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ORIGINAL RESEARCH

Phylogenomics, divergence times and notes of orders in Basidiomycota

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Abstract
Basidiomycota is one of the major phyla in the fungal tree of life. The outline of Basidiomycota provides essential taxonomic information for researchers and workers in mycology. In this study, we present a time-framed phylogenomic tree with 487 species of Basidiomycota from 127 families, 47 orders, 14 classes and four subphyla; we update the outline of Basidiomycota based on the phylogenomic relationships and the taxonomic studies since 2019; and we provide notes for each order and discuss the history, defining characteristics, evolution, justification of orders, problems, significance, and plates. Our phylogenomic analysis suggests that the subphyla diverged in a time range of 443–490 Myr (million years), classes in a time range of 312–412 Myr, and orders in a time range of 102–361 Myr. Families diverged in a time range of 50–289 Myr, 76–224 Myr, and 62–156 Myr in Agaricomycotina, Pucciniomycotina, and Ustilaginomycotina, respectively. Based on the phylogenomic relationships and divergence times, we propose a new suborder Mycenineae in Agaricales to accommodate Mycenaceae. In the current outline of Basidiomycota, there are four subphyla, 20 classes, 77 orders, 297 families, and 2134 genera accepted. When building a robust taxonomy of Basidiomycota in the genomic era, the generation of molecular phylogenetic data has become relatively easier. Finding phenotypical characters, especially those that can be applied for identification and classification, however, has become increasingly challenging.

Keywords Classification · Fungi · Molecular clock · Systematics · Taxonomy

Introduction

Fungi are crucial components of life on Earth with essential ecological and economic impacts. Their interactions with other organisms contribute significantly to the proper functioning of terrestrial ecosystems and previous research

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Mao-Qiang He, Bin Cao and Fei Liu have contributed equally to this work.

Extended author information available on the last page of the article indicates that they have promoted the evolution of many terrestrial clades (Berbee et al. 2017; Loron et al. 2019; Gan et al. 2021). They are involved in symbiotic associations with photosynthetic bacteria or algae to produce lichen; have mycorrhizal relationships with plant roots; and can act as pathogens or decomposers that help recycle organic materials in ecosystems (Peay et al. 2016; Yuan et al. 2023). They are of direct benefit to humanity and are estimated to contribute 54.57 trillion USD to the global economy as contributors to food, medicine production and other products (Willis 2018; Pérez-Moreno et al. 2021; Mapook et al. 2022; Niego et al. 2023). The number of species of Fungi is estimated to be in the range of 2.2 to 13.2 million, with the latest estimate of 2 to 3 million species, indicating they make up a major portion of Earth's biodiversity (Hawksworth and Lücking 2017; Willis 2018; Wu et al. 2019a; Antonelli et al. 2020; Niskanen et al. 2023).

The phylum Basidiomycota R.T. Moore is one of the major branches in the fungal tree of life, with global estimates of 1.4–4.2 million species in the phylum and latest estimates of 0.7 to 1 million species, which represents about 28–40% of all fungal diversity (Tedersoo et al. 2021; Baldrian et al. 2022; He et al. 2022; Niskanen et al. 2023). The typical members of this group are mushrooms, bracket fungi, smuts, rusts, and yeasts, which are grouped into the subphyla Agaricomycotina Doweld, Ustilaginomycotina Doweld and Pucciniomycotina R. Bauer et al. The phylum also contains a small subphylum Wallemiomycotina Doweld composed of xerophilic microfungi (Kirk et al. 2008; He et al. 2019a).

Systematics seeks to classify organisms by their phylogenetic relationships, using robust criteria such that these classifications can stand the test of time. (Cai et al. 2011). Fungal classification was traditionally based on comparative morphology, anatomy, biochemistry, physiology, and ecology. The systematics of fungi has been revolutionized by advances in molecular biology, phylogenetics, and bioinformatics. Nowadays, DNA sequence-based classification and identification has become the standard approach in fungal taxonomy (Hibbett et al. 2007; Xu 2020; Lücking et al. 2021). Fungal systematics has undergone a transformation due to the phylogenetic era, with a massive number of single-gene and/or multiple-gene analyses having been conducted in the past two decades. Next-generation and single-molecule real-time (SMRT) sequencing has ushered fungal systematics further into the phylogenomic era (James et al. 2020). Numerous trees have been generated based on a large number of samples, and sequence markers with the aim of employing diverse sets of species to resolve phylogenetic relationships among different ranks. Phylogenomics aims to recover the most accurate species tree from a multitude of gene trees and is considered to be the most powerful tool to unify and stabilize fungal taxonomy (Nagy and Szöllősi 2017; Xu 2020).

In a previous study conducted in 2017, we provided a phylogenomic perspective of Basidiomycota from available genomes (Zhao et al. 2017). In 2019, we performed multigene phylogenetic analyses for each subphylum in Basidiomycota and provided an outline (He et al. 2019a); we also estimated divergence times to suggest a criterion for rank standardization (Zhao et al. 2016a, 2017). Since then, new genomes of Basidiomycota have been published, amounting up to 199 and 559 deposited in the MycoCosm of Joint Genome Institute (JGI) fungal portal and in the National Center for Biotechnology Information (NCBI), respectively (data from 2017 to August 2022).

This current work aims to update the outline of Basidiomycota based on the progress made since our previous outline (He et al. 2019a). We used the data available to date to build a time-framed phylogenomic tree of Basidiomycota. Genome data were selected to represent as many families as possible resulting in a relatively comprehensive coverage of this phylum. We also summarize, evaluate, and integrate advances made since our previous study (He et al. 2019a) such as recent multigene phylogenetic analyses which led to novel taxonomic propositions. Furthermore, we provide notes for each order with comprehensive information, including introductory information, taxonomic history, evolution, and plates (due to the similar morphology of yeasts, only representative orders are presented).

Materials and methods

Samples selection and data obtention for phylogenomic analyses

All publicly available genomic data used in this study were obtained from the MycoCosm of Joint Genome Institute (JGI) fungal portal and the National Center for Biotechnology Information (NCBI) GenBank database (by March 2022). In sample selection, the following samples were given priority when: (1) type materials of taxa, and (2) genomes of better quality. Whenever possible, a minimum of two species per family were selected to examine the monophyly of families. Detailed information on selected specimens is presented in Supplementary Table 1.

Genome completeness assessment and phylogenetic analyses

Genome completeness with single-copy orthologues was calculated using BUSCO v5.2.0 (Simão et al. 2015) using default parameters based on the presence/absence of predefined orthologs in the basidiomycota_odb10 database. We conducted a tBLASTn search for each BUSCO gene using its consensus orthologous protein sequence against each genome assembly. Gene structures in the putative genomic regions were predicted using AUGUSTUS v3.2.2 (Stanke and Waack 2003). Subsequently, the predicted gene sequences were aligned to the BUSCO gene's hidden Markov model profile. BUSCO genes in each genome assembly were categorized as "Full-Length" (if one complete gene was present), "Duplicated" (if two or more complete genes were found for one BUSCO gene), "Fragmented" (if the predicted gene was shorter than 95% of the aligned sequence lengths from the reference species), or "Missing" (if no predicted gene was detected in the genome).

To construct the phylogenomic data matrix, we started with 1764 single-copy, full-length BUSCO genes from representatives of the phylum Basidiomycota, and one Ascomycota outgroup. Each gene was aligned with MAFFT v7.490 with default options (Katoh and Standley 2013). Ambiguously aligned regions were removed using trimAl version 1.4 with the gappyout option (Capella-Gutiérrez et al. 2009). The AA alignments of these 1764 BUSCO genes, each with more than 90% taxon occupancy, were then concatenated into the full data matrix. Phylogenetic analyses were conducted using IQ-TREE (Katoh and Standley 2013) version 2.0.3, with the best-fit amino acid substitution model automatically selected. Divergence time estimates were obtained through penalized likelihood analyses using a truncated Newton optimization algorithm implemented in the program r8s version 1.81 (Sanderson 2003).

Phylogenomics relationships (higher level above family) and genera number of Basidiomycota

A total of 488 samples was included in the phylogenomic analyses, consisting of 487 samples from Basidiomycota and one Ascomycota outgroup, namely *Xylaria arbuscula*. The dataset contained a set of 1764 single-copy ortholog genes. There are 487 species of Basidiomycota from 127 families, 47 orders, 14 classes and four subphyla included in our analyses. Divergence times shown in Figs. 1, 2 were estimated based on the ML tree topology. Divergence times (crown ages) and genera number of each rank (family, order, class, and subphylum) are presented in Table 1.

Phylogenomic relationships among the four subphyla (Agaricomycotina, Wallemiomycotina, Ustilaginomycotina, and Pucciniomycotina) agreed well with previous studies of Zhao et al. (2017) and Li et al. (2021c).

Phylogenetic relationships between classes of Agaricomycotina are the same as in previous studies (Hibbett 2006; Zhao et al. 2017; Varga et al. 2019). Nineteen orders in Agaricomycetes included in the analyses, while the position of Lepidostromatales, Stereopsidales, and Tremellodendropsidales were not resolved due to a lack of genomic data. Two subclasses in Agaricomycetes were resolved: (1) Agaricomycetidae composed of Agaricales, Amylocorticiales, Atheliales, and Boletales. (2) Phallomycetidae composed of Gomphales, Geastrales, Phallales, Hysterangiales, and Trechisporales. This agrees well with previous studies (Hibbett 2006; James et al. 2020). The clade sister to Agaricomycetidae is composed of six orders viz. Polyporales, Thelephorales, Russulales, Gloeophyllales, Jaapiales, and Corticiales. Hymenochaetales is sister to the clade composed of the Agaricomycetidae and the six-order clade. The remaining three orders, Auriculariales, Sebacinales and Cantharellales, were at the base of Agaricomycetes and did not cluster with any other order. All five orders of Tremellomycetes viz. Tremellales, Trichosporonales, Holtermanniales, Filobasidiales, and Cystofilobasidiales, were included in the analyses. The phylogenetic relationships among these orders agreed well with previous studies (Liu et al. 2015b; He et al. 2019a). Wallemiomycotina is grouped as a sister taxon to Agaricomycotina.

Almost all recognized classes and orders of Ustilaginomycotina were sampled in the analyses, except for Cintractiellales and Uleiellales which lacked genomic data. Phylogenetic relationships among classes agreed well with previous studies (Begerow et al. 2006; Wang et al. 2014b, 2015d; Li et al. 2021c) with the recognition of four classes: Exobasidiomycetes, Malasseziomycetes, Moniliellomycetes, and Ustilaginomycetes. The phylogenomic relationships among orders of Ustilaginomycetes are the same as in a previous study (Begerow et al. 2006). Exobasidiomycetes was found to be polyphyletic. Two main clades were found in Exobasidiomycetes. One clade was composed of Ceraceosorales, Entylomatales, Exobasidiales, Golubeviales, and Microstromatales; and the other one was composed of Georgefischeriales, Moniliellomycetes, and Tilletiales.

Of the ten classes of Pucciniomycotina five were included in the analyses (Agaricostilbomycetes, Cystobasidiomycetes, Microbotryomycetes, Mixiomycetes, and Pucciniomycetes), but Atractiellomycetes, Classiculomycetes, Cryptomycocolacomycetes, Spiculogloeomycetes, and Tritirachiomycetes were not included because of lack of available genomic data. Phylogenomic relationships between classes confirmed the results of previous studies (Wang et al. 2015b; Li et al. 2021c). Four orders were included in Microbotryomycetes (Leucosporidiales, Microbotryales, Sporidiobolales, and Heterogastridiales), and their taxonomic positions showed the same relationships as previous studies (Wang et al. 2015b; Li et al. 2021c). Two clades were recognized within Cystobasidiomycetes: Cystobasidiales and another composing Erythrobasidiales and Symmetosporaceae. It should be noted, however, that classes Cystobasidiomycetes and Microbotryomycetes lacked genome sequences of many taxa, including representatives of orders Heitmaniales, Kriegeriales, and Rosettozymales.

Fig. 1 Backbone-constrained Maximum Likelihood phylogenomic tree of orders in Basidiomycota. Bootstrap values lower than 100 and divergence times are noted around the nodes

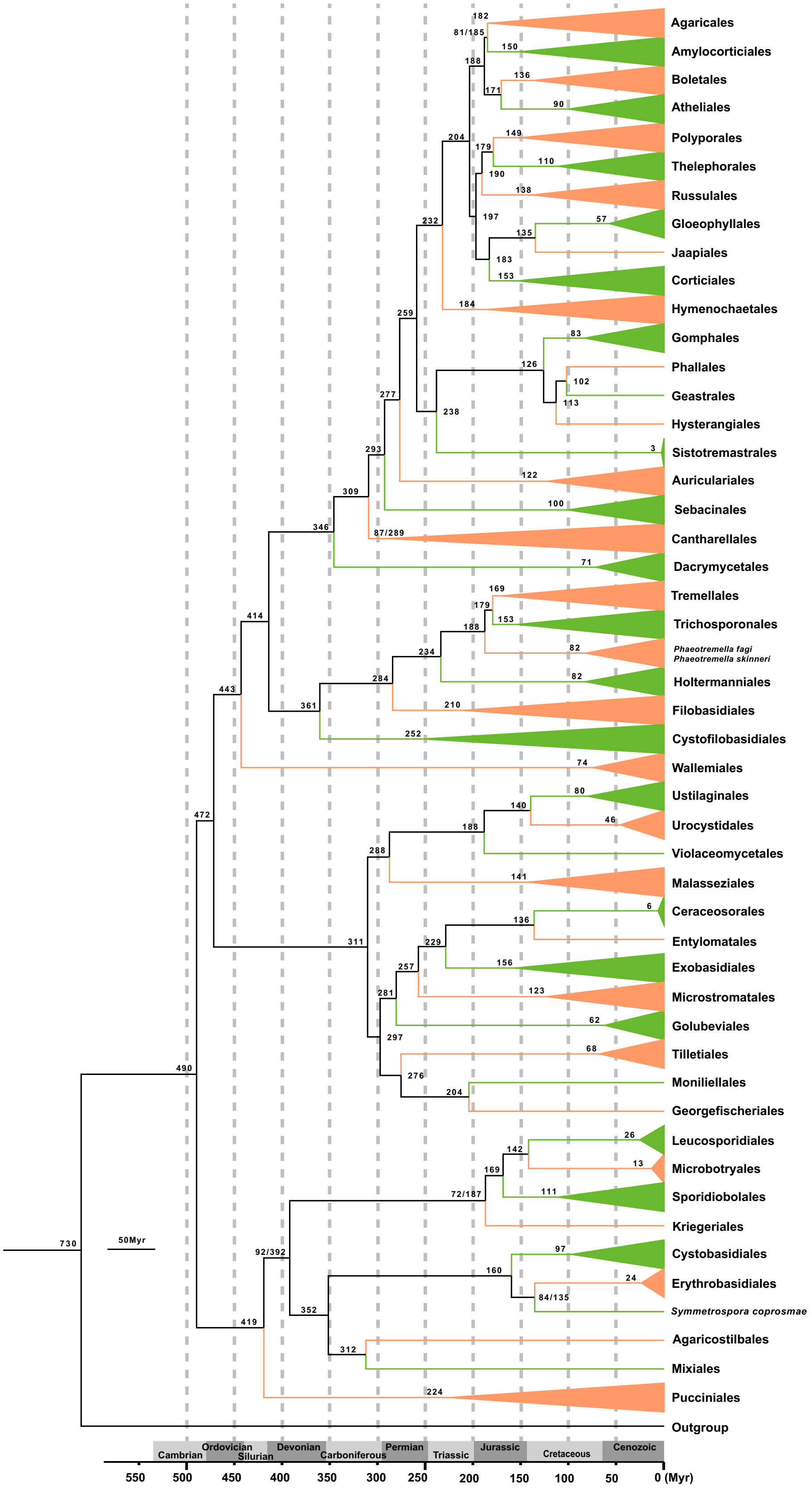

Fig. 2 Time calibrated Maximum Likelihood phylogenomic tree of Basidiomycota based on 1764 single-copy ortholog genes of 487 species from 127 families, 47 orders, 14 classes, and four subphyla. The tree is rooted with the ascomycetes species *Xylaria arbuscula*. Bootstrap values and divergence times are noted around the nodes. Nodes with bootstrap values lower than 100 are marked with star symbols

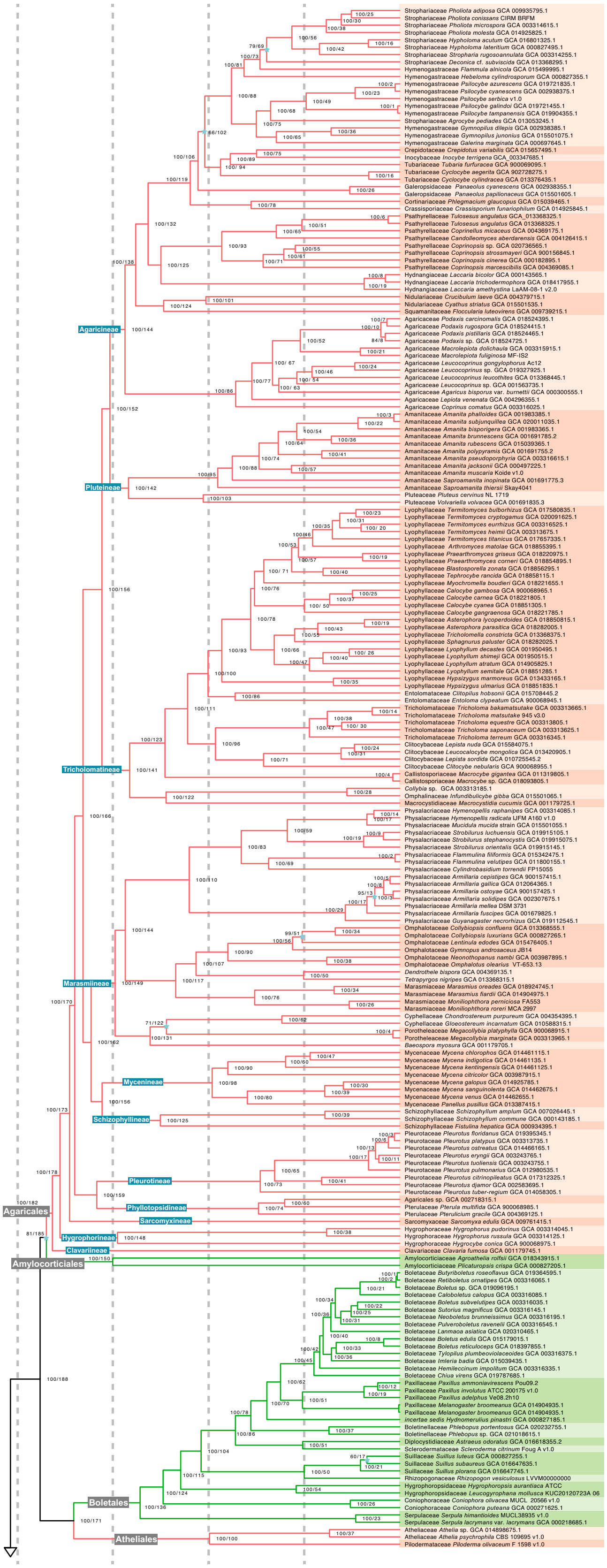

Fig. 2 (continued)

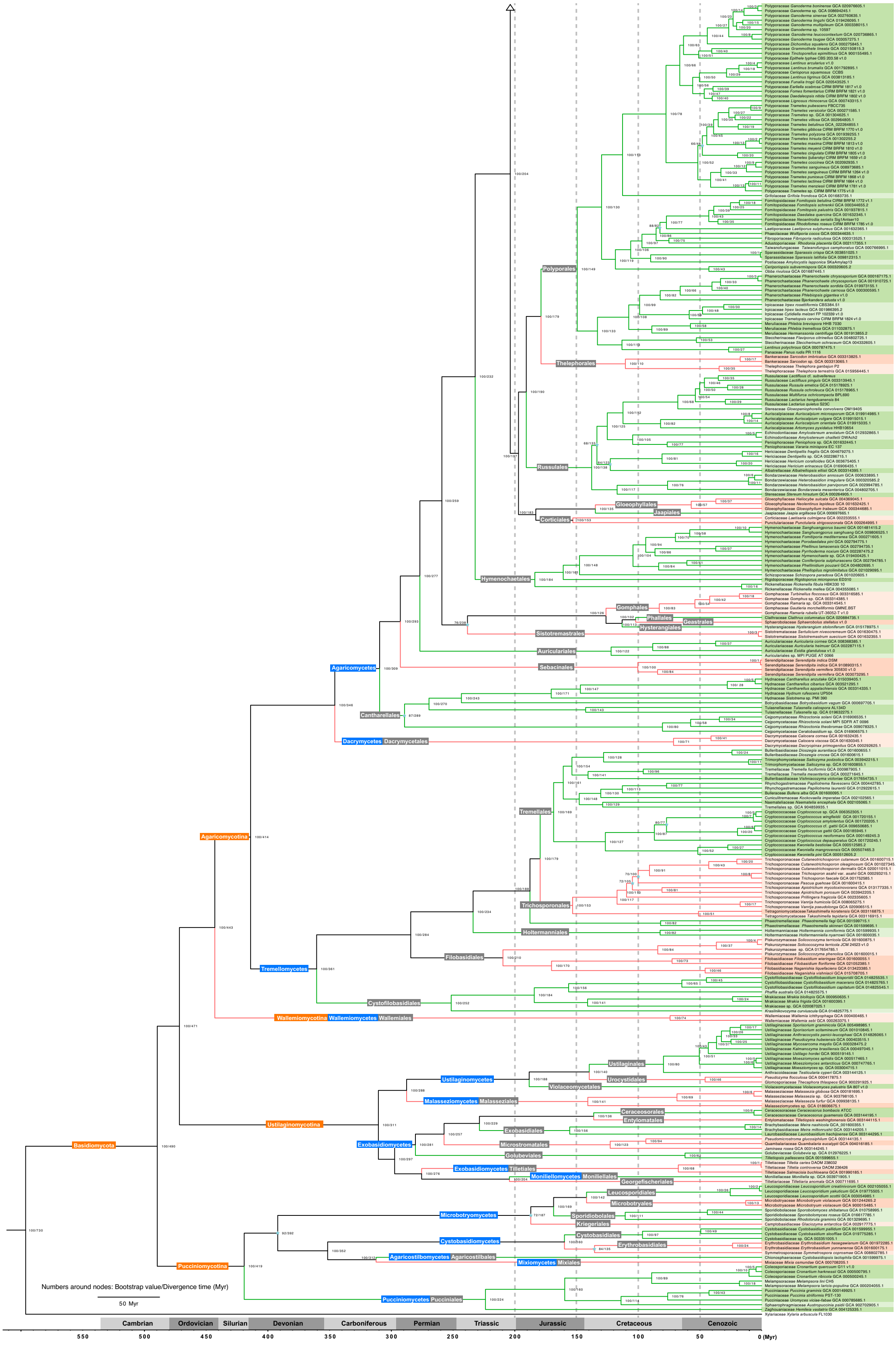

Table 1 Divergence times (steam ages) and genera number of ranks in Basidiomycota (family, order, class, and subphylum)

Higher	Order/suborder	Family	Genus number	Divergence time (Myr)
Basidiomycota			2134	–
Agaricomycotina			1680	443
Agaricomycetes			1592	346
	Agaricales		560	185
	Agaricineae		194	152
		Agaricaceae	51	144
		Bolbitiaceae	15	–
		Cortinariaceae	11	78
		Crassisporiaceae	2	78
		Crepidotaceae	7	75
		Galeropsidaceae	3	106
		Hydnangiaceae	4	125
		Hymenogastraceae	13	88
		Inocybaceae	7	75
		Lycoperdaceae	16	–
		Mythicomycetaceae	2	–
		Nidulariaceae	7	124
		Psathyrellaceae	20	125
		Squamanitaceae	6	124
		Strophariaceae	11	88
		Tubariaceae	7	89
		incertae sedis	12	–
	Clavariineae		11	182
		Clavariaceae	11	–
	Hygrophorineae		31	178
		Hygrophoraceae	30	–
		incertae sedis	1	–
	Marasmiineae		119	162
		Cyphellaceae	22	–
		Cystostereaceae	7	–
		Marasmiaceae	13	117
		Omphalotaceae	16	107
		Physalacriaceae	32	144
		Porotheleaceae	19	122
		incertae sedis	10	–
	Mycenineae		11	156
		Mycenaceae	11	–
	Phyllotopsidineae		18	159
		Phyllotopsidaceae	4	–
		Pterulaceae	9	–
		Radulomycetaceae	4	–
		incertae sedis	1	
	Pleurotineae		13	159
		Pleurotaceae	6	–
		Stephanosporaceae	5	–
		Typhulaceae	2	–
	Pluteineae		11	152
		Amanitaceae	6	142
		Limnoperdaceae	1	–
		Pluteaceae	4	142

Table 1 (Continued)

Higher	Order/suborder	Family	Genus number	Divergence time (Myr)
	Sarcomyxineae		1	173
		Sarcomyxaceae	1	–
	Schizophyllineae		19	156
		Cyphellopsidaceae	14	–
		Schizophyllaceae	5	156
	Tricholomatineae		90	156
		Asproinocybaceae	2	–
		Biannulariaceae	3	–
		Callistosporiaceae	6	123
		Clitocybaceae	8	96
		Entolomataceae	9	100
		Fayodiaceae	5	–
		Lyophyllaceae	28	100
		Macrocystidiaceae	1	122
		Omphalinaceae	2	–
		Pseudoclitocybaceae	5	–
		Tricholomataceae	10	96
		incertae sedis	11	–
	incertae sedis		42	–
		Broomeiaceae	1	–
		Hemigasteraceae	2	–
		incertae sedis	39	–
	Amylocorticiales		14	185
		Amylocorticiaceae	14	–
	Atheliales		19	171
		Atheliaceae	11	100
		Byssocorticiaceae	3	–
		Lobuliciaceae	1	–
		Pilodermataceae	2	100
		Tylosporaceae	2	–
	Auriculariales		57	277
		Auriculariaceae	15	122
		Hyaloriaceae	3	–
		incertae sedis	39	–
	Boletales		166	171
		Boletaceae	112	62
		Boletinellaceae	2	78
		Calostomataceae	1	–
		Coniophoraceae	6	124
		Diplocystidiaceae	4	51
		Gasterellaceae	1	–
		Gomphidiaceae	4	–
		Gyroporaceae	1	–
		Hygrophoropsidaceae	2	115
		Paxillaceae	11	–
		Protogastraceae	1	–
		Rhizopogonaceae	3	50
		Sclerodermataceae	5	51
		Serpulaceae	3	136
		Suillaceae	3	50

Table 1 (Continued)

Higher	Order/suborder	Family	Genus number	Divergence time (Myr)
		Tapinellaceae	3	–
		incertae sedis	4	–
	Cantharellales		27	309
		Botryobasidiaceae	2	243
		Cejpomycetaceae	3	289
		Hydnaceae	18	243
		Tulasnellaceae	3	270
		incertae sedis	1	–
	Corticiales		29	183
		Corticiaceae	13	153
		Dendrominiaceae	1	–
		Punctulariaceae	4	153
		Vuilleminiaceae	3	–
		incertae sedis	8	–
	Geastrales		8	102
		Geastraceae	4	–
		Schenellaceae	1	–
		Sphaerobolaceae	1	–
		Sclerogastraceae	2	–
	Gloeophyllales		14	135
		Gloeophyllaceae	10	–
		incertae sedis	4	–
	Gomphales		20	126
		Clavariadelphaceae	2	–
		Gomphaceae	13	–
		Lentariaceae	4	–
		incertae sedis	1	–
	Hymenochaetales		84	232
		Chaetoporellaceae	2	–
		Hymenochaetaceae	45	148
		Hyphodontiaceae	1	–
		Odonticiaceae	2	–
		Peniophorellaceae	1	–
		Repetobasidiaceae	1	–
		Resiniciaceae	1	–
		Rickenellaceae	1	184
		Rigidoporaceae	3	–
		Schizocorticiaceae	1	–
		Schizoporaceae	3	148
		Sideraceae	1	–
		Skvortzoviaceae	1	–
		Tubulicrinaceae	1	–
		incertae sedis	20	–
	Hysterangiales		17	113
		Gallaceaceae	3	–
		Hysterangiaceae	3	–
		Mesophelliaceae	8	–
		Phallogastraceae	1	–
		incertae sedis	2	–
	Jaapiales		1	135

Table 1 (Continued)

Higher	Order/suborder	Family	Genus number	Divergence time (Myr)
		Jaapiaceae	1	–
	Lepidostromatales		3	–
		Lepidostromataceae	3	–
	Phallales		38	102
		Clathraceae	9	–
		Claustulaceae	5	–
		Gastrosporiaceae	1	–
		Lysuraceae	1	–
		Phallaceae	11	–
		Protophallaceae	1	–
		Trappeaceae	4	–
		incertae sedis	6	–
	Polyporales		346	179
		Adustoporiaceae	5	75
		Auriporiaceae	1	–
		Cerrenaceae	5	–
		Climacocystaceae	2	–
		Dacryobolaceae	1	–
		Fibroporiaceae	2	75
		Fomitopsidaceae	28	77
		Fragiliporiaceae	1	–
		Gelatoporiaceae	4	–
		Gloeoporellaceae	1	–
		Grifolaceae	2	113
		Hyphodermataceae	1	–
		Incrustoporiaceae	4	–
		Irpicaceae	15	99
		Ischnodermataceae	1	–
		Laetiporaceae	5	77
		Laricifomitaceae	3	–
		Meripilaceae	1	–
		Meruliaceae	30	108
		Panaceae	2	–
		Phaeolaceae	3	82
		Phanerochaetaceae	24	99
		Piptoporellaceae	1	–
		Podoscyphaceae	3	–
		Polyporaceae	111	113
		Postiaceae	15	–
		Pycnoporellaceae	2	–
		Sarcoporiaceae	1	–
		Sparassidaceae	1	90
		Steccherinaceae	24	113
		Taiwanofungaceae	1	97
		incertae sedis	46	–
	Russulales		97	190
		Albatrellaceae	8	123
		Auriscalpiaceae	6	112
		Bondarzewiaceae	9	117
		Echinodontiaceae	4	105

Table 1 (Continued)

Higher	Order/suborder	Family	Genus number	Divergence time (Myr)
		Hericiaceae	6	123
		Peniophoraceae	17	105
		Russulaceae	7	68
		Stereaceae	22	68
		Terrestriporiaceae	1	–
		Xenasmataceae	2	–
		incertae sedis	15	–
	Sebacinales		9	293
		Sebacinaceae	8	–
		Serendipitaceae	1	–
	Sistotremastrales		2	–
		Sistotremastraceae	2	–
	Stereopsidales		3	–
		Stereopsidaceae	1	–
		incertae sedis	2	–
	Thelephorales		17	179
		Bankeraceae	5	110
		Thelephoraceae	10	110
		incertae sedis	2	–
	Trechisporales		13	–
		Hydnodontaceae	11	–
		incertae sedis	2	–
	Tremellodendropsidales		1	–
		Tremellodendropsidaceae	1	–
	Xenasmatellales		1	–
		Xenasmatellaceae	1	–
	incertae sedis	*incertae sedis*	46	–
Bartheletiomycetes			1	–
	Bartheletiales		1	–
		Bartheletiaceae	1	–
Dacrymycetes			14	346
	Dacrymycetales		14	–
		Cerinomycetaceae	1	–
		Dacryonaemataceae	1	–
		Dacrymycetaceae	11	–
		Unilacrymaceae	1	–
Tremellomycetes			73	414
	Chionasterales		1	–
		Chionasteraceae	1	–
	Cystofilobasidiales		8	361
		Cystofilobasidiaceae	1	156
		Mrakiaceae	7	184
	Filobasidiales		8	284
		Filobasidiaceae	6	210
		Piskurozymaceae	2	210
	Holtermanniales		2	234
		Holtermanniaceae	2	–
	Tremellales		38	179
		Bulleraceae	4	113
		Bulleribasidiaceae	6	–

Table 1 (Continued)

Higher	Order/suborder	Family	Genus number	Divergence time (Myr)
		Carcinomycetaceae	1	–
		Cryptococcaceae	3	169
		Cuniculitremaceae	3	130
		Naemateliaceae	2	–
		Phragmoxenidiaceae	1	–
		Rhynchogastremaceae	2	113
		Sirobasidiaceae	2	–
		Tremellaceae	3	141
		Trimorphomycetaceae	4	128
		incertae sedis	7	–
	Trichosporonales		12	179
		Tetragoniomycetaceae	4	153
		Trichosporonaceae	8	153
	incertae sedis		4	–
		Phaeotremellaceae	2	–
		incertae sedis	2	–
Pucciniomycotina			302	490
Agaricostilbomycetes			17	312
	Agaricostilbales		17	–
		Agaricostilbaceae	3	–
		Chionosphaeraceae	6	–
		Jianyuniaceae	3	–
		Kondoaceae	2	–
		Ruineniaceae	1	–
		Crittendeniaceae	1	–
		incertae sedis	1	–
Atractiellomycetes			11	–
	Atractiellales		11	–
		Atractogloeaceae	1	–
		Hoehnelomycetaceae	2	–
		Mycogelidiaceae	1	–
		Phleogenaceae	7	–
Classiculomycetes			2	–
	Classiculales		2	–
		Classiculaceae	2	–
Cryptomycocolacomycetes			2	–
	Cryptomycocolacales		2	–
		Cryptomycocolacaceae	2	–
Cystobasidiomycetes			16	352
	Buckleyzymales		1	–
		Buckleyzymaceae	1	–
	Cystobasidiales		5	160
		Cystobasidiaceae	3	–
		incertae sedis	2	–
	Erythrobasidiales		5	135
		Erythrobasidiaceae	2	–
		incertae sedis	3	–
	Naohideales		1	–
		Naohideaceae	1	–
	Sakaguchiales		1	–

Table 1 (Continued)

Higher	Order/suborder	Family	Genus number	Divergence time (Myr)
		Sakaguchiaceae	1	–
	incertae sedis		3	–
		Microsporomycetaceae	1	–
		Symmetrosporaceae	1	–
		incertae sedis	1	–
Microbotryomycetes			46	392
	Heitmaniales		1	–
		Heitmaniaceae	1	–
	Heterogastridiales		3	–
		Heterogastridiaceae	3	–
	Kriegeriales		9	187
		Camptobasidiaceae	4	–
		Kriegeriaceae	5	–
	Leucosporidiales		1	142
		Leucosporidiaceae	1	–
	Microbotryales		9	142
		Microbotryaceae	5	–
		Ustilentylomataceae	4	–
	Rosettozymales		1	–
		Rosettozymaceae	1	–
	Sporidiobolales		3	169
		Sporidiobolaceae	3	–
	incertae sedis		19	–
		Chrysozymaceae	4	–
		Colacogloeaceae	1	–
		incertae sedis	14	–
Mixiomycetes			1	312
	Mixiales		1	–
		Mixiaceae	1	–
Pucciniomycetes			199	419
	Helicobasidiales		1	–
		Helicobasidiaceae	1	–
	Pachnocybales		1	–
		Pachnocybaceae	1	–
	Platygloeales		10	–
		Eocronartiaceae	5	–
		Platygloeaceae	5	–
	Pucciniales		181	–
		Araucariomycetaceae	1	–
		Coleosporiaceae	10	–
		Crossopsoraceae	6	–
		Endoraeciaceae	1	–
		Gymnosporangiaceae	3	–
		Melampsoraceae	2	89
		Milesinaceae	4	–
		Ochropsoraceae	3	–
		Phakopsoraceae	12	–
		Neophysopellaceae	1	–
		Nyssopsoraceae	1	–
		Phragmidiaceae	9	–

Table 1 (Continued)

Higher	Order/suborder	Family	Genus number	Divergence time (Myr)
		Pileolariaceae	1	–
		Pucciniaceae	33	76
		Pucciniastraceae	5	–
		Raveneliaceae	32	–
		Rogerpetersoniaceae	1	–
		Skierkaceae	1	–
		Sphaerophragmiaceae	5	114
		Tranzscheliaceae	2	–
		Uncolaceae	2	–
		Uromycladiaceae	1	–
		Zaghouaniaceae	9	224
		incertae sedis	36	–
	Septobasidiales		6	–
		Septobasidiaceae	6	–
Spiculogloeomycetes			3	–
	Spiculogloeales		3	–
		Spiculogloeaceae	3	–
Tritirachiomycetes			2	–
	Tritirachiales		2	–
		Tritirachiaceae	2	–
incertae sedis	*incertae sedis*	*incertae sedis*	3	–
Ustilaginomycotina			138	471
Exobasidiomycetes			61	–
	Ceraceosorales		1	136
		Ceraceosoraceae	1	–
	Doassansiales		13	–
		Doassansiaceae	11	–
		Melaniellaceae	1	–
		Rhamphosporaceae	1	–
	Entylomatales		2	136
		Entylomataceae	2	–
	Exobasidiales		20	229
		Brachybasidiaceae	8	156
		Cryptobasidiaceae	5	–
		Exobasidiaceae	4	–
		Graphiolaceae	2	–
		Laurobasidiaceae	1	156
	Franziozymales		1	–
		Franziozymaceae	1	–
	Georgefischeriales		7	204
		Eballistraceae	1	–
		Georgefischeriaceae	2	–
		Gjaerumiaceae	1	–
		Tilletiariaceae	3	–
	Golubeviales		1	281
		Golubeviaceae	1	62
	Microstromatales		8	257
		Microstromataceae	1	–
		Quambalariaceae	1	94
		Volvocisporiaceae	1	–

Table 1 (Continued)

Higher	Order/suborder	Family	Genus number	Divergence time (Myr)
		incertae sedis	5	–
	Robbauerales		1	–
		Robbaueraceae	1	–
	Tilletiales		7	276
		Tilletiaceae	6	–
		Erratomycetaceae	1	–
Malasseziomycetes			1	288
	Malasseziales		1	–
		Malasseziaceae	1	–
Moniliellomycetes			1	204
	Moniliellales		1	–
		Moniellaceae	1	–
Peribolosporomycetes			1	–
	Peribolosporales		1	–
		Peribolosporaceae	1	–
Ustilaginomycetes			72	288
	Quasiramulariales		1	–
		Quasiramulariaceae	1	–
	Uleiellales		1	–
		Uleiellaceae	1	–
	Urocystidales		13	140
		Doassansiopsidaceae	1	–
		Fereydouniaceae	1	–
		Floromycetaceae	2	–
		Glomosporiaceae	1	46
		Mycosyringaceae	1	–
		Urocystidaceae	7	–
	Ustilaginales		53	140
		Anthracoideaceae	19	80
		Clintamraceae	1	–
		Geminaginaceae	1	–
		Melanotaeniaceae	3	–
		Pericladiaceae	1	–
		Ustilaginaceae	26	80
		Websdaneaceae	2	–
	Violaceomycetales		1	188
		Violaceomycetaceae	1	–
incertae sedis	Cintractiellales		1	–
		Cintractiellaceae	1	–
	incertae sedis	*incertae sedis*	2	–
Wallemiomycotina			4	443
Wallemiomycetes			4	–
	Geminibasidiales		2	–
		Geminibasidiaceae	2	–
	Wallemiales		1	–
		Wallemiaceae	1	–
	incertae sedis	*incertae sedis*	1	–
Basidiomycota *incertae sedis*	*incertae sedis*	*incertae sedis*	10	–

Outline of orders in Basidiomycota

Phylum Basidiomycota R.T. Moore 1980
Subphylum Agaricomycotina Doweld 2001
Class Agaricomycetes Doweld 2001

Agaricales Underw. 1899
Amylocorticiales K.H. Larss., Manfr. Binder & Hibbett 2010
Atheliales Jülich 1982
Auriculariales Bromhead 1840
Boletales E.-J. Gilbert 1931
Cantharellales Gäum. 1926
Corticiales K.H. Larss. 2007
Geastrales K. Hosaka & Castellano 2007
Gloeophyllales Thorn 2007
Gomphales Jülich 1982
Hymenochaetales Oberw. 1977
Hysterangiales K. Hosaka & Castellano 2007
Jaapiales Manfr. Binder, K.H. Larss. & Hibbett 2010
Lepidostromatales B.P. Hodk. & Lücking 2013
Phallales E. Fisch. 1898
Polyporales Gäum. 1926
Russulales Kreisel ex P.M. Kirk, P.F. Cannon & J.C. David 2001
Sebacinales M. Weiss, Selosse, Rexer, A. Urb. & Oberw. 2004
Sistotremastrales L.W. Zhou & S.L. Liu 2022
Stereopsidales Sjökvist, E. Larss., B.E. Pfeil & K.H. Larss. 2013
Thelephorales Corner ex Oberw. 1976
Trechisporales K.H. Larss. 2007
Tremellodendropsidales Vizzini 2014
Xenasmatellales L.W. Zhou & S.L. Liu 2023

Class Bartheletiomycetes Thines 2017

Bartheletiales Thines 2017

Class Dacrymycetes Doweld 2001

Dacrymycetales Henn. 1897

Class Tremellomycetes Doweld 2001

Chionasterales N.A.T. Irwin, C.S. Twynstra, V. Mathur & P.J. Keeling 2021
Cystofilobasidiales Fell et al. 1999
Filobasidiales Jülich 1982
Holtermanniales Libkind, Wuczk., Turchetti & Boekhout 2011
Tremellales Fr. 1821
Trichosporonales Boekhout & Fell 2000

Subphylum Pucciniomycotina R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw. 2006

Class Agaricostilbomycetes R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw. 2006

Agaricostilbales Oberw. & R. Bauer 1989

Class Atractiellomycetes R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw. 2006

Atractiellales Oberw. & Bandoni 1982

Class Classiculomycetes R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw. 2006

Classiculales R. Bauer, Begerow, Oberw. & Marvanová 2003

Class Cryptomycocolacomycetes R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw. 2006

Cryptomycocolacales Oberw. & R. Bauer 1990

Class Cystobasidiomycetes R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw. 2006

Buckleyzymales R.L. Zhao & K.D. Hyde 2017
Cystobasidiales R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw. 2006
Erythrobasidiales R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw. 2006
Naohideales R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw. 2006
Sakaguchiales R.L. Zhao & K.D. Hyde 2017

Class Microbotryomycetes R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw. 2006

Heitmaniales Q.M. Wang & F.Y. Bai 2020
Heterogastridiales Oberw. & R. Bauer 1990
Kriegeriales Toome & Aime 2013
Leucosporidiales J.P. Samp., M. Weiss & R. Bauer 2003
Microbotryales R. Bauer & Oberw. 1997
Rosettozymales Q.M. Wang & F.Y. Bai 2020
Sporidiobolales Doweld 2001

Class Mixiomycetes R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw. 2006

Mixiales R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw. 2006

Class Pucciniomycetes R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw. 2006

Helicobasidiales R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw. 2006
Pachnocybales R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw. 2006
Platygloeales R.T. Moore 1990

Pucciniales Caruel 1881
Septobasidiales Couch ex Donk 1964

Class Spiculogloeomycetes Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout 2015

Spiculogloeales R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw. 2006

Class Tritirachiomycetes Aime & Schell 2011

Tritirachiales Aime & Schell 2011

Subphylum Ustilaginomycotina Doweld 2001
Class Exobasidiomycetes Begerow, M. Stoll & R. Bauer 2007

Ceraceosorales Begerow, M. Stoll & R. Bauer 2007
Doassansiales R. Bauer & Oberw. 1997
Entylomatales R. Bauer & Oberw. 1997
Exobasidiales Henn. 1898
Franziozymales Q.M. Wang, Begerow & M. Groenew. 2022
Georgefischeriales R. Bauer, Begerow & Oberw. 1997
Golubeviales Q.M. Wang, F.Y. Bai, Begerow & Boekhout 2023
Microstromatales R. Bauer & Oberw. 1997
Robbauerales Boekhout, Begerow, Q.M. Wang & F.Y. Bai 2015
Tilletiales Haeckel 1894

Class Malasseziomycetes Denchev & T. Denchev 2014

Malasseziales R.T. Moore 1980

Class Moniliellomycetes Q.M. Wang, F.Y. Bai & Boekhout 2014

Moniliellales Q.M. Wang, F.Y. Bai & Boekhout 2014

Class Peribolosporomycetes Witfeld, M. A. Guerreiro, H.D.T. Nguyen, Begerow 2023

Peribolosporales Witfeld, M. A. Guerreiro, H.D.T. Nguyen, Begerow 2023

Class Ustilaginomycetes R. Bauer, Oberw. & Vánky 1997

Quasiramulariales R. Kirschner, M. Kolařík & M. Piepenbr. 2021
Uleiellales Garnica, K. Riess, M. Schön, H. Butin, M. Lutz, Oberw. & R. Bauer 2016
Urocystidales R. Bauer & Oberw. 1997
Ustilaginales G. Winter 1880
Violaceomycetales Albu et al. 2015

Ustilaginomycotina order ***incertae sedis***

Cintractiellales McTaggart & R.G. Shivas 2020

Subphylum Wallemiomycotina Doweld 2014

Class Wallemiomycetes Zalar, de Hoog & Schroers 2005

Geminibasidiales H.D.T. Nguyen, N.L. Nick. & Seifert 2013
Wallemiales Zalar, de Hoog & Schroers 2005

Notes of orders in Basidiomycota

Agaricales Underw. 1899

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Introduction

Agaricales is the most conspicuous and largest group of macrofungi characterized by highly diverse basidiome types and nutritional modes. It is cosmopolitan in distribution and contains mostly gill-forming species, but also those with clavarioid, poroid, corticoid, cyphelloid, gasteroid, secotioid or reduced basidiomes. Members of the order occur in a wide range of terrestrial habitats (forests, grasslands, and wetlands) and one freshwater aquatic species is known, *Psathyrella aquatica* J.L. Frank, Coffan & D. South (Frank et al. 2010). Nutritional modes of Agaricales species are mostly saprotrophic, ectomycorrhizal, or parasitic, while endophytic and lichenized lifestyles are less represented (Põlme et al. 2020). More than 25,350 species have been ascribed to Agaricales (Roskov et al. 2023), which contains 553 genera, encompassing six extinct genera (Hibbet et al. 2003; Heads et al. 2017), harbored in 46 families. The accuracy of the infraorder classification of Agaricales was finally proposed with suborders: Agaricineae, Clavariineae, Hygrophorineae, Marasmiineae, Mycenineae, Pleurotineae, Pluteineae, Phyllotopsidineae, Sarcomyxineae, Schizophyllineae, and Tricholomatineae (Dentinger et al. 2016; Olariaga et al. 2020; Wang et al. 2023c).

History

From the beginning, within Linnaean taxonomic systems (Linnaeus 1753), Agaricales was almost all classified in a single genus *Agaricus* L. with few exceptions, one being *Lycoperdon pedunculatum* L. (now *Tulostoma brumale* Pers., Agaricales). However, many of Linnaeus's *Agaricus* belong in other orders, e.g., *Agaricus chantarellus* L. now *Cantharellus cibarius* Fr. in Cantharellales, *A. integer* L. now *Russula integra* (L.) Fr. in Russulales, and *A. quercinus* L. now *Daedalea quercina* (L.) Pers. in Polyporales. Additionally, among 'Algae' was *Byssus botryoides* L. now *Lichenomphalia umbellifera* (L.) Redhead, Lutzoni, Moncalvo & Vilgalys in Agaricales, with an alternative simultaneously published name *Agaricus umbellifera* L. (1753), which is a basionym for *Lichenomphalia umbellifera*. *Agaricus* was one of only 10 genera in 'Fungi' that itself was distinguished from 'Algae', 'Musci', and 'Filices' in 'class' Cryptogamia. Others were: *Boletus* L., *Clathrus* P. Micheli ex L., *Clavaria* Vaill. ex L., *Elvella* L., *Hydnum* L., *Lycoperdon* Tourn. ex L., *Mucor* P. Micheli ex L., *Peziza* L., and *Phallus* Junius ex L.

Following the introduction of Linnaean classification system with genera and species binomials, there was a frenzied, chaotic half century of naming fungi and plants without rules or regulation or formal attributes, largely by persons having royal or wealthy patrons or being clergy and supported by churches, or as a hobby or by physicians interested in medicinal or poisonous properties. Christiaan Hendrik Persoon (1761–1836) was exceptional, being a physician without wealth and dedicated to studying fungi. In his Tentamen dispositionis methodicae fungorum (Persoon 1797), roughly translated as 'An attempt at the methodical arrangement of fungi', he formulated a taxonomic classification of classes, orders, genera, and families.

In 1797, it was evident from his illustrations of slime mold fructifications and rust spores that Persoon was using either a powerful hand lens or a microscope, hence breakthroughs in systematics via new technology. Nearly all modern Agaricales had hymenia he could see and were classified in the order Hymenothecium (Gymnothecium), while several powdery-spored gastromycetes lacking hymenia but currently in Agaricales, were then in order Dermatocarpon (Angiothecium). Another (*Cyathus*) with macroscopic disseminules, was in the order Sarcothecium (Gymnothecium). Persoon's advances in science were so *avant garde*, that his next major publication, Synopsis methodica fungorum (Persoon 1801) was selected as a starting point book by later generations of mycologists, but restricted to names in "Uredinales", "Ustilaginales", and "Gasteromycetes", the latter being vague.

Elias Magnus Fries (1794–1878) was the next major influencer in the classification of fungi and especially those in Agaricales. Fries (1815–1818, 1821–1832) recognized many genera and subgeneric 'families'. Then, Fries (1874) elevated some of them and recognized 12 genera of lamellar fungi and suggested a classification system based on macromorphological characters, such as the morphology of basidiome and color of spore print (Matheny et al. 2006; Zhao et al. 2008). Subsequently, Fayod (1889) incorporated micromorphological characters in agaricoid fungi study, proposing 108 genera (Fayod 1889). Underwood (1899) proposed Agaricales with seven families in his work, including "Moulds, mildews and mushrooms". Clements (1909) followed Underwood's proposal in "The genera of Fungi", considering Agaricales but with six families. Currently, Agaricales in the sense of Underwood and Clements, who also called them "Hymenomycetes", could correspond to the modern Agaricomycotina and their family Agaricaceae to the current order Agaricales. Singer (1951, 1962, 1975, 1986), in his very important work "The Agaricales in modern taxonomy", divided Agaricales in three suborders: Agaricineae Fr., Boletineae Rea, and Russulineae Singer. These groups are currently recognized as orders on their own, leaving the first one as Agaricales s.s. (Hibbett et al. 2014). Horak (1968) in "Synopsis generum Agaricalium" provided full descriptions and illustrations of approximately 330 genera of agaricoid and boletoid fungi. Another relevant work is that of Kühner (1980, 1984), who emphasized on cytological characteristics, in addition of other morphological characters, and proposed five orders: Agaricales s.s., Boletales, Pluteales, Russulales, and Tricholomatales, to accommodate fungi with lamellar hymenophore. Moreover, Kühner (1984) recognized six families within Agaricales: Agaricaceae, Bolbitiaceae, Coprinaceae, Cortinariaceae, Crepidotaceae, and Strophariaceae. Modern concept of Agaricales arrived with Moncalvo et al. (2002), who presented the first phylogeny of Agaricales and resolved 117 clades. However, Hibbett et al. (1997) had already recovered the euagarics clade before this work. Then, Matheny et al. (2006) presented the first multilocus phylogeny where they found six clades: agaricoid, tricholomatoid, marasmioid, hygrophoroid, pluteoid, and plicaturopsidoid. The most recent compilation of names of Agaricales in a phylogenetic context was made by Kalichman et al. (2020). These authors identified and analyzed 1383 generic names of this group, in addition, they provided a schematic phylogenetic tree of families that contain agarics and others belonging to Agaricales.

Characters that define the taxa in the order

There is no morphological synapomorphy that unites Agaricales. The order evolved several basidiome types from resupinate (corticioid) to conchate, cyphelloid, stereoid, clavarioid, pileostipitate (with open or enclosed hymenophore), and gasteroid/sequestrate (epigeous or hypogeous). Dominating the forms are pileostipitate forms, characterized by a lamellate hymenophore. However, hymenophores can also be smooth, wrinkled, odontoid or poroid. Presence of protective veils (universal and partial) is quite common in pileostipitate forms. Sequestrate forms showing locules and a columella (vestigial structure of the stipe) that can be present, reduced or absent. Hyphal system is mainly monomitic, with or without clamp-connections, rarely dimitic or sarcodimitic. Basidia are holobasidiate, usually sterigmate, ballistosporic (when the hymenophore is very early exposed to air) or statismosporic (in gasteroid/

sequestrate epigeous to hypogeous forms). Dolipore septa are usually provided with perforate parenthesomes. Basidiospores features are extremely diverse with regards to the broad range of shapes, wall thickness, colour in mass (white, pink, brown, purple-brown, black); they can be smooth or ornamented in many ways, dextrinoid/amyloid or not. Cystidia, setae and other sterile structures may be present in hymenium, on pileus and/or stipe surface, on basal mycelium or absent.

Taxa delimitation mainly relies on molecular phylogenetic results, but their integration with macro- and micromorphological and ecological/trophic traits is very useful and strongly recommended. Microscopically, there are particularly important taxonomic characters including the size, shape and wall features (thickness, ornamentation, and chemical reactions) of basidiospores; the arrangement of covering layers of basidiomes (pileipellis, stipitipellis), veils, and hymenophoral trama; the presence/absence of clamp-connections; and the presence, character and distribution of specialized sterile elements (cystidia, setae). All these features have played a central role in defining the 553 genera and 46 families in Agaricales.

Plates

Fig. 3 Selected basidiome types of suborders in Agaricales. **a**, **b** *Agaricus bisporus* (ZRL20181488, Gansu province, China) and *Apioperdon pyriforme* from Agaricineae (QL20170019, Gansu province, China); **c** *Hygrophorus russula* from Hygrophorineae (ZRL20201408, Sichuan province, China); **d** *Marasmiellus candidus* from Marasmiineae (ZRL20151342, Zhejiang province of China); **e** *Pleurotus abieticola* from Pleurotineae (ZRL20201486, Sichuan province, China); **f** *Amanita chepangiana* from Pluteineae (ZRL20190425, Sichuan province, China); **g** *Clavulinopsis laeticolor* from Clavariineae (ZRL2015793, Sichuan province, China); **h** *Schizophyllum commune* from Schizophyllineae (GX2017001, Guangxi province, China); **i** *Tricholoma matsutake* from Tricholomatineae (ZRL20191536, Sichuan province, China)

Genera included

Suborder **Agaricineae** Fr. 1825
Family Agaricaceae Chevall. 1826
= Family Coprinaceae Overeem & Weese 1924
= Family Podaxaceae Corda 1842
= Family Tulostomataceae E. Fisch. 1900
Agaricus L. 1753
= *Araneosa* Long 1941
= *Gyrophragmium* Mont. 1843
= *Hypophyllum* Paulet 1793
= *Longula* Zeller 1945
= *Psalliota* (Fr.) P. Kumm. 1871
= *Pratella* (Pers.) Gray 1821
Asperosporus Karlsen-Ayala, Gazis & M.E. Sm. 2021
Barcheria T. Lebel 2004
Battarrea Pers. 1801
= *Dendromyces* Libosch. 1810
= *Sphaericeps* Welw. & Curr. 1868
Battarreoides T. Herrera 1953
= *Battarraeastrum* R. Heim & T. Herrera 1960
Chamaemyces Battarra ex Earle 1909
= *Drosella* Maire 1935
= *Lepiotella* (E.-J. Gilbert) Konrad 1934
Chlamydopus Speg. 1898
Chlorolepiota Sathe & S.D. Deshp. 1979
Chlorophyllum Massee 1898
Clarkeinda Kuntze 1891
= *Chitonia* (Fr.) P. Karst. 1879
= *Chitoniella* Henn. 1898
= *Chitonis* Clem. 1909
= *Secotium* Kunze 1840
Clavogaster Henn. 1896
Coniolepiota Vellinga 2011
Coprinus Pers. 1797
= *Coprinusella* (Peck) Zerov 1979
= *Onchopus* P. Karst. 1879
Crucispora E. Horak 1971
Cystolepiota Singer 1952
= *Pulverolepiota* Bon 1993
Dictyocephalos L.M. Underwood ex V.S. White 1901
= *Battarreopsis* Henn. 1902
= *Whetstonia* Lloyd 1906
Echinoderma (Locq. ex Bon) Bon 1991
Endolepiotula Singer 1963
Eriocybe Vellinga 2011
Gasterellopsis Routien 1940
Heinemannomyces Watling 1999
Hiatulopsis Singer & Grinling 1967
Holocotylon Lloyd 1906
Hymenagaricus Heinem. 1981
Janauaria Singer 1986
Lepiota (Pers.) Gray 1821
= *Amogaster* Castellano 1995
= *Cribrospora* Pacioni & P. Fantini 2000
= *Cryptolepiota* Kropp & Trappe 2012
= *Fusispora* Fayod 1889
= *Lepiota* P. Browne 1756
= *Lepiotula* (Maire) Locq. ex E. Horak 1968
= *Morobia* E. Horak 1979
Leucoagaricus Locq. ex Singer 1948
= *Coccobotrys* Boud. & Pat. 1900
= *Schulzeria* Bres. & Schulzer 1886
= *Sericeomyces* Heinem. 1978
Leucocoprinus Pat. 1888
= *Mastocephalus* Battarra ex Earle 1909
Macrolepiota Singer 1948
= *Lepiotella* Rick 1938
= *Volvolepiota* Singer 1959
Melanophyllum Velen. 1921
= *Chlorosperma* Murrill 1922
= *Chlorospora* Massee 1898
= *Glaucospora* Rea 1922
Metrodia Raithelh. 1971
Micropsalliota Höhn. 1914
= *Allopsalliota* Nauta & Bas 1999
Montagnea Fr. 1836
Mycenastrum Desv. 1842
= *Endonevrum* Czern. 1845
Neosecotium Singer & A.H. Sm. 1960
Phellorinia Berk. 1843
= *Areolaria* Kalchbr. 1884
= *Cyphellomyces* Speg. 1906
= *Xylopodium* Mont. 1845
Phyllogaster Pegler 1969
Podaxis Desv. 1809
= *Catachyon* (Ehrenb. ex Fr.) Fr. 1832
= *Cauloglossum* Grev. ex Fr. 1829
= *Chainoderma* Massee 1890
= *Schweinitzia* Grev. 1823
Pseudoauricularia Kobayasi 1982
Pseudolepiota Z.W. Ge 2017
Queletia Fr. 1872
Rugosospora Heinem. 1973
Schinzinia Fayod 1889
Schizostoma Ehrenb. ex Lév. 1846
Singerina Sathe & S.D. Deshp. 1981
Smithiogaster J.E. Wright 1975
Smithiomyces Singer 1944
Termiticola E. Horak 1979
Tulostoma Pers. 1794
= *Tulasnodea* Fr. 1849
Xanthagaricus (Heinem.) Little Flower, Hosag. & T.K. Abraham 1997
Xerocoprinus Maire 1907
Family Bolbitiaceae Singer 1948
Agrogaster D.A. Reid 1986

Bolbitius Fr. 1838
= *Pluteolus* (Fr.) Gillet 1876
Conocybe Fayod 1889
= *Gastrocybe* Watling 1968
= *Pseudoconocybe* Hongo 1967
= *Raddetes* P. Karst. 1887
Cyttarophyllopsis R. Heim 1968
Descolea Singer 1952
= *Descomyces* Bougher & Castellano 1993
= *Hymenangium* Klotzsch 1839
= *Pseudodescolea* Raithelh. 1980
= *Setchelliogaster* Pouzar 1958
= *Timgrovea* G. Cunn. 1993
Galerella Earle 1909
Galeropsis Velen. 1930
= *Cyttarophyllum* (R. Heim) Singer 1936
= *Psammomyces* Lebedeva 1932
Gymnoglossum Massee 1891
Pholiotina Fayod 1889
Ptychella Roze & Boud. 1879
Rhodoarrhenia Singer 1964
Tubariella E. Horak & Hauskn. 2002
Tubariopsis R. Heim 1931
Tympanella E. Horak 1971
Wielandomyces Raithelh. 1988

Family Cortinariaceae Singer 1951
Aureonarius Niskanen & Liimat. 2022
Austrocortinarius Niskanen & Liimat. 2022
Calonarius Niskanen & Liimat. 2022
Cortinarius (Pers.) Gray 1821
= *Cuphocybe* R. Heim 1951
= *Cystocybe* Velen. 1921
= *Dermocybe* (Fr.) Wünsche 1877
= *Gomphos* Kuntze 1891
= *Hydrocybe* (Fr. ex Rabenh.) Wünsche 1877
= *Hydrocybium* Earle 1909
= *Hydrotelamonia* Rob. Henry 1957
= *Hygromyxacium* Locq. 1979
= *Inoloma* (Fr.) Wünsche 1877
= *Leucopus* P. Kumm. 1871
= *Myxacium* (Fr.) P. Kumm. 1871
= *Myxopholis* Locq. 1979
= *Protoglossum* Massee 1891
= *Quadrispora* Bougher & Castellano 1993
= *Rozites* P. Karst. 1879
= *Sericeocybe* Rob. Henry 1993
= *Sphaerotrachys* Fayod 1889
= *Telamonia* (Fr.) Wünsche 1877
Cystinarius Niskanen & Liimat. 2022
Hygronarius Niskanen & Liimat. 2022
Mystinarius Niskanen & Liimat. 2022
Phlegmacium (Fr.) Wünsche 1877
= *Bulbopodium* Earle 1909
= *Cyanicium* Locq. 1979
= *Meliderma* Velen. 1920
Pyrrhoglossum Singer 1944
Thaxterogaster Singer 1951
= *Hygramaricium* Locq. 1979
= *Gigasperma* E. Horak 1971
= *Rapacea* E. Horak 1999
Volvanarius Niskanen & Liimat. 2022

Family Crassisporiaceae Vizzini, Consiglio & M. Marchetti 2019
Crassisporium Matheny, P.-A. Moreau & Vizzini 2014
Romagnesiella Contu, Matheny, P.-A. Moreau, Vizzini & A. de Haan 2014

Family Crepidotaceae (S. Imai) Singer 1951
Crepidotus (Fr.) Staude 1857
= *Calathinus* Quél. 1886
= *Cyphellathelia* Jülich 1972
= *Dochmiopus* Pat. 1887
= *Octojuga* Fayod 1889
= *Phaeoglabrotricha* W.B. Cooke 1961
= *Phaeomyces* E. Horak 2005
= *Phialocybe* P. Karst. 1879
= *Pleurotellus* Fayod 1889
= *Tremellastrum* Clem. 1909
= *Tremellopsis* Pat. 1903
Episphaeria Donk 1962
Nanstelocephala Oberw. & R.H. Petersen 1990
Neopaxillus Singer 1948
Pellidiscus Donk 1959
Pleuroflammula Singer 1946
Simocybe P. Karst. 1879
= *Ramicola* Velen. 1929

Family Galeropsidaceae Singer 1962
Panaeolopsis Singer 1969
Panaeolina Maire 1933
Panaeolus (Fr.) Quél. 1872
= *Anellaria* P. Karst. 1879
= *Campanularius* Roussel 1806
= *Chalymmota* P. Karst. 1879
= *Copelandia* Bres. 1912
= *Coprinarius* (Fr.) P. Kumm. 1871

Family Hydnangiaceae Gäum. & C.W. Dodge 1928
Hydnangium Wallr. 1839
Laccaria Berk. & Broome 1883
= *Russuliopsis* J. Schröt. 1889
Maccagnia Mattir. 1922
Podohydnangium G.W. Beaton, Pegler & T.W.K. Young 1984

Family Hymenogastraceae Vittad. 1831
= Family Chromocyphellaceae Knudsen 2010
Anamika K.A. Thomas, Peintner, M.M. Moser & Manim. 2002

Chromocyphella De Toni & Levi 1888
= *Cymbella* Pat. 1886
= *Phaeocarpus* Pat. 1887
= *Phaeocyphella* Pat. 1900
Flammula (Fr.) P. Kumm. 1871
Galerina Earle 1909
= *Galera* (Fr.) P. Kumm. 1871
= *Galerula* P. Karst. 1879
= *Pseudogalera* Velen. 1947
= *Phaeogalera* Kühner 1973
= *Pholidotopsis* Earle 1909
= *Velomycena* Pilát 1953
Gymnopilus P. Karst. 1879
= *Pseudogymnopilus* Raithelh. 1974
Hebeloma (Fr.) P. Kumm. 1871
= *Hebelomatis* Earle 1909
= *Hebelomina* Maire 1935
= *Myxocybe* Fayod 1889
= *Picromyces* Battarra ex Earle 1909
Hymenogaster Vittad. 1831
= *Dendrogaster* Bucholtz 1901
= *Fechtneria* Velen. 1939
= *Hysterogaster* C.W. Dodge 1928
= *Radiogaster* Lloyd 1924
= *Rhizopogoniella* Soehner 1953
= *Roumeguerites* P. Karst. 1879
= *Sarcoloma* Locq. 1979
Naucoria (Fr.) P. Kumm. 1871
= *Alnicola* Kühner 1926
Phaeocollybia R. Heim 1931
= *Quercella* Velen. 1921
Phaeosolenia Speg. 1902
Psathyloma Soop, J.A. Cooper & Dima 2016
Psilocybe (Fr.) P. Kumm. 1871
= *Delitescor* Earle 1909
= *Naematoloma* P. Karst. 1879
= *Stropholoma* (Singer) Balletto 1989
= *Weraroa* Singer 1958
Synnematomyces Kobayasi 1981

Family Inocybaceae Jülich 1982
Auritella Matheny & Bougher 2006
Inocybe (Fr.) Fr. 1863
= *Agmocybe* Earle 1909
= *Astrosporina* J. Schröt. 1889
= *Clypeus* (Britzelm.) Fayod 1889
= *Inocibium* Earle 1909
= *Inocybella* Zerova 1974
Inosperma (Kühner) Matheny & Esteve-Rav. 2019
Mallocybe (Kuyper) Matheny, Vizzini & Esteve-Rav. 2019
Nothocybe Matheny & K.P.D. Latha 2019
Pseudosperma Matheny & Esteve-Rav. 2019
Tubariomyces Esteve-Rav. & Matheny 2010

Family Lycoperdaceae Chevall. 1826
Abstoma G. Cunn. 1926
Acutocapillitium P. Ponce de León 1976
Apioperdon (Kreisel & D. Krüger) Vizzini 2017
= *Lycoperdon* subgenus *Apioperdon* (Kreisel & D. Krüger) Jeppson & E. Larss. 2008
Arachnion Schwein. 1822
= *Scoleciocarpus* Berk. 1843
Bovista Pers. 1794
= *Globaria* Quél. 1873
= *Piesmycus* Raf. 1808
= *Pseudolycoperdon* Velen. 1947
= *Sackea* Rostk. 1844
Bryoperdon Vizzini 2017
Calvatiopsis Hollós 1929
Calbovista Morse ex M.T. Seidl 1995
= *Calbovista* Morse 1935
Calvatia Fr. 1849
= *Bovistaria* (Fr.) P. Karst. 1889
= *Eriosphaera* Reichardt 1866
= *Hypoblema* Lloyd 1902
= *Langermannia* Rostk. 1839
= *Lanopila* Fr. 1847
= *Lasiosphaera* Reichardt 1870
Disciseda Czern. 1845
= *Bovistina* Long & Stouffer 1941
= *Catastoma* Morgan 1892
Gastropila Homrich & J.E. Wright 1973
= *Pila* Speg. 1923
Glyptoderma R. Heim & Perr.—Bertr. 1971
Japonogaster Kobayasi 1989
Lycoperdon Pers. 1794
= *Bovistella* Morgan 1892
= *Calvatiella* C.H. Chow 1936
= *Capillaria* Velen. 1947
= *Cerophora* Raf. 1814
= *Handkea* Kreisel 1989
= *Priapus* Raf. 1808
= *Sufa* Adans. 1763
= *Utraria* Quél. 1873
= *Vascellum* F. Šmarda 1958
Lycoperdopsis Henn. 1900
Morganella Zeller 1948

Family Mythicomycetaceae Vizzini, Consiglio & M. Marchetti 2019
Mythicomyces Redhead & A.H. Sm. 1986
Stagnicola Redhead & A.H. Sm. 1986
Family Nidulariaceae Dumort. 1822
Crucibulum Tul. & C. Tul. 1844
Cyathella Brot. 1804
Cyathus Haller 1768
= *Cyathia* P. Browne 1756
= *Cyathodes* P. Micheli ex Kuntze 1891

= *Peziza* L. 1753
Mycocalia J.T. Palmer 1961
Nidula V.S. White 1902
Nidularia Fr. 1817
= *Granularia* Roth 1791
Retiperidiolia Kraisit., Choeyklin, Boonprat. & M.E. Sm. 2022
Family Psathyrellaceae Vilgalys, Moncalvo & Redhead 2001
= Zerovaemycetaceae Gorovij 1977
Britzelmayria D. Wächt. & A. Melzer 2020
Candolleomyces D. Wächt. & A. Melzer 2020
Coprinellus P. Karst. 1879
= *Annularius* Roussel 1806
= *Ephemerocybe* Fayod 1889
= *Ozonium* Link 1809
= *Pseudocoprinus* Kühner 1928
Coprinopsis P. Karst. 1881
= *Hormographiella* Guarro & Gené 1992
= *Lentispora* Fayod 1889
= *Pselliophora* P. Karst. 1879
= *Rhacophyllus* Berk. & Broome 1871
= *Zerovaemyces* Gorovij 1977
Cystoagaricus Singer 1947
Gasteroagaricoides D.A. Reid 1986
Hausknechtia D. Wächt. & A. Melzer 2020
Heteropsathyrella T. Bau & J.Q. Yan 2021
Homophron (Britzelm.) Örstadius & E. Larss. 2015
Jugisporipsathyra J.Q. Yan, Y.G. Fan & S.N. Wang 2022
Kauffmania Örstadius & E. Larss. 2015
Lacrymaria Pat. 1887
= *Cortiniopsis* J. Schröt. 1889
= *Glyptospora* Fayod 1889
Macrometrula Donk & Singer 1948
Narcissea D. Wächt. & A. Melzer 2020
Olotia D. Wächt. & A. Melzer 2020
Parasola Redhead, Vilgalys & Hopple 2001
Psathyrella (Fr.) Quél. 1872
= *Astylospora* Fayod 1889
= *Drosophila* Quél. 1886
= *Gymnochilus* Clem. 1896
= *Hypholomopsis* Earle 1909
= *Pannucia* P. Karst. 1879
= *Pluteopsis* Fayod 1889
= *Psalliotina* Velen. 1939
= *Psathyra* (Fr.) P. Kumm. 1871
= *Psilocybe* Fayod 1889
Punjabia D. Wächt. & A. Melzer 2020
Tulosesus D. Wächt. & A. Melzer 2020
Typhrasa Örstadius & E. Larss. 2015
Family Squamanitaceae Jülich1982
Cystoderma Fayod 1889
Dissoderma (A.H. Sm. & Singer) Singer 1973
Floccularia Pouzar 1957
Leucopholiota (Romagn.) O.K. Mill., T.J. Volk & Bessette 1996
= *Amylolepiota* Harmaja 2002
Phaeolepiota Maire ex Konrad & Maubl. 1928
Squamanita Imbach 1946
= *Coolia* Huijsman 1943
Family Strophariaceae Singer & A.H. Sm. 1946
Agrocybe Fayod 1889
= *Bulla* Battarra ex Earle 1909
= *Bulla* Battarra 1755
= *Cyclopus* (Quél.) Barbier 1907
= *Togaria* W.G. Sm. 1908
Brauniella Rick ex Singer 1955
= *Braunia* Rick 1934
Deconica (W.G. Sm.) P. Karst. 1879
Hypholoma (Fr.) P. Kumm. 1871
= *Bogbodia* Redhead 2013
Kuehneromyces Singer & A.H. Sm. 1948
Leratiomyces Bresinsky & Manfr. Binder ex Bridge, Spooner, Beever & D.C. Park 2008
= *Cytophyllopsis* R. Heim 1958
Melanotus Pat. 1900
Pholiota (Fr.) P. Kumm. 1871
= *Derminus* (Fr.) Staude 1857
= *Dryophila* Quél. 1886
= *Flammopsis* Fayod 1889
= *Gymnocybe* P. Karst. 1879
= *Hemipholiota* (Singer) Romagn. 1980
= *Hemipholiota* (Singer) Bon 1986
= *Hypodendrum* Paulet ex Earle 1909
= *Nemecomyces* Pilát 1933
= *Nivatogastrium* Singer & A.H. Sm. 1959
= *Phaeonematoloma* (Singer) Bon 1994
= *Ryssospora* Fayod 1889
= *Visculus* Earle 1909
Protostropharia Redhead, Moncalvo & Vilgalys 2013
Pyrrhulomyces E.J. Tian & Matheny 2020
Stropharia (Fr.) Quél. 1872
Family Tubariaceae Vizzini 2008
Cyclocybe Velen. 1939
Flammulaster Earle 1909
Hemistropharia Jacobsson & E. Larss. 2007
Pachylepyrium Singer 1958
Phaeomarasmius Scherff. 1897
= *Epicorticium* Velen. 1926
= *Flocculina* P.D. Orton 1960
= *Marasmiopsis* Henn. 1898
Pleuromyces Dima, P.-A. Moreau & V. Papp 2018
Tubaria (W.G. Sm.) Gillet 1876
Genera *incertae sedis*
Cercopemyces T.J. Baroni, Kropp & V.S. Evenson 2014

Cereicium Locq. 1979
Cystodermella Harmaja 2002
Fissolimbus E. Horak 1979
Meottomyces Vizzini 2008
Phaeopholiota Locq. & Sarwal 1983
Ripartitella Singer 1947
Squamaphlegma Locq. 1979
Stephanopus M.M. Moser & E. Horak 1975
Verrucospora E. Horak 1967
Volvigerum (E. Horak & M.M. Moser) R. Heim 1966
Weinzettlia Velen. 1921
Suborder **Clavariineae** Olariaga, Huhtinen, Læssøe, J.H. Petersen & K. Hansen 2020
Family Clavariaceae Chevall. 1826
Camarophyllopsis Herink 1958
=*Hygrotrama* Singer 1959
Ceratellopsis Konrad & Maubl. 1937
Clavaria Vaill. ex L. 1753
=*Holocoryne* (Fr.) Bonord. 1851
=*Stichoclavaria* Ulbr. 1928
Clavicorona Doty 1947
Clavulinopsis Overeem 1923
=*Donkella* Doty 1950
=*Ramaria* Holmsk. 1790
Hirticlavula J.H. Petersen & Læssøe 2014
Hodophilus R. Heim 1958
Hyphodontiella Å. Strid 1975
Lamelloclavaria Birkebak & Adamčík 2016
Mucronella Fr. 1874
=*Myxomycidium* Massee 1901
Ramariopsis (Donk) Corner 1950
Suborder **Hygrophorineae** Aime, Dentinger & Gaya 2015
Family Hygrophoraceae Lotsy 1907
Acantholichen P.M. Jørg. 1998
Aeruginospora Höhn. 1908
Ampulloclitocybe Redhead, Lutzoni, Moncalvo & Vilgalys 2002
=*Clavicybe* Harmaja 2002
Aphroditeola Redhead & Manfr. Binder 2013
Arrhenia Fr. 1849
=*Boehmia* Raddi 1806
=*Corniola* Gray 1821
=*Dictyolus* Quél. 1886
=*Geotus* Pilát & Svrček 1953
=*Leptotus* P. Karst. 1879
=*Omphalia* (Fr.) Gray 1821
Cantharellula Singer 1936
Cantharocybe H.E. Bigelow & A.H. Sm. 1973
Chromosera Redhead, Ammirati & Norvell 1995
Chrysomphalina Clémençon 1982
=*Chrysobostrychodes* G. Kost 1985
Cora Fr. 1825
=*Wainiocora* Tomas. 1950
Corella Vain. 1890
Cuphophyllus (Donk) Bon 1985
=*Dermolomopsis* Vizzini 2012
Cyphellostereum D.A. Reid 1965
Dictyonema C. Agardh ex Kunth 1822
=*Coraemyces* Cif. & Tomas. 1954
=*Dichonema* Blume & T. Nees 1826
=*Dictyonematomyces* Cif. & Tomas. 1954
=*Gyrolophium* Kunze ex Krombh. 1831
=*Laudatea* Johow 1884
=*Rhipidonema* Mattir. 1881
=*Rhipidonematomyces* Cif. & Tomas. 1954
=*Rhizonema* Thwaites 1849
Eonema Redhead, Lücking & Lawrey 2009
Gliophorus Herink 1958
Gloioxanthomyces Lodge, Vizzini, Ercole & Boertm. 2013
Haasiella Kotl. & Pouzar 1966
Humidicutis (Singer) Singer 1959
Hygroaster Singer 1955
Hygrocybe (Fr.) P. Kumm. 1871
=*Bertrandia* R. Heim 1936
=*Bertrandia* R. Heim 1966
=*Godfrinia* Maire 1902
=*Hydrophorus* Battarra ex Earle 1909
=*Pseudohygrocybe* (Bon) Kovalenko 1988
Hygrophorus Fr. 1836
=*Camarophyllus* (Fr.) P. Kumm. 1871
=*Limacium* (Fr. ex Rabenh.) P. Kumm. 1871
Lichenomphalia Redhead, Lutzoni, Moncalvo & Vilgalys 2002
=*Botrydiopsis* Trevis. 1845
=*Coriscium* Vain. 1890
=*Phalomia* Nieuwl. 1916
=*Phytoconis* Bory 1797
Melanomphalia M.P. Christ. 1936
=*Horakomyces* Raithelh. 1983
Neohygrocybe Herink 1958
Porpolomopsis Bresinsky 2008
Pseudoarmillariella Singer 1956
Semiomphalina Redhead 1984
Sinohygrocybe C.Q. Wang, Ming Zhang & T.H. Li 2018
Spodocybe Z. M. He & Zhu L. Yang 2021
Genera *incertae sedis*
Xeromphalina Kühner & Maire 1934
=*Phlebomarasmius* R. Heim 1967
=*Valentinia* Velen. 1939
Suborder **Marasmiineae** Aime, Dentinger & Gaya 2015
Family Cyphellaceae Burnett 1835
Asterocyphella W.B. Cooke 1961

Atheniella Redhead, Moncalvo, Vilgalys, Desjardin & B.A. Perry 2012
Campanophyllum Cifuentes & R.H. Petersen 2003
Catilla Pat. 1915
Cheimonophyllum Singer 1955
Chondrostereum Pouzar 1959
Cunninghammyces Stalpers 1985
Cyphella Fr. 1822
= *Dendrocyphella* Petch 1922
= *Phaeocoryne* Clem. 1902
Gloeocorticium Hjortstam & Ryvarden 1986
Gloeostereum S. Ito & S. Imai 1933
Granulobasidium Jülich 1979
Hyphoradulum Pouzar 1987
Incrustocalyptella Agerer 1983
Mycopan Redhead, Moncalvo & Vilgalys 2013
Phaeoporotheleum (W.B. Cooke) W.B. Cooke 1961
Phloeomana Redhead 2013
Pleurella E. Horak 1971
Scytinotus P. Karst. 1879
Seticyphella Agerer 1983
Setigeroclavula R.H. Petersen 1988
Sphaerobasidioscypha Agerer 1983
Thujacorticium Ginns 1988

Family Cystostereaceae Jülich 1982
Cericium Hjortstam 1995
Crustomyces Jülich 1978
Cystidiodontia Hjortstam 1983
Cystostereum Pouzar 1959
Parvobasidium Jülich 1975
Parvodontia Hjortstam & Ryvarden 2004
Rigidotubus J. Song, Y.C. Dai & B.K. Cui 2018

Family Marasmiaceae Roze ex Kühner 1980
Amyloflagellula Singer 1966
Aphyllotus Singer 1973
Brunneocorticium Sheng H. Wu 2007
Campanella Henn. 1895
Cellypha Donk 1959
Chaetocalathus Singer 1943
Crinipellis Pat. 1889
Hymenogloea Pat. 1900
Marasmius Fr. 1836
= *Androsaceus* (Pers.) Pat. 1887
= *Chamaeceras* Rebent. ex Kuntze 1898
= *Chaenocarpus* Rebent. 1804
= *Coenocarpus* Fr. 1825
= *Cryptothamnium* Wallr. 1842
= *Discocyphella* Henn. 1900
= *Heliomyces* Lév. 1844
= *Hymenoconidium* Zukal 1888
= *Hymenomarasmius* Overeem 1927
= *Polymarasmius* Murrill 1915
= *Protomarasmius* Overeem 1927
= *Scorteus* Earle 1909
= *Tephrophana* Earle 1909
Moniliophthora H.C. Evans, Stalpers, Samson & Benny 1978
Neocampanella Nakasone, Hibbett & Goranova 2009
Paramarasmius Antonín & Kolařík 2023
Tetrapyrgos E. Horak 1987
= *Pterospora* Métrod 1949

Family Omphalotaceae Bresinsky 1985
Anthracophyllum Ces. 1879
Caripia Kuntze 1898
Collybiopsis (J. Schröt.) Earle 1909
= *Marasmiellus* Murrill 1915
Connopus R.H. Petersen 2010
Gymnopanella Sand.-Leiva, J.V. McDonald & Thorn 2016
Gymnopus (Pers.) Gray 1821
= *Setulipes* Antonín 1987
Hymenoporus Tkalčec, Mešić & Chun Y. Deng 2015
Lentinula Earle 1909
Mycetinis Earle 1909
Neonothopanus R.H. Petersen & Krisai 1999
Omphalotus Fayod 1889
= *Lampteromyces* Singer 1947
= *Monodelphus* Earle 1909
Paragymnopus J.S. Oliveira 2019
Paramycetinis R.H. Petersen 2020
Pseudomarasmius R.H. Petersen & K.W. Hughes 2020
Pusillomyces J.S. Oliveira 2019
Rhodocollybia Singer 1939

Family Physalacriaceae Corner 1970
Anastrophella E. Horak & Desjardin 1994
Armillaria (Fr.) Staude 1857
= *Acurtis* Fr. 1849
= *Armillariella* (P. Karst.) P. Karst. 1881
= *Aphotistus* Humb. 1793
= *Polymyces* Battarra ex Earle 1909
= *Rhizomorpha* Roth 1791
Cibaomyces Zhu L. Yang, Y.J. Hao & J. Qin 2014
Cribbea A.H. Sm. & D.A. Reid 1962
Cryptomarasmius T.S. Jenkinson & Desjardin 2014
Cylindrobasidium Jülich 1974
Cyptotrama Singer 1960
= *Xerulina* Singer 1962
Dactylosporina (Clémençon) Dörfelt 1985
Deigloria Agerer 1980
Desarmillaria (Herink) R. A. Koch & Aime 2017
Epicnaphus Singer 1960
Flammulina P. Karst. 1891
= *Collybidium* Earle 1909
= *Myxocollybia* Singer 1936
Gloiocephala Massee 1892

Guyanagaster T.W. Henkel, M.E. Sm. & Aime 2010
Hymenopellis R.H. Petersen 2010
Laccariopsis Vizzini 2013
Manuripia Singer 1960
Mucidula Pat. 1887
Mycaureola Maire & Chemin 1922
Mycotribulus Nag Raj & W.B. Kendr. 1970
Naiadolina Redhead, Labbé & Ginns 2013
Oudemansiella Speg. 1881
= *Coprinopsis* Beeli 1929
= *Oudemansia* Speg. 1880
= *Phaeolimacium* Henn. 1899
Paraxerula R.H. Petersen 2010
Physalacria Peck 1882
= *Baumanniella* Henn. 1897
= *Eoagaricus* L. Krieg. 1923
= *Hormomitaria* Corner 1950
Ponticulomyces R.H. Petersen 2010
Protoxerula R.H. Petersen 2010
Pseudohiatula (Singer) Singer 1938
Pseudotyphula Corner 1953
Rhizomarasmius R.H. Petersen 2000
Rhodotus Maire 1926
Strobilurus Singer 1962
Xerula Maire 1933

Family Porotheleaceae Murrill 1916
Acanthocorticium Baltazar, Gorjón & Rajchenb. 2015
Calyptella Quél. 1886
Chrysomycena Vizzini, Picillo, Perrone & Dovana 2019
Clavomphalia E. Horak 1987
Clitocybula (Singer) Singer ex Métrod 1952
Delicatula Fayod 1889
= *Retocybe* Velen. 1947
Gerronema Singer 1951
Henningsomyces Kuntze 1898
= *Solenia* Pers. 1794
Hydropodia Vizzini & Consiglio 2022
Hydropus Kühner ex Singer 1948
Leucoinocybe Singer ex Antonín, Borovička, Holec & Kolařík 2019
Lignomphalia Antonín, Borovička, Holec & Kolařík 2019
Megacollybia Kotl. & Pouzar 1972
Porotheleum Fr. 1818
= *Stromatoscypha* Donk 1951
Pseudohydropus Vizzini & Consiglio 2022
Pulverulina Matheny & K.W. Hughes 2020
Rectipilus Agerer 1973
Trogia Fr. 1836
Vanromburghia Holterm. 1898
Genera *incertae sedis*
Baeospora Singer 1938
Callistodermatium Singer 1981
Hispidocalyptella E. Horak & Desjardin 1994
Lactocollybia Singer 1939
= *Bertrandiella* R. Heim 1959
= *Bertrandiella* R. Heim 1966
Lecanocybe Desjardin & E. Horak 1999
Mycenella (J.E. Lange) Singer 1938
Neoclitocybe Singer 1962
Pegleromyces Singer 1981
Phaeomycena R. Heim ex Singer & Digilio 1952
Physocystidium Singer 1962
Suborder **Mycenineae** R.L. Zhao, Vizzini & M.Q. He

Family Mycenaceae Overeem 1926
Cruentomycena R.H. Petersen, Kovalenko & O.V. Morozova 2008
Cynema Maas Geest. & E. Horak 1995
Favolaschia (Pat.) Pat. 1892
= *Hologloea* Pat. 1900
= *Mycomedusa* R. Heim 1945
= *Mycomedusa* R. Heim 1966
= *Poroauricula* McGinty 1917
= *Porolaschia* Pat. 1897
= *Porolaschia* Pat. 1898
Flabellimycena Redhead 1984
Heimiomyces Singer 1942
= *Perona* Pers. 1825
Hemimycena Singer 1938
Mycena (Pers.) Roussel 1806
= *Bactroboletus* Clem. 1909
= *Basidopus* Earle 1909
= *Collopus* Earle 1909
= *Corrugaria* Métrod 1949
= *Decapitatus* Redhead & Seifert 2000
= *Dictyoploca* Mont. ex Pat. 1890
= *Eomycenella* G.F. Atk. 1902
= *Filoboletus* Henn. 1900
= *Galactopus* Earle 1909
= *Hiatula* (Fr.) Mont. 1854
= *Insiticia* Earle 1909
= *Leiopoda* Velen. 1947
= *Leptomyces* Mont. 1856
= *Linopodium* Earle 1909
= *Mycenoporella* Overeem 1926
= *Mycenopsis* Velen. 1947
= *Phlebomycena* R. Heim 1945
= *Phlebomycena* R. Heim 1966
= *Poromycena* Overeem 1926
= *Prunulus* Gray 1821
= *Pseudomycena* Cejp 1929
= *Stereopodium* Earle 1909
= *Zephirea* Velen. 1947
Panellus P. Karst. 1879
= *Dictyopanus* Pat. 1900

= *Urospora* Fayod 1889
= *Urosporellina* E. Horak 1968
Resinomycena Redhead & Singer 1981
Roridomyces Rexer 1994
= *Roridella* E. Horak 2005
Tectella Earle 1909
Suborder **Phyllotopsidineae** Zhu L. Yang & G. S. Wang 2023
Family Phyllotopsidaceae Locquin ex Olariaga, Huhtinen, Læssøe, J.H. Petersen & K. Hansen 2020
Conoloma Zhu L. Yang & G. S. Wang 2023
Phyllotopsis E.-J. Gilbert & Donk ex Singer 1936
= *Tilotus* Kalchbr. 1881
= *Tomentifolium* Murrill 1903
Pleurocybella Singer 1947
Tricholomopsis Singer 1939
Family Pterulaceae Corner 1970
Allantula Corner 1952
Chaetotyphula Corner 1950
Coronicium J. Erikss. & Ryvarden 1975
Lepidomyces Jülich 1979
Merulicium J. Erikss. & Ryvarden 1976
Myrmecopterula Leal-Dutra, Dentinger & G.W. Griff. 2020
Phaeopterula (Henn.) Sacc. & D. Sacc. 1905
Pterula Fr. 1825
Pterulicium Corner 1950
= *Deflexula* Corner 1950
Family Radulomycetaceae Leal-Dutra, Dentinger & G.W. Griff. 2020
Aphanobasidium Jülich 1979
Globuliciopsis Hjortstam & Ryvarden 2004
Radulomyces M.P. Christ. 1960
= *Adustomyces* Jülich 1979
= *Cerocorticium* Henn. 1900
= *Chrysoderma* Boidin & Gilles 1991
= *Flavophlebia* (Parmasto) K.H. Larss. & Hjortstam 1977
Radulotubus Y.C. Dai, S.H. He & C.L. Zhao 2016
Genus family *incertae sedis*
Macrotyphula R.H. Petersen 1972
Suborder **Pleurotineae** Aime, Dentinger & Gaya 2015
Family Pleurotaceae Kühner 1980
Agaricochaete Eichelb. 1906
Hohenbuehelia Schulzer 1866
= *Acanthocystis* (Fayod) Kühner 1926
= *Nematoctonus* Drechsler 1941
Lignomyces R.H. Petersen & Zmitr. 2015
Pleurotus (Fr.) P. Kumm. 1871
= *Antromycopsis* Pat. & Trab. 1897
= *Crepidopus* Nees ex Gray 1821
= *Lentodiopsis* Bubák 1895
= *Nothopanus* Singer 1944
= *Pterophyllus* Lév. 1844
= *Scleroma* Fr. 1838
= *Velolentinus* Overeem 1927
Radulomycetopsis Dhingra, Priyanka & J. Kaur 2012
Resupinatus Nees ex Gray 1821
= *Asterotus* Singer 1943
= *Phyllotremella* Lloyd 1920
= *Phyllotus* P. Karst. 1879
= *Pleurotopsis* (Henn.) Earle 1909
= *Rhodocyphella* W.B. Cooke 1961
= *Scytinotopsis* Singer 1943
= *Stigmatolemma* Kalchbr. 1882
= *Stromatocyphella* W.B. Cooke 1961
= *Urceolus* Velen. 1939
Family Stephanosporaceae Oberw. & E. Horak 1979
Athelidium Oberw. 1965
Cristinia Parmasto 1968
= *Dacryobasidium* Jülich 1982
Lindtneria Pilát 1938
= *Cyanobasidium* Jülich 1979
= *Sulphurina* Pilát 1953
Mayamontana Castellano, Trappe & Lodge 2007
Stephanospora Pat. 1914
Family Typhulaceae Jülich 1982
Lutypha Khurana, K.S. Thind & Berthier 1977
Typhula (Pers.) Fr. 1818
= *Astoma* Gray 1821
= *Bromicolla* E.V. Eichw. 1843
= *Cnazonaria* Corda 1829
= *Coccopleum* Ehrenb. 1818
= *Dacryopsella* Höhn. 1915
= *Gliocoryne* Maire 1909
= *Phacorhiza* Pers. 1822
= *Pistillaria* Fr. 1821
= *Pistillina* Quél. 1881
= *Scleromitra* Corda 1829
= *Sclerotiomyces* Woron. 1926
= *Sphaerula* Pat. 1883
= *Tygervalleyomyces* Crous 2017
= *Xylochoeras* Fr. 1849
Suborder **Pluteineae** Aime, Dentinger & Gaya 2015
Family Amanitaceae E.-J. Gilbert 1940
Amanita Pers. 1797
= *Agaricus* Raf. 1830
= *Amanitaria* E.-J. Gilbert 1940
= *Amanitina* E.-J. Gilbert 1940
= *Amanitella* Earle 1909
= *Amanitopsis* Roze 1876
= *Amarrendia* Bougher & T. Lebel 2002
= *Amidella* E.-J. Gilbert 1940
= *Amplariella* E.-J. Gilbert 1940
= *Ariella* E.-J. Gilbert 1940

= *Boletium* Clem. 1909
= *Leucomyces* Battarra ex Earle 1909
= *Pseudofarinaceus* Battarra ex Kuntze 1891
= *Torrendia* Bres. 1902
= *Vaginaria* Forq. 1886
= *Vaginarius* Roussel 1806
= *Vaginata* Nees ex Gray 1821
= *Venenarius* Earle 1909
= *Volvella* E.-J. Gilbert & Beeli 1940
= *Volvoamanita* (Beck) E. Horak 1968
= *Volvoboletus* Henn. 1898
Catatrama Franco-Mol. 1991
Limacella Earle 1909
= *Amanitella* Maire 1913
Limacellopsis Zhu L. Yang, Q. Cai & Y.Y. Cui 2018
Saproamanita Redhead, Vizzini, Drehmel & Contu 2016
= *Lepidella* E.-J. Gilbert 1925
= *Aspidella* E.-J. Gilbert 1940
Zhuliangomyces Redhead 2019
= *Myxoderma* Fayod ex Kühner 1926
Family Limnoperdaceae G.A. Escobar 1976
Limnoperdon G.A. Escobar 1976
Family Pluteaceae Kotl. & Pouzar 1972
Melanoleuca Pat. 1897
= *Kinia* Consiglio, Contu, Setti & Vizzini 2008
= *Psammospora* Fayod 1893
Pluteus Fr. 1836
= *Annularia* (Schulzer) Gillet 1876
= *Chamaeota* (W.G. Sm.) Earle 1909
= *Hyporrhodius* (Fr.) Staude 1857
= *Rhodosporus* J. Schröt. 1889
Volvariella Speg. 1898
= *Volva* Adans. 1763
= *Volvaria* (Fr.) P. Kumm. 1871
= *Volvariopsis* Murrill 1911
= *Volvarius* Roussel 1806
Volvopluteus Vizzini, Contu & Justo 2011
= *Pseudofarinaceus* Earle 1909
Suborder **Sarcomyxineae** Zhu L. Yang & G. S. Wang 2023
Family Sarcomyxaceae Olariaga, Huhtinen, Læssøe, J.H. Petersen & K. Hansen 2020
Sarcomyxa P. Karst. 1891
Suborder **Schizophyllineae** Aime, Dentinger & Gaya 2015
Family Cyphellopsidaceae Jülich 1982
= Niaceae Jülich 1982
Akenomyces G. Arnaud 1954
Calathella D.A. Reid 1962
Dendrothele Höhn. & Litsch. 1907
= *Aleurocorticium* P.A. Lemke 1964
Digitatispora Doguet 1962
Eoscyphella Silva-Filho, Stevani & Menolli 2023
Flagelloscypha Donk 1951
Halocyphina Kohlm. & E. Kohlm. 1965
Lachnella Fr. 1836
Merismodes Earle 1909
= *Cyphellopsis* Donk 1931
= *Maireina* W.B. Cooke 1961
= *Phaeocyphellopsis* W.B. Cooke 1961
= *Pseudodasyscypha* Velen. 1939
Nia R.T. Moore & Meyers 1961
Peyronelina P.J. Fisher, J. Webster & D.F. Kane 1976
Phaeodepas D.A. Reid 1961
Pseudolasiobolus Agerer 1983
Woldmaria W.B. Cooke 1961
Family Schizophyllaceae Quél. 1888
Auriculariopsis Maire 1902
Fistulina Bull. 1791
= *Agarico-carnis* Paulet 1793
= *Buglossus* Wahlenb. 1820
= *Confistulina* Stalpers 1983
= *Hypodrys* Pers. 1825
Porodisculus Murrill 1907
= *Enslinia* Fr. 1836
= *Porodiscus* Murrill 1903
Pseudofistulina O. Fidalgo & M. Fidalgo 1963
Schizophyllum Fr. 1815
= *Apus* Gray 1821
= *Hyponevris* Earle 1909
= *Petrona* Adans. 1763
= *Phaeoschizophyllum* W.B. Cooke 1962
= *Rhipidium* Wallr. 1833
= *Scaphophoeum* Ehrenb. ex Wallr. 1833
= *Scaphophorum* Ehrenb. 1820
= *Schizonia* Pers. 1828
Suborder **Tricholomatineae** Aime, Dentinger & Gaya 2015
Family Asproinocybaceae T. Bau & G.F. Mou 2021
Asproinocybe R. Heim 1970
Tricholosporum Guzmán 1975
Family Biannulariaceae Jülich 1982
= Catathelasmataceae Wasser 1985
Bonomyces Vizzini 2014
Catathelasma Lovejoy 1910
= *Biannularia* Beck 1922
Cleistocybe Ammirati, A.D. Parker & Matheny 2007
Family Callistosporiaceae Vizzini, Consiglio, M. Marchetti & P. Alvarado 2020
Anupama K.N.A. Raj, K.P.D. Latha & Manim. 2019
Callistosporium Singer 1944
= *Pleurocollybia* Singer 1947
Guyanagarika Sánchez-García, T.W. Henkel & Aime 2016
Macrocybe Pegler & Lodge 1998

Pseudolaccaria Vizzini, Contu & Z.W. Ge 2015
Xerophorus (Bon) Vizzini, Consiglio & M. Marchetti 2020
Family Clitocybaceae Vizzini, Consiglio & M. Marchetti 2020
Clitocybe (Fr.) Staude 1857
= *Pseudolyophyllum* Raithelh. 1977
= *Rubeolarius* Raithelh. 1981
= *Singerella* Harmaja 1974
= *Trigonipes* Velen. 1939
Collybia (Fr.) Staude 1857
= *Microcollybia* Métrod 1952
= *Microcollybia* Lennox 1979
Dendrocollybia R.H. Petersen & Redhead 2001
= *Sclerostilbum* Povah 1932
= *Tilachlidiopsis* Keissl. 1924
Lepista (Fr.) W.G. Sm. 1870
= *Rhodopaxillus* Maire 1913
Lepistella T.J. Baroni & Ovrebo 2007
Leucocalocybe X.D. Yu & Y.J. Yao 2011
Paralepistopsis Vizzini 2012
Singerocybe Harmaja 1988
Family Entolomataceae Kotl. & Pouzar 1972
Clitocella Kluting, T.J. Baroni & Bergemann 2014
Clitopilopsis Maire 1937
Clitopiloides (Romagn.) Largent 1994
Clitopilus (Fr. ex Rabenh.) P. Kumm. 1871
= *Hexajuga* Fayod 1889
= *Orcella* Battarra ex Clem. 1896
Entocybe T.J. Baroni, V. Hofst. & Largent 2011
Entoloma (Fr.) P. Kumm. 1871
= *Alboleptonia* Largent & R.G. Benedict 1970
= *Arenicola* Velen. 1947
= *Calliderma* (Romagn.) Largent 1994
= *Claudopus* Gillet 1876
= *Eccilia* (Fr.) P. Kumm. 1871
= *Fibropilus* (Noordel.) Largent 1994
= *Inocephalus* (Noordel.) P.D. Orton 1991
= *Inopilus* (Romagn.) Pegler 1983
= *Lanolea* Nieuwl. 1916
= *Latzinaea* Kuntze 1891
= *Leptonia* (Fr.) P. Kumm. 1871
= *Leptoniella* Earle 1909
= *Nigropogon* Coker & Couch 1928
= *Nolanea* (Fr.) P. Kumm. 1871
= *Omphaliopsis* (Noordel.) P.D. Orton 1991
= *Paraeccilia* Largent 1994
= *Paraleptonia* (Romagn. ex Noordel.) P.D. Orton 1991
= *Pouzarella* Mazzer 1976
= *Pouzaromyces* Pilát 1953
= *Rhodocybella* T.J. Baroni & R.H. Petersen 1987
= *Rhodogaster* E. Horak 1964
= *Rhodophyllus* Quél. 1886
= *Richoniella* Costantin & L.M. Dufour 1900
= *Trichopilus* (Romagn.) P.D. Orton 1991
Lulesia Singer 1970
Rhodocybe Maire 1926
Rhodophana Kühner 1971
Family Fayodiaceae Jülich 1982
Caulorhiza Lennox 1979
Conchomyces Overeem 1927
Fayodia Kühner 1930
Gamundia Raithelh. 1979
= *Stachyomphalina* H.E. Bigelow 1979
Myxomphalia Hora 1960
Family Lyophyllaceae Jülich 1982
Arthromyces T.J. Baroni & Lodge 2007
Asterophora Ditmar 1809
= *Asterophora* Corda 1840
= *Asterophora* Fr. 1849
= *Asterosperma* Pers. 1818
= *Asterotrichum* Bonord. 1851
= *Nyctalis* Fr. 1825
= *Ugola* Adans. 1763
Atractosporocybe P. Alvarado, G. Moreno & Vizzini 2015
Australocybe T.J. Baroni, N. Fechner & van de Peppel 2022
Blastosporella T.J. Baroni & Franco-Mol. 2007
Calocybe Kühner ex Donk 1962
= *Calocybe* Kühner 1938
= *Rugosomyces* Raithelh. 1979
Calocybella Vizzini, Consiglio & Setti 2015
Clitolyophyllum Sesli, Vizzini & Contu 2016
Gerhardtia Bon 1994
Hypsizygus Singer 1947
Leucocybe Vizzini, P. Alvarado, G. Moreno & Consiglio 2015
Lyophyllopsis Sathe & J.T. Daniel 1981
Lyophyllum P. Karst. 1881
= *Caesposus* Nüesch 1937
Myochromella V. Hofst., Clémençon, Moncalvo & Redhead 2015
Nigrocarnea Sparre P. & Læssøe 2022
Ossicaulis Redhead & Ginns 1985
Phaeotephrocybe T.J. Baroni, T.W. Kuyper & van de Peppel 2022
Praearthromyces T.J. Baroni, T.W. Kuyper & van de Peppel 2022
Rhizocybe Vizzini, G. Moreno, P. Alvarado & Consiglio 2015
Sagaranella V. Hofst., Clémençon, Moncalvo & Redhead 2014
Sphagnurus Redhead & V. Hofst. 2014
= *Bryophyllum* Vizzini 2014
Tephrocybe Donk 1962
Tephrocybella Picillo, Vizzini & Contu 2015
Tephroderma Contu & Musumeci 2014

Termitomyces R. Heim 1942
=*Podabrella* Singer 1945
=*Rajapa* Singer 1945
=*Sinotermitomyces* M. Zang 1981
Termitosphaera Cif. 1935
Tricholomella Zerova ex Kalamees 1992
=*Echinosporella* Contu 1992
Tricholyophyllum Qing Cai, G. Kost & Zhu L. Yang 2020

Family Macrocystidiaceae Kühner 1979
Macrocystidia Joss. 1934
=*Galeromycena* Velen. 1947

Family Omphalinaceae Vizzini, Consiglio & M. Marchetti 2020
Infundibulicybe Harmaja 2003
Omphalina Quél. 1886
=*Phaeotellus* Kühner & Lamoure 1972

Family Pseudoclitocybaceae Vizzini, Consiglio, P.-A. Moreau & P. Alvarado 2018
Clitopaxillus G. Moreno, Vizzini, Consiglio & P. Alvarado 2018
Harmajaea Dima, P. Alvarado & Kekki 2018
Musumecia Vizzini & Contu 2011
Pogonoloma (Singer) Sánchez-García 2014
Pseudoclitocybe (Singer) Singer 1956

Family Tricholomataceae R. Heim ex Pouzar 1983
Albomagister Sánchez-García, Birkebak & Matheny 2014
Corneriella Sánchez-García 2014
Dennisiomyces Singer 1955
Dermoloma J.E. Lange ex Herink 1958
=*Dermoloma* J.E. Lange ex Singer 1951
=*Dermoloma* J.E. Lange ex Singer 1955
Leucopaxillus Boursier 1925
Porpoloma Singer 1952
Pseudobaeospora Singer 1942
Pseudoporpoloma Vizzini & Consiglio 2016
Pseudotricholoma (Singer) Sánchez-García & Matheny 2014
Tricholoma (Fr.) Staude 1857
=*Cortinellus* Roze 1876
=*Glutinaster* Earle 1909
=*Gyrophila* Quél. 1886
=*Mastoleucomyces* Battarra ex Kuntze 1891
=*Megatricholoma* G. Kost. 1984
=*Monomyces* Battarra ex Earle 1909
=*Phlebophora* Lév. 1841
=*Sphaerocephalus* Battarra ex Earle 1909
Genera *incertae sedis*
Aspropaxillus Kühner & Maire 1934
Giacomia Vizzini & Contu 2012
Leucocortinarius (J.E. Lange) Singer 1945
Notholepista Vizzini & Contu 2012
Omphaliaster Lamoure 1971
Paralepista Raithelh. 1981
Pseudoclitopilus Vizzini & Contu 2012
Pseudoomphalina (Singer) Singer 1956
=*Neohygrophorus* Singer 1962
Rimbachia Pat. 1891
=*Mniopetalum* Donk & Singer 1962
=*Pleuromycenula* Singer 1973
Ripartites P. Karst. 1879
Trichocybe Vizzini 2010
Agaricales families *incertae sedis*

Family Broomeiaceae Zeller 1948
Broomeia Berk. 1844

Family Hemigasteraceae Gäum. & C.W. Dodge 1928
Hemigaster Juel 1895
Flammulogaster Locq. & Sarwal 1987
Agaricales genera *incertae sedis*
Acinophora Raf. 1808
Actiniceps Berk. & Broome 1876
=*Dimorphocystis* Corner 1950
=*Wiesnerina* Höhn. 1907
Albocoprinus Voto 2020
Aleurocystis Lloyd ex G. Cunn. 1956
=*Matula* Massee 1888
Amparoina Singer 1958
Arthrosporella Singer 1970
=*Nothoclavulina* Singer 1970
Austroclitocybe Raithelh. 1972
Austroomphaliaster Garrido 1988
Cephaloscypha Agerer 1975
Cheilophlebium Opiz & Gintl 1856
Cymatella Pat. 1899
Cymatellopsis Parmasto 1985
Cyphellocalathus Agerer 1981
Fibulochlamys A.I. Romero & Cabral 1989
Glabrocyphella W.B. Cooke 1961
Gramincola Velen. 1947
Hertzogia R. Wiest 2022
Hygrophorocybe Vizzini & Contu 2014
Laterradea Raspail 1824
Locellina Gillet 1876
Lycogalopsis E. Fisch. 1886
=*Enteromyxa* Ces. 1879
Masseerina Lloyd 1920
Mesophelliopsis Bat. & A.F. Vital 1957
Metraria (Cooke) Cooke & Massee 1891
Metulocyphella Agerer 1983
Mycoalvimia Singer 1981
Mycodendron Massee 1891
Mycospongia Velen. 1939
Nochascypha Agerer 1983
Palaeocephala Singer 1962
Peglerochaete Sarwal & Locq. 1983
Phlebonema R. Heim 1929

Polygaster Fr. 1823
Pseudohygrophorus Velen. 1939
Retiperidiolia Kraisit., Choeyklin, Boonprat. & M.E. Sm. 2022
Skepperiella Pilát 1927
Stanglomyces Raithelh. 1986
Stemastrum Raf. 1808
Stylobates Fr. 1837

Evolution

Evolution of Agaricales is a field of intense research, due to the multifaceted importance of the order. Agaricales includes species with the most stereotypical and best-known mushroom morphologies such as the pileate-stipitate button mushroom and shiitake. Research attention focuses on various aspects of the order. For example, many studies examined the morphology of species, including transitions in complexity level, basidiomes morphologies, and macro- and microscopic trait evolution (Varga et al. 2019, 2022; Sánchez-García et al. 2020). It has been shown that morphological novelties such as pileus formation or the protection of the developing primordia by veil tissue (Varga et al. 2022), could have a higher impact on the speciation rate of lineages (Sánchez-García et al. 2020). This is in contrast to early studies (Sánchez-García and Matheny 2017; Wilson et al. 2017), which focused on nutritional modes. Agaricales lineages could also have a major contribution to the radiation of Agaricomycetes in the Jurassic period, coinciding with the emergence of complex basidiome types (Varga et al. 2019). Researchers addressed questions about genomic repertoires, with special attention on the evolution of substrate utilization, wood-decay properties (Ruiz-Dueñas et al. 2020), ectomycorrhizal genomics (Miyauchi et al. 2020), and chemical biology, to name a few. It was demonstrated that the peroxidase diversity was increased in this order by adapting to new substrates such as grass or forest litter (Ruiz-Dueñas et al. 2020). A significant body of research also concerns resolving phylogenetic and phylogenomic relationships within the order (Matheny et al. 2006; Dentinger et al. 2016). This aspect has probably experienced the most progress in the last two decades due to the broad accessibility of diverse sequencing technologies. Global ‘megaphylogenies’ have the promise to provide a bird’s eye view on phylogenetic relationships within the order (Varga et al. 2019; Sánchez-García et al. 2020). Simultaneously, genomic data can be expected to continue proliferating and contributing to resolving phylogenetic relationships even at smaller phylogenetic scales, as in the Cortinariaceae (Liimatainen et al. 2022). Agaricales includes the most widely produced crop mushroom species and thus one of the most widely researched fields is the evolution, development, and cultivation of edible mushroom-forming fungi, on which increasing taxonomic, genomic and transcriptomic attention has focused lately (Thakur 2020; Fu et al. 2022; Lin et al. 2022).

Justification of order and problems

Delimitation of Agaricales has been rather stable for the past 20 years since the beginning of the molecular era (Moncalvo et al. 2002; Hibbett 2006; Li et al. 2021c) and it also receives full support in our phylogenomic analyses. However, the internal classification of the group is still in progress. Dentinger et al. (2016) divided the order in seven suborders based on genomics level data: Agaricineae, Hygrophorineae, Marasmiineae, Pleurotineae, Pluteineae, Schizophyllineae and Tricholomatineae. Later Olariaga et al. (2020) separated a new suborder Clavariineae from Hygrophorineae based on a six-gene phylogeny, a division also supported by our phylogenomic tree. The other suborders recognized in Dentinger et al. (2016) are recovered with good support in our analyses but the delimitation of Marasmiineae requires further consideration. The placement of Mycenaceae as the basal taxon of Marasmiineae was poorly supported (59% bootstrap) in Dentinger et al. (2016) and their Tree Certainty Dataset recovered Schizophyllaceae forming a clade with Mycena (63% bootstrap). Based on our phylogenomic analyses Mycenaceae is indeed placed as sister to Schizophyllineae. Thus, Mycenaceae may need its own suborder and is here treated as *incertae sedis*. A recent study updated Agaricales system with two new suborders, Phyllotopsidaceae and Sarcomyxineae (Wang et al. 2023a, b, c). There are now 10 suborders accepted in Agaricales.

Family level classification of Agaricales is still far from stabilized in many parts. Several new families have been described during the past 10 years, i.e., Pseudoclitocybaceae (Alvarado et al. 2018a), Mythicomycetaceae (Vizzini et al. 2019), Phyllotopsidaceae (Olariaga et al. 2020), and Asproinocybaceae (Mou and Bau 2021), whilst old family names have been reintroduced or amended, i.e. Biannulariaceae (Vizzini et al. 2020a), Galeropsidaceae (Kalichman et al. 2020), and Squamanitaceae (Liu et al. 2021) to accommodate taxa that have previously been included in different families. The traditionally used loci (LSU, rpb1, rpb2, tef1) are only sometimes enough for resolving the family-level relationships and genomic level data would be needed for more solid conclusions. For example, delimitation of Hymenogastraceae and Strophariaceae (Agaricineae) has remained problematic and results from our -omics data analyses challenge the previous delimitations proposed (see more detailed discussion below). At the moment, over 80% genera of Agaricales are lacking genomic level data. Thus, many more changes in the internal classification of Agaricales are expected to be seen in the near future. Discussion on problems and the latest changes in selected families is presented below under each suborder.

Agaricineae

Hymenogastraceae

Matheny et al. (2006) used the name Hymenogastraceae for a clade that included: *Alnicola, Anamika, Flammula, Galerina*, *Hebeloma*, *Phaeocollybia*, and *Psilocybe*. This family was recovered in later phylogenies (e.g., Tian and Matheny 2021). In Moreno et al. (2017) two additional genera, *Chromocyphella* and *Psathyloma*, were recovered in Hymenogastraceae. In the phylogeny obtained by Varga et al. (2019), Hymenogastraceae was not recovered. To provide a family to place most of the genera of Agaricales, Kalichman et al. (2020) proposed to apply Hymenogastraceae sensu lato to the group of 28 genera, which included Strophariaceae. Nested within Hymenogastraceae sensu lato, Kalichman et al. (2020) considered Hymenogastraceae sensu stricto, with only *Alnicola*, *Hebeloma*, *Hymenogaster*, and *Psathyloma*, partially based on one of the subclades recovered by Moreno et al. (2017) in Hymenogastraceae. In this study, Hymenogastraceae was not recovered as a monophyletic group. The type of the family and two important members, *Alnicola* and *Psathyloma*, were not sampled. The clade that includes *Agrocybe pediades* (Fr.) Fayod, *Galerina*, *Gymnopilus*, and *Psilocybe*, labeled as Hymenogastraceae, needs a new family name, as was already suggested by Kalichman et al. (2020).

Inocybaceae

It is estimated that Inocybaceae comprises approximately 1250 species (Wijayawardene et al. 2020), making this family one of the most species-rich groups in Basidiomycota. The higher-level classification of this family has been vague: three genera were formally described (*Inocybe*, *Auritella*, *Tubariomyces*) but, for example, *Inocybe* was paraphyletic, and many subgenera or section-level groups existed with informal names (Matheny et al. 2009). Matheny et al. (2020a, b) resolved many discrepancies regarding the higher level of classification of Inocybaceae and formally recognized seven genera (viz. *Inocybe* sensu stricto, *Auritella*, *Inosperma*, *Mallocybe*, *Nothocybe*, *Pseudosperma*, and *Tubariomyces*) based on a 6-loci phylogeny of 63 species.

Psathyrellaceae

Wächter and Melzer (2020) proposed a subdivision of *Psathyrellaceae* based on a taxon-rich phylogenetic analysis and an iterative multigene guide tree. Seventeen monophyletic genera, among which seven new, viz. *Candolleomyces*, *Britzelmayria*, *Hausknechtia*, *Narcissea*, *Olotia*, *Punjabia,* and *Tulosesus*, were recognized. Bau and Yan (2021) described a new monotypic genus *Heteropsathyrella* which is sister to a clade consisting of genera *Cystoagaricus*, *Kauffmania* and *Typhrasa*, according to the ITS, LSU, *tef-1α*, and *β-tub* sequences analysis. Wang et al. (2022) described another monotypic genus *Jugisporipsathyra* based on morphology (e.g. ridge-ornamented basidiospores with suprahilar plage) and phylogenetic analysis (ITS, LSU, and *β-tub* sequences).

Squamanitaceae

Liu et al. (2021) emended *Squamanitaceae* and presented a detailed taxonomic treatment of it to accommodate five genera, viz. *Cystoderma*, *Floccularia*, *Leucopholiota*, *Phaeolepiota*, and *Squamanita*. Saar et al. (2022) resurrected *Dissoderma* for those species, previously included in *Squamanita*, with small, collybioid or mycenoid basidiomes, not volvate, without cystidia, and with purplish grey tinges on the pileus and often upper part of the stipe.

Strophariaceae

Strophariaceae sensu stricto, as was conceived by Matheny et al. (2006), has been modified over time. Formerly it was composed of the following genera: *Agrocybe*, *Deconica*, *Hypholoma*, *Kuehneromyces*, *Pholiota*, and *Stropharia*. Then, in Tian and Matheny (2021), two genera, *Bogbodia* and *Pyrrhulomyces*, were added. Later, in Varga et al. (2019), *Deconica* and *Kueheneromyces* were placed outside the Strophariaceae sensu stricto. The clade named Strophariaceae sensu stricto by Varga et al. (2019) was consistent across multiple trees and highly supported and included: *Bogbodia*, *Clavogaster*, *Leratiomyces*, *Phaeonematoloma*, *Pholiota*, *Protostropharia*, *Hypholoma*, and *Stropharia*. Kalichman et al. (2020) followed Varga et al. (2019) but with the addition of *Pyrrhulomyces* in Strophariaceae. In the phylogenomic tree of this work, not all the genera previously considered in the family were sampled, thus the clade that could correspond to Strophariaceae sensu stricto, in this case highly supported, was formed only by: *Hypholoma*, *Pholiota*, and *Stropharia*. If we follow Matheny et al. (2006) and the results obtained here, *Deconica* could also be part of this family; however, support for this node of Strophariaceae, including *Deconica*, is moderately low (79%) in our phylogenomic tree (Fig. 2). Basal to this clade were *Flammula* and *Hebeloma*, but with the inclusion of wider taxonomic sampling, these relationships could change. Finally, *Agrocybe* that was considered in Strophariaceae is polyphyletic (Matheny et al. 2006; Vizzini et al. 2014), with at least four lineages. In our phylogenomic tree (Fig. 2), one of these lineages, *Agrocybe pediades*, is the sister group to *Psilocybe*. Another sampled lineage is labeled *Cyclocybe* [e.g., *C. aegerita* (V. Brig.) Vizzini (=*Agrocybe aegerita* (V. Brig.) Singer)], which resulted as a sister group of *Crepidotus* and *Tubaria*.

Placement of *Gymnopilus* has always been problematic; sensu Singer (1986) it was a Cortinariaceae based on the ornamentation of the basidiospores, but for Kühner (1980) it was Strophariaceae due to the styrilpyrones found in these mainly lignicolous mushrooms. Matheny et al. (2006)

found it in its own clade, Gymnopileae, basal of a clade that included Crepidotaceae, Hymenogastraceae, Inocybaceae, Panaeoleae, Strophariaceae sensu stricto, and Tubarieae. Then, based again in Varga et al. (2019), Kalichman et al. (2020) considered *Gymnopilus* as part of Hymenogastraceae sensu lato, result also found here, or in need of a new family as already mentioned, along with *Psilocybe* and others.

In future works it is necessary to include all the members of Hymenogastraceae sensu lato, since in the phylogenomic tree presented here only 10 genera of the 28 tentatively considered in the family were sampled. Therefore, it is still difficult to make precise decisions about the correct placement of the genera involved, whether they belong to two or more families.

Clavariineae

Olariaga et al. (2020) established the new suborder Clavariineae Olariaga, Huhtinen, Læssøe, J.H. Petersen & K. Hansen for the family Clavariaceae Chevall. which in their analysis includes the clavarioid genera *Ceratellopsis*, *Clavaria*, *Clavulinopsis*, *Hirticlavula*, *Mucronella*, *Ramariopsis*, the corticioid genus *Hyphodontiella* and the agaricoid genera *Camarophyllopsis*, *Hodophilus,* and *Lamelloclavaria*.

Hygrophorineae

Cuphophylloideae

Phylogenetically, *Ampulloclitocybe*, *Cantharocybe* and *Cuphophyllus* were considered as basal in Hygrophoraceae, where they constituted the so-called cuphophylloid grade (Lodge et al. 2014). However, exact phylogenetic position of these three genera have remained unresolved until He and Yang (2021) that based on multigenic phylogenetic inference datasets, established a new subfamily Cuphophylloideae, which includes *Ampulloclitocybe, Cantharocybe*, *Cuphophyllus*, and *Spodocybe*.

Marasmiineae

In Marasmiaceae, a new genus *Paramarasmius* Antonín & Kolařík (Antonín et al. 2022), forming a monophyletic lineage within this family, was described with the type species *P. palmivorus* (Sharples) Antonín & Kolařík, a causal agent for bunch rot disease on oil palm.

In Omphalotaceae, Petersen and Hughes (2021) accepted *Collybiopsis* [as *Collybiopsis* Earle, not *Collybiopsis* (J. Schröt.) Earle] as a correct generic name for *Marasmiellus* Murrill. This concept, however, probably needs a multi-gene analysis, if this large group really represents a monophyletic lineage. Petersen and Hughes (2020) described two new genera—*Paramycetinis* as a lineage related to *Mycetinis*, and *Pseudomarasmius* accommodating species previously placed in *Marasmius* (clade D by Oliveira et al. 2019) and related to some *Rhodocollybia* species.

Consiglio et al. (2021), on the basis of morphological and phylogenetic analysis, emended Porotheleaceae to also encompass agaricoid taxa with descriptions of two new genera, *Hydropodia* and *Pseudohydropus*. Vizzini et al. (2022) proposed an updated taxonomic arrangement of Cyphellaceae and Porotheleaceae, based on phylogenetic results of analysis of a large dataset. Vizzini et al. (2020b) also included their newly described genus *Chrysomycena* in this family.

Physalacriaceae

Among Physalacriaceae we found a question whether *Oudemansiella* s.l. must be split or not. Singer (1951) already suggested that the hairy pileus can be used to separate *Xerula* from *Oudemasiella*. Later, Singer (1964) proposed to consider both under the same genus *Oudemansiella*, followed by his last system (Singer 1986). Alternatively, Dörfelt (1979, 1980a, 1980b, 1981a, b, 1983a, b, c, 1984, 1985) considered all radicate species with and without hairs under *Xerula*, or in *Dacytilosporina* in case of species with digitate basidiospores. This interpretation was partially followed by Petersen and Nagasawa (2005) and Petersen (2008a, b, c), but considering the digitate spored members of *Dactylosporina* under *Xerula*. Alternatively, Yang et al. (2009) proposed a more conservative arrangement for the group including *Dactylosporina*, *Mucidula* and the radicate members without hairs under *Oudemansiella*. Petersen and Hughes (2010) proposed a huge systematic rearrangement who erected the genera *Oudemansiella* s.str., *Dactylosporina*, *Hymenopellis*, *Mucidula*, *Paraxerula*, *Ponticulomyces*, and *Protoxerula*. This generic classification was suppressed by Hao et al. (2014) after more robust analyses, who considered *Oudemansiella* (including *Dactylosporina*, *Hymenopellis*, *Mucidula*, *Ponticulomyces*, and *Protoxerula*), *Paraxerula*, *Xerula* (for hairy species), and the glutinous fungus bearing digitate basidiospores as the new genus *Cibaomyces*.

Mycenineae R.L. Zhao, Vizzini & M.Q. He, subord. nov.

Fungal Names: FN 571792

Type genus: *Mycena* (Pers.) Roussel 1806

Etymology: From the type genus *Mycena*.

Diagnosis: Mycenineae differs from other suborders of Agaricales by its small to medium-sized basidiome, lamellate and poroid hymenophore.

Description: Spore print white. Basidiomes small-, medium-sized, mycenoid, pleurotoid, or clitocyboid. Hymenophore lamellate or poroid. Pileus conic, campanulate, plane, or conchate; surface dry or viscid; smooth, rarely fibrillose or pruinose; margin often striate. Stipe equal, central, or lateral; hollow; surface dry or viscid, smooth, fibrillose, or pruinose; base smooth or with mycelium. Basidiospores hyaline, smooth, thin-walled, amyloid or inamyloid. Cheilocystidia present or absent, shape various, globose, ellipsoid, pyriform, fusiform, cylindrical; hyaline or pigmented; pleurocystidia present or absent. Hyphal system usually monomitic, rarely sarcodimitic. Pileipellis ranging from a cutis to a trichoderm to a hymeniderm, often with diverticulate hyphae. Clamp connections present or absent. Some species are bioluminescent. Saprotrophic (terricolous, foliicolous, lignicolous), sometimes symbiotic with orchids.

Family included: Mycenaceae Overeem 1926

Notes: In the previous study, Mycenaceae represented by a single species, *Mycena luteopallens* (Peck) Peck, was shown to be sister to the rest of Marasmiineae with a bootstrap value of 59, and it is accepted as a member of Marasmiineae (Dentinger et al. 2016). In the phylogenomic tree of Wang et al. (2023a, b, c), Mycenaceae representing by three species is sister to the clade comprising Marasmiineae and Schizophyllineae. It is a distinct clade which cannot been classified in any suborders thus remained as Mycenaceae clade in Agaricales (Wang et al. 2023a, b, c). In this study, with a broader sampling in taxa and genes, [(27 genes from one species in Dentinger et al. (2016); 555 genes from three species in Wang et al. (2023a, b, c); 1286 genes from eight species in this study)], the Mycenaceae clade is found to be sister to Schizophyllineae with a full bootstrap value. Additionally, molecular dating analysis indicates its divergence time (156 Myr) is relatively equal to other suborders in Agaricales (152–182 Myr). Based on the phylogenomic relationships and divergence time, we propose the suborder Mycenineae to accommodate Mycenaceae in Agaricales.

Mycenaceae

Atheniella was treated as a member of Mycenaceae (He et al. 2019a), however, previous phylogenies on Agaricales using LSU (Moncalvo et al. 2002) and multigenes (Matheny et al. 2006) found species of *Mycena* sect. *Adonidae* (=*Atheniella*) in a separated clade from *Mycena* and Mycenaceae. On the other hand, in Cooper's (2016b) phylogeny, *Atheniella* resulted as a member of Porotheleaceae and with a sister relationship to *Hydropus scabripes* (Murrill) Singer, although the support was relatively low. Later, Matheny et al. (2020b) performed a phylogeny using ITS and LSU, where *Atheniella* also resulted in a well-supported clade within Porotheleaceae. Kalichman et al. (2020) considered the genus in Cyphellaceae s. l. A recent phylogeny also based on ITS and LSU by Vizzini et al. (2022) partially supported the proposal to accommodate *Atheniella* within the Cyphellaceae, as the sister clade to *Mycopan.* We accepted the criterion of considering *Atheniella* as part of the Cyphellaceae in the current outline.

Mycopan was treated in Mycenaceae in previous outline (He et al. 2019a). In Moncalvo et al. (2002), *Hydropus scabripes* [=*Mycopan scabripes* (Murrill) Redhead, Moncalvo & Vilgalys] was recovered in the baeosporoid clade, independently of the type species of *Hydropus*. In the phylogeny of Agaricales carried out by Matheny et al. (2006), *Hydropus* aff. *scabripes* was recovered as a member of the hydropoid clade and as a sister group to the *Mycena* sect. *Adonidae* (=*Atheniella*). Cooper (2016b), Eberhardt et al. (2018), Kalichman et al. (2020) and Vizzini et al. (2022) considered *Mycopan* as a member of Cyphellaceae s. l. In current outline, we accepted *Mycopan* as a member of Cyphellaceae s. l.

Hydropus was erected by Singer (1948) and has traditionally been treated as part of the Mycenaceae, a position also followed by He et al. (2019a, b). Results of the phylogenetic analysis made by Moncalvo et al. (2002) suggested that *Hydropus* is polyphyletic and an independent lineage of the Mycenaceae; therefore, the hydropoid clade was proposed for *H. fuliginarius* (Batsch) Singer, the type species of the genus, and other related genera (Moncalvo et al. 2002; Matheny et al. 2006), and considered as Porotheleaceae (Cooper 2016b). Eberhardt et al. (2018), Kalichman et al. (2020), Consiglio et al. (2021) and Vizzini et al. (2022) also considered *Hydropus* as member of Porotheleaceae. In the current outline, we accepted *Hydropus* as a member of Porotheleaceae.

Pluteineae

Limits and composition of Pluteaceae are currently not well-defined. Early phylogenetic work (Justo et al. 2011a, b) split *Volvariella* in two genera: *Volvopluteus* (closely related to *Pluteus*), and *Volvariella* s. s., apparently not in Pluteaceae, and of uncertain phylogenetic position in Agaricales. These phylogenies, based on ribosomal loci, suggested a close relationship of Pluteaceae with *Limnoperdon*, *Macrocystidia*, and *Melanoleuca*, and Amanitaceae.

Phylogenomic data presented here (Fig. 2) do support a close relationship of Pluteaceae and Amanitaceae but offer limited insight into the composition of Pluteaceae itself. *Macrocystidia* is shown to belong in Tricholomatineae, and currently it is the only member of Macrocystidiaceae. In our analyses, *Volvariella*, represented by a single species, *V. volvacea* (Bull.) Singer, appears as sister to *Pluteus*, represented by *P. cervinus* (Schaeff.) P. Kumm. These results would suggest a return to a “classical” concept of the Pluteaceae, with these two genera as its only members. However, we lack full-genome data for two critical genera, viz. *Volvopluteus* and *Melanoleuca*, to understand relationships within Pluteaceae. Aditionally, the aquatic genus *Limnoperdon* appeared close to Pluteaceae in analyses of ribosomal loci, and it is currently classified in its own family (Limnoperdaceae) in Pluteineae. To further clarify the relationships of genera in

Pluteineae, full-genome data is needed for *Limnoperdon*, *Melanoleuca*, and, *Volvopluteus* and ideally for additional species of *Pluteus* and *Volvariella*.

Amanitaceae

Currently the phylogenetic analyses and resulting taxonomic organization regarding the obligately ectomycorrhizal (ECM) *Amanita* and presumably saprotrophic *Saproamanita* species is unsettled. Bas (1969) suspected that members of *Amanita* subsect. *Vittadiniae* Bas were not ECM with regard to their habitat (meadows, prairies, lawns, pampa). Later, Wolfe et al. (2011) studied stable isotopes of *A. thiersii* Bas and found less depleted ^{13}C in basidiomes of this species than commonly observed for ECM fungi. Subsequent studies by Wolfe et al (2012) proposed an evolutive overview on this and, considering *Amanita* an integrative genus with sequences of taxa of *Amanita* subsect. *Vittadiniae* basally, concluded that loss of saprotrophic mode was irreversible and all other amanitas evolved from this basal group acquired ECM biotrophic mode. On the other hand, Vizzini et al. (2012a, b, c) interpreted this basal clade as the independent genus *Aspidella*, later renamed to *Saproamanita* for nomenclatural purposes (Redhead et al. 2015). The proposal to treat a weaklier supported basal clade of *Amanita* as independent genus was immediately contested by Tulloss et al. (2016) who argued in favour of placing greater importance on the morphological feature, the schizohymenial ontogeny of all members of the three supported clades, using it as synapomorphy of the integrated genus *Amanita*. This taxonomical and nomenclatural controversy was particularly solved when Cui et al. (2018) performed a robust multigene phylogeny also including *Catatrama*, *Limacella*, *Limacellopsis*, and *Myxoderma* Kühner (now = *Zhuliangomyces*), and confirmed a monophyletic Amanitaceae containing an integral *Amanita* with three subgenera subg. *Amanita*, subg. *Amanitina*, and subg. *Lepidella*, the last one containing the basal clade of saprotrophic taxa traditionally included in *Vittadiniae*.

Li et al. (2020a), on the other hand, analyzed the mitochondrial genome of six *Amanita* (sensu stricto) and two putative *Saproamanita*, suggesting that they did not form a distinct clade whereas the rest of *Amanita* did form a monophyletic clade. Interpreted differently in the classification by Tulloss et al. (2016) and of Cui et al. (2018), it would mean that *Amanita* subg. *Lepidella* is not monophyletic. Unfortunately, Li et al. (2020a) did not include the other Amanitaceae genera used by Cui et al. (2018) nor additional *Saproamanita*, including the type. Their results suggest that either *Amanita* should include *Saproamanita* (= *Lepidella*), or that *Saproamanita* should be split, contradicting Tulloss et al. (2016) and Cui et al. (2018). This possibility was raised by Redhead et al. (2015) and Tulloss et al. (2016). This solution was observed in the Lyophyllaceae to maintain *Termitomyces* (van de Peppel et al. 2022). Additional research is required.

Schizophyllineae

Cyphellopsidaceae

Cyphellopsidaceae, described by Jülich (1982) with *Cyphellopsis anomala* (Pers.) Donk as type species has the same nomenclatural priority that Niaceae, also described by Jülich in the same work (Jülich 1982). However, Cyphellopsidaceae has been firstly selected and legitimate over Niaceae by Knudsen and Vesterholt (2018). Jülich (1982) recognized within Cyphellopsidaceae the genera *Calathella*, *Cyphellopsis*, *Merismodes*, and *Woldmaria*. Additionally, in Niaceae, Jülich (1982) recognized the genus *Nia*, typified by the marine species *Nia vibrissa* R.T. Moore & Meyers. Later, based on molecular data, *N. vibrissa* was included in the euagaric clade, specifically in *Nia* clade and related to *Calathella mangrovei* E.B.G. Jones & Agerer and *Halocyphina villosa* Kohlm. & E. Kohlm (Binder et al. 2001; Hibbett and Binder 2002), confirming a putative synonym of Cyphellopsidaceae and Niaceae. Within the Nia clade was later confirmed the phylogenetic positioning of other cyphelloid genera such as *Cyphellopsis*, *Flagelloscypha*, *Lachnella*, *Maireina*, *Merismodes*, and *Woldmaria*, as well as the corticioid genus *Dendrothele* (Bodensteiner et al. 2004; Læssøe et al. 2016; Silva-Filho et al. 2023). Recently, Silva-Filho et al. (2023) emended the morphological concept of *Merismodes* and, based on the phylogenetic positioning of the epitype of the type species of *Maireina* [= *Maireina monacha* (Speg.) W.B. Cooke], considered *Maireina* is a synonym of *Merismodes*, which also has the genera *Cyphellopsis*, *Phaeocyphellopsis*, and *Pseudodasyscypha* as synonyms. The placement of the genera *Peyronelina* and *Pseudolasiobolus* also has been highlighted in Cyphellopsidaceae by Silva-Filho et al. (2023). *Digitatispora*, and *Phaeodepas* must be further investigated based on molecular data, as well as of *Akenomyces* and *Dendrothele* based on their type species.

Tricholomatineae

Asproinocybaceae

Asproinocybaceae was established by Mou and Bau (2021) for accommodating the genera *Asproinocybe* and *Tricholosporum*. The family is sister to Callistosporiaceae and includes species with a tricholomatoid habit, purplish, violaceous, or lilac-vinaceous distinctive coloured basidiomes; colourless, inamyloid, thin-walled, cyanophilous or not, subglobose to subellipsoid, tuberculate to stellate (*Asproinocybe*), or cruciform to stauriform (*Tricholosporum*) spores; hymenial cystidia present or absent, colourless or golden brown, or sometimes with pinkish violet content or grey-violet pigment; clamp connections present or absent; laticifers present (Angelini et al. 2014).

Biannulariaceae and Callistosporiaceae

Vizzini et al. (2020a) proposed a new classification of the taxa formerly ascribed to Biannulariaceae (≡ Catathelasmataceae), viz. *Catathelasma* (type), *Anupama*, *Callistosporium*, *Guyanagarika*, *Macrocybe*, *Pleurocollybia*, and *Pseudolaccaria* (Sánchez-García et al. 2016). Phylogenetic inference of Tricholomatineae based on the analysis of a combined multigene dataset supported the monophyletic origin of the aforementioned genera with the exception of *Catathelasma*, which is related with *Bonomyces* and *Cleistocybe* (Vizzini et al. 2020a). Biannulariaceae was therefore emended to include the clade formed by *Bonomyces*, *Catathelasma*, and *Cleistocybe*. Callistosporiaceae was proposed to name the clade containing *Callistosporium* (=*Pleurocollybia*) and related genera (Vizzini et al. 2020a). Species of *Callistosporium* with distant lamellae, long hygrophoroid basidia and large amygdaliform basidiospores were accommodated in *Xerophorus* (Vizzini et al. 2020a).

Clitocybaceae

Matheny et al. (2006), Binder et al. (2010), Vizzini et al. (2011), Vizzini and Ercole (2012), Raj et al. (2019), and Olariaga et al. (2020) recovered evidence for a monophyletic clade consisting of *Clitocybe*, *Collybia* s. s., and *Lepista* (Tribe Clitocybeae Fayod). Alvarado et al. (2015, 2018a, b), Sánchez-García et al. (2016), Sesli et al. (2016), Sánchez-García and Matheny (2017) and He et al. (2023a) found also that the genus *Singerocybe* is nested inside it. The informal name "Clitocybaceae" was used for this clade in some works (Cooper 2016a; Kalichman et al. 2020; Kibby 2021), but it was only recently validly published by Vizzini et al. (2020c).

Lyophyllaceae

Termitomycetoid clade was circumscribed within Lyophyllaceae by van de Peppel et al. (2022). All species within this clade produce a rooting stipe (pseudorhiza). In addition to *Termitomyces*, also *Blastosporella* and *Arthromyces* in the clade contain insect-associated species. van de Peppel et al. (2022) described four new genera belonging to the termitomycetoid clade, viz. *Australocybe* (from Australia), *Phaeotephrocybe* (from Belize), *Nigrocarnea* (from Laos) and *Praearthromyces* (from Asia: Malaysia, Singapore, and Thailand).

Omphalinaceae

Omphalinaceae was established by Vizzini et al. (2020c) based on the molecular results of several works (e.g., Moncalvo et al. 2000, 2002; Vizzini et al. 2011, 2012a,b; Vizzini and Ercole 2012; Lodge et al. 2014; Sánchez-García et al. 2016; Sánchez-García and Matheny 2017). It encompasses *Omphalina* and *Infundibulicybe* characterized by a usually depressed at centre pileus, dry, usually with ochre, reddish brown, rusty, orangish brown tinges; decurrent lamellae; colourless, smooth, inamyloid, acyanophilous, cyanophobic thin-walled spores; hymenophoral trama of interwoven hyphae; pileipellis arranged as a cutis to a trichoderm; pigments intracellular and wall-encrusting; clamp-connections present; habitat on soil, litter, or associated with bryophytes (Vizzini et al. 2020c).

Incertae sedis, Hertzogia

Wiest (2022) proposed *Hertzogia* to accommodate *Clitocybe martiorum* J. Favre, which occupied an uncertain position within Tricholomatineae. Since his phylogenetic analysis was based only on an ITS sequence from a single collection, the results of the work are considered here as doubtful and need future confirmation with more materials and data.

Significance

Some species of Agaricales contain harmful toxins, while many are edible (Retnowati et al. 2020; Li et al. 2021b). This includes the popular edible button mushroom (*Agaricus bisporus*), ink caps (*Coprinus* and other genera), lethal death cap (*Amanita phalloides*), and the world's largest *Armillaria* spp. (Schmitt and Tatum 2008; Money 2016). Most fatal mushroom poisonings are caused by several Agaricales species, mainly in *Amanita* (Garcia et al. 2015; Chen et al. 2016). Almost all hallucinogenic, which produce psilocybin, belong to Agaricales (Boyce et al. 2019). Most members of this order play an important role in the environment and are of great economic value (Kusuma et al. 2021).

Vast majority of Agaricales species are terrestrial, found in almost any habitat, from woods and grasslands to deserts and dunes (Kusuma et al. 2021), and they vary a lot from one species to another (Sfetcu 2006). In addition, some grow in limited, specific, or extensive geographical areas. Agaricoid species were long thought to be terrestrial only until the discovery of *Psathyrella aquatica*, an only gilled agaric known to grow underwater (Frank et al. 2010). The wide variety of habitats and substrates colonizes indicates that Agaricales exhibits diverse lifestyles, including saprotrophic, symbiotic, and parasitic (Põlme et al. 2020) which play important roles in maintaining environmental balance (Yang et al. 2017).

Agaricales plays important roles, especially in organic matter decomposition, nutrient cycling, soil structure, and retention, food sources for wild animals, pathogens in plants, and mycorrhizae (Kusuma et al. 2021). Saprotrophic species of Agaricales feed on decaying leaf litter, plant debris, and decaying wood, and include coprophilous, humicolous, and lignicolous species. Lignicolous Agaricales are mainly associated with white rot (Worrall et al. 1997; Zhang et al. 2023b). Brown rot is a rare feeding strategy in Agaricales, associated with the small genera such as *Fistulina*, *Hypsizygus*, and *Ossicaulis* (Redhead and Ginns 1985; Zhou et al. 2022a). According to Kalichman et al. (2020), Agaricales exhibit a wide variety of life strategies, ranging from unusual wood decomposition in the gilled *Cylindrobasidium* and *Fistulina*, nematode trapping by the gilled *Hohenbuehelia,* and economically destructive parasitism in cocoa plants by gilled *Moniliophthora* (Kalichman et al. 2020). Most studies of wood decay have focused on Polyporales and Gloeophyllales with less attention given to members of the order Agaricales (Floudas et al. 2015; Zhang et al. 2022b). Enzymes secreted by Agaricales fungi responsible for wood rot are highly relevant to carbon and nutrient cycling in nature (Ruiz-Dueñas et al. 2020; Sánchez-Ruiz et al. 2021). Agaricales also includes species that function as ectomycorrhizae associated with the roots of conifers and dicotyledons (Raj et al. 2021) and absorb sugars from the roots of living trees and shrubs. A few species form mutualistic symbiosis with ants and termites, and some are important plant pathogens (Money 2016).

More than half of the world's production of edible mushrooms comes from four genera in Agaricales, viz., *Agaricus*, *Flammulina*, *Lentinula*, and *Pleurotus* (Royse 2014). *Lentinula* is the most important genus of major edible mushrooms grown in the world today; accounting for approximately 22% of the global supply based on the production of *Lentinula edodes* (Royse et al. 2017). *Pleurotus* follows with five or six taxa, accounting for around 19% of world production (Royse et al. 2017). Two other genera, *Agaricus* and *Flammulina*, represent 15% and 11% of the total production, respectively (Royse et al. 2017). The genus *Agaricus* has two main cultivated species viz. *A. bisporus* (temperate button mushroom) and *A. bitorquis* (tropical or heat-tolerant white button mushroom), which are the most popular cultivated mushroom in the world and the first mushrooms to be commercially exploited on an industrial scale (Gupta et al. 2018). Apart from these main commercial species, it is recorded 2189 edible fungi species worldwide with records for almost 100 countries, being within Agaricales the genera *Amanita*, *Cortinarius*, and *Agaricus* the most representative in terms of the number of known edible species (Li et al. 2021b).

Mushrooms have been consumed by humans for thousands of years for their sensory properties, flavours, medicinal substances, and other beneficial uses. They are widely marketed as nutritional supplements and are considered beneficial to human health (Barbisan et al. 2003; Bellini et al. 2003; Li et al. 2023c). Agaricales includes many macro delicacies that are rich in carbohydrates, proteins, and vitamins B and D, which are beneficial to human health (Naeem et al. 2020; Kumar et al. 2021). The carbohydrates in mushrooms include polysaccharides such as glucans, mono and disaccharides, sugar alcohols, glycogen, and chitin (Kurtzman 1997). On a dry weight basis, *Pleurotus* species contains 46.6 to 81.8% carbohydrates, compared to an average of 60% in *A. bisporus* (Rahi and Malik 2016). Considering protein content, González et al. (2020) showed that *A. bisporus*, *A. subrufescens*, and *P. ostreatus* have a higher protein-to-energy ratio than beef jerky. *Agaricus bisporus* shows a protein/energy ratio comparable to lentils, *P. djamor, P. eryngii*, and *P. ostreatus* show protein/energy ratios similar to black beans, while *Flammulina filiformis* (Wang et al. 2018) and *L. edodes* have the lowest protein to energy ratio comparable to that of whole milk. Mushrooms are said to be a good source of several vitamins (Rahi and Malik 2016). The thiamine content (mg per 100 g dry weight of mushroom) is about 0.35 mg in *Volvariella volvacea*, 1.14 mg in *A. bisporus*, 1.16–4.80 mg in *Pleurotus* spp., and 7.8 mg in *L. edodes* (Rahi and Malik 2016). High riboflavin content is reported in *A. bisporus* (5.0 mg), *L. edodes* (4.9 mg), and *V. volvacea* (1.63 –2.98 mg) (Rahi and Malik 2016). *Lentinula edodes* mushrooms are reported to have the highest amount of vitamin C (9.4 mg/100 g dry sample) followed by *P. sajor-caju*, *A. bisporus*, and *V. volvacea* with 7.4 mg, 1.8 mg, and 1.4 mg, respectively (Chang and Miles 1989). Fiber is considered an important part of a balanced diet (Rahi and Malik 2016). The consumption of fiber-rich foods has garnered considerable interest due to their ability to lower triglycerides and blood cholesterol via the gut microbiomes (Asad et al. 2020). Agaricales mushrooms have sufficient fiber content to be considered a source of prebiotics in dietary supplements (Oyetayo and Oyetayo 2007; Van Doan et al. 2016; Roy and Fahim 2019; Asad et al. 2020). In addition, a variety of food products (biscuits, chips, ketchup, soup, mushroom tikki, vegetable mixture diets, noodles and pasta) have been developed from fungi in Agaricales as forms of ready-to-eat and ready-to-cook (Kumar et al. 2021) due to their nutritional values.

In addition to their obvious importance in the global agricultural and food industry, taxa in Agaricales are also considered important objects for medicinal purposes. Mushrooms in Agaricales have pharmacological effects that can improve the quality of life of humans and are used to treat diseases such as cancer (Jong et al. 1991; Mizuno and Zhuang 1995; Dai et al. 2009). Polysaccharides, glycoproteins, steroids, and riboglycans in *Agaricus* mushrooms have been shown to regulate antitumor, antimutagenic, bactericidal, and antibiotic activities and the immune system. The various effects on the enhancement of immunomodulation, reduction of tumor growth through cytostatic effects, and inhibition of tumor angiogenesis are due to different mechanisms of action of fungi in Agaricales (Novaes et al. 2007). Also, fibers in Agaricales mushrooms are important for the regulation of body function and the reduction of tumor development (Novaes et al. 2007). Agaricales mushrooms contain different chemical substances/bioactive compounds such as estrogel, lectine, β-glucans, terpenes, arginine, and protein-glucans that are responsible for different healing activities and significant numbers of cases reported that these substances can have positive effects on patient's quality of life (Table 2).

Agaricales mushrooms and their by-products are widely used in many fields and have many uses other than

Table 2 Bioactive ingredients of selected edible and medicinal Agaricales mushrooms and their medicinal properties

Species	Secondary metabolites	Bioactivities	References
Agaricus bisporus	Flavonoids, terpenoids, alkaloids and saponins, ergosterol, ergothioneine, glucans and chitin	Anti-diabetic, anti-cancer and may improve metabolic syndrome, immune function and gastrointestinal health	Ekowati et al. (2018), Blumfield et al. (2020)
Agaricus subrufescens	Ergosterols, lignins, and polysaccharides	Reduces physical and mental stress, strengthens the immune system and helps manage diabetes, high cholesterol, and digestive problems	Firenzuoli et al. (2008)
Flammulina filiformis	Polysaccharides	Anti-oxidation, immune regulation, anti-inflammation, liver protection, anti-tumor, and anti-hyperlipidemia	Wang and Zhang (2021), Wang et al. (2018), Dai et al. (2021)
Lentinula edodes	Lentinan, eritadenina	Anti-carcinogenic, antioxidant, and hypocholesterolemic action	Rivera et al. (2017)
Pleurotus spp.	Lectins, glucan, glycopeptides, β-D-Glucan (pleuran), polysaccharides, and lovastatin	Antioxidants, immunomodulating, antitumor, antibiotic, antiviral, anti-inflammatory, and anticholesterol agents	Cohen et al. (2002), Castro-Alves et al. (2017), Galappaththi et al. (2021)

nutritional and pharmaceutical values. Edible members of Agaricales have been shown to play an important role in the production of films/coatings, biosorbents, nanoparticles. Edible films/coatings are promising applications in the agricultural, food, and pharmaceutical industries. Fungi and their residues have many applications in the food industry, but much less research has been done on edible films/coatings (Antunes et al. 2020). Several studies have shown that polysaccharides, chitosan, fibers, and flours extracted from members of Agaricales can be used to produce edible films/coatings (Du et al. 2016; Bilbao-Sainz et al. 2018; Poverenov et al. 2018; Olufunmilola et al. 2019; Zhang et al. 2020).

Studies have been conducted to produce biosorbents from edible fungi for the removal of metal ions and dyes from aqueous solutions. Members of Agaricales, such as *Agaricus*, *Flammulina*, *Lentinula* and *Pleurotus*, are capable of bleaching dyes, biodegrading pollutants, and binding heavy metals (Akar et al. 2009; Si et al. 2013; Qu et al. 2015; Zhao et al. 2016a, b; Sekan et al. 2019; Eliescu et al. 2020; Yang et al. 2020; Lee and Tang 2020; Menaga et al. 2021).

Mushroom-based nanoparticles synthesized from components such as enzymes and metabolites secreted by fungal cells grade is higher than bacteria-based metal nanoparticles, which can reduce the toxicity of substances (Owaid et al. 2017; Owaid and Ibraheem 2017; Bhardwaj et al. 2020). Bhat et al. (2013), Madhanraj et al. (2017), Chaturvedi et al. (2020), and Sriramulu et al. (2020) reported that Agaricales fungi have a probability of synthesizing mushroom-derived nanoparticles and can use them for different pharmaceuticals applications.

Edible mushrooms are relatively inexpensive and contain various chemical constituents such as carbon, oxygen, phosphorus, and nitrogen, and are often described as carboxyl and amine groups. The presence of carbohydrates, amino acids, polysaccharides, citric acid, flavonoids, lipids, vitamins and proteins make them ideal candidates for the development of carbon dots (Boobalan et al. 2020; Wen et al. 2023). Carbon dots have also been shown to be effective in biomedical applications and energy storage systems, including water purification, pathogen identification, environmental research, and the detection of heavy metals and additives in food. Agaricales mushrooms such as *Pleurotus* spp. and *F. filiformis* act as carbon sources for preparing carbon dots (Pacquiao et al. 2018; Boobalan et al. 2020).

Cosmetics, made from natural ingredients, are increasingly in demand due to their organic, healthy, and eco-friendly properties (Antignac et al. 2011). Several studies have focused on skin care formulations made from fungi of Agaricales, such as creams, moisturizers, and gels. They have been reported to treat health issues such as fine lines, wrinkles, and uneven skin tone and texture due to their antioxidant and anti-inflammatory properties (Hyde et al. 2010; Hapsari et al. 2012; Gupta et al. 2015; Taofiq et al. 2016, 2018).

However, these mushrooms in Agaricales are still an untapped resource with many industrial uses. Therefore, further studies and responsible management are needed to explore and identify the potential of these mushrooms and use them in the most practical way.

Agaricostilbales Oberw. & R. Bauer 1989

Contributed by: Nathan Schoutteten, Teun Boekhout, Andrey Yurkov

Introduction

Agaricostilbales comprises dimorphic basidiomycetes and species currently only known from a yeast stage. Most species are thought to be saprotrophic, although there are indications that mycoparasitism and lichen parasitism occur in some lineages. *Agaricostilbum* was introduced to accommodate dimorphic basidiomycetes that form small, synnematoid, stilboid basidiomes that grow in clusters on plants, especially palm leaves (Bandoni and Boekhout 2011a). *Agaricostilbum* species were initially classified in the former 'Deuteromycetes', and several species were described multiple times by different authors, which resulted in a long list of circulating species names of which the synonymy often remains to be assessed. Basidiomycetous nature of *Agaricostilbum* species were only recognized by Oberwinkler and Bandoni (1982). Basidia formed directly on hyphae, are transversely three-septate, and give rise to statismosporic basidiospores. These basidiospores germinate with an ontogenetic yeast stage. Hyphal septa are referred to as 'simple' in that they form diaphragma with a single central pore, which is not surrounded by microbodies. Comparative morphological and molecular phylogenetic analyses demonstrated that these fungi form a distinct phylogenetic lineage that is now recognized at the ordinal level as Agaricostilbales (Oberwinkler and Bauer 1989; Weiss et al. 2004a, b) and at class level as Agaricostilbomycetes (Bauer et al. 2006).

History

Agaricostilbales was proposed by Oberwinkler and Bauer (1989) to accommodate basidiomycetes that form small stilboid-capitate basidiomes that mainly grow on plant surfaces, and which are characterized by transversally septate basidia producing successively statismospores. The stilboid basidiome morphology is shared with some species of the basidiomycete genera *Atractiella*, *Phleogena* (Atractiellales), and *Pachnocybe* (Pachnocybales). In a seminal work, Oberwinkler and Bauer (1989) compared these genera at micromorphological and ultrastructural level, and combined with early comparisons of 5.8S rDNA sequence data, the authors arranged a higher systematic placement of these different genera. Early phylogenetic sequence analysis of 5.8S rDNA revealed an isolated position of *Agaricostilbum pulcherrimum*, and which the authors translated into an isolated taxonomic position proposing Agaricostilbales (Oberwinkler and Bauer 1989). Early molecular phylogenetic studies using the D1/D2 domains of the LSU rDNA revealed that *Agaricostilbum* clade also comprised many species that are only known as yeasts and belong to genera such as *Sterigmatomyces, Bensingtonia, Kondoa, Sporobolomyces, Kurtzmanomyces* and *Chionosphaera* (Fell et al. 2000). Based on combined SSU and LSU phylogenetic reconstructions, Bauer et al. (2006) proposed the class Agaricostilbomycetes for a clade that comprised *Agaricostilbum*, *Bensingtonia, Chionosphaera*, *Kondoa*, *Kurtzmanomyces*, *Mycogloea*, *Sterigmatomyces*, and *Stilbum*. A multigene-based phylogeny supported the above conclusions and several new genera were introduced to reduce the polyphyletic nature of previous large genera such as *Bensingtonia* and *Sporobolomyces* (Wang et al. 2015a, b; Li et al. 2020b). More recently, *Crittendenia* (Millanes et al. 2016) and Crittendeniaceae (Diederich et al. 2022a) were proposed to accommodate a diverse group of stilboid, holobasidiate fungi growing in various lichen hosts. In early phylogenetic reconstructions, members of Agaricostilbales and Spiculogloeales often clustered together, and both orders were both viewed as members of Agaricostilbomycetes (Weiss et al. 2004a, b; Bauer et al. 2006). Based on multigene phylogenetic reconstructions, Wang et al. (2015a, b) recognised the clade of Spiculogloeales as a separate lineage and raised it to class level, Spiculogloeomycetes.

Characters that define the taxa in the order

Initially the order was recognized by the presence of synnematoid to stilboid basidiomes, composed of hyaline hyphae, without cystidia. Basidial morphology in this class is diverse. Most taxa have transversely one- or three-septate basidia, and form repeatedly statismosporic basidiospores that are hyaline and germinate with yeast cells. *Kondoa* and *Mycogloea* species on the other hand are characterized by basidia that produce ballistorspores (= active spore discharge), whereas *Chionosphaera* and *Crittendenia* species are holobasidiate, that means, basidia consisting of one cell. A peculiar type of basidium occurs in *Mycogloea*, in which the three-septate basidia detach from the hyphae on which they were formed, prior to producing basidiospores (Bandoni 1998; Kirschner et al. 2002). Teliospores are not present. Fucose is present in cell walls. Ultrastructural features of the order are the lack of microbodies surrounding septal pores, lack of colacosomes, spindle pole bodies (SPB) present inside the nucleus during metaphase, and separation of the SPBs inside the nucleus (Bauer et al. 2006). For two species, i.e., *Kondoa myxariophila* and *Stilbum vulgare*, tremelloid haustoria have been observed in culture conditions, which may hint towards a mycoparasitic strategy (Seifert et al. 1992; Li et al. 2020b). Lichen-inhabiting species of *Crittendenia* form tiny stipitate-capitate basidiomes that emerge from lichen thalli. *Crittendenia* species have holobasidia with 3–8 sterigmata on which basidospores are formed that are not actively discharged. Two types of hyphae occur: primary hyphae with clamp connections and secondary hyphae that are thinner and lack clamp connections (Diederich et al. 2022a, b).

Plates

Fig. 4 Culture of *Mycogloea* sp. on PDA. Also see figures in Oberwinkler and Bandoni (1982), Oberwinkler and Bauer (1989), and Bauer et al. (2006)

Genera included

Family Agaricostilbaceae Oberw. & R. Bauer 1989

Agaricostilbum J.E. Wright 1970

= *Amerobotryum* Subram. & Natarajan 1976
Pseudobensingtonia F.Y. Bai, Q.M. Wang, M. Groenewald & Boekhout 2015
Sterigmatomyces Fell 1966

Family Chionosphaeraceae Oberw. & Bandoni 1982

Ballistosporomyces Nakase, G. Okada & Sugiy. 1989
Boekhoutia Q.M. Wang & F.Y. Bai 2020
Chionosphaera D.E. Cox 1976
= *Fibulostilbum* Seifert & Oberw. 1992
Cystobasidiopsis R. Bauer, B. Metzler, Begerow & Oberw. 2009
Kurtzmanomyces Y. Yamada, Itoh, H. Kawas., I. Banno & Nakase 1989
Stilbum Tode 1790

Family Jianyuniaceae Q.M. Wang & F.Y. Bai 2020

Jianyunia Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout 2015
Pseudosterigmatospora Q.M. Wang & F.Y. Bai 2020
Sterigmatospora Q.M. Wang & F.Y. Bai 2020

Family Kondoaceae R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw. 2006

Bensingtonia Ingold 1986
Kondoa Y. Yamada, Nakagawa & I. Banno 1989

Family Ruineniaceae Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout 2015

Ruinenia Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout 2015

Family Crittendeniaceae Millanes, Diederich & Wedin 2022

Crittendenia Diederich, Millanes, M. Westb., Etayo, J.C. Zamora & Wedin 2021
Agaricostilbales genera *incertae sedis*
Mycogloea L.S. Olive 1950 pro parte

Evolution

Agaricostilbales contains filamentous, dimorphic, and unicellular yeast species. The evolutionary mechanisms among fungi of the order remain unclear, and it is expected that only the tip of the iceberg is known in terms of diversity, biology and ecology of these fungi. The notion that the ecology of most species is poorly known, also hampers insight into the evolutionary patterns of ecological strategies. In general, several members of Agaricostilbales are found on long branches in phylogenetic reconstructions (Weiss et al. 2004a, b; Bauer et al. 2006; Wang et al. 2015a). The mean time of origin of the order is estimated at 268 million years ago (Zhao et al. 2017).

Justification of order and problems

Multiple molecular phylogenetic analyses supported the circumscription of the order (Fell et al. 2000; Bauer et al. 2006; Wang et al. 2015a, b). It remains to be seen whether the species that are only known by their yeast morph can form stilboid basidiomes. Especially for the genera containing filamentous and dimorphic species, e.g., *Agaricostilbum*, *Mycogloea* and *Stilbum*, many names are in circulation, and type material or living cultures are often lacking. This impedes the establishment of a stable nomenclature of these genera, especially when molecular data for type species of these genera is unavailable (e.g., for *Mycogloea*).

Significance

Ecological and economical roles

Many species of Agaricostilbales were found and isolated from plant surfaces, especially leaves, and possibly they play an important role in the phyllosphere. Some species were isolated from terrestrial soils and marine environments (Diederich et al. 2022b). As far as known, none of the species have been used in agricultural or biotechnological applications. Members of Crittendeniaceae are remarkably diverse on lichen thalli (Diederich et al. 2022b). However, no interaction structures are known, and the specific type of interaction with their lichen hosts remains to be investigated.

Amylocorticiales K.H. Larss., Manfr. Binder & Hibbett 2010

Contributed by: Sergio P. Gorjón

Introduction

Amylocorticiales is a small order comprising about 10 genera and 50 species, among which resupinate forms predominate (He et al. 2019a). It has been regarded as the sister clade to Agaricales by most authors (Binder et al. 2010; He et al. 2019a), even though some controversy still exist when delimiting relationships among Agaricales, Boletales, Atheliales, Amylocorticiales, and Lepidostromatales in Agaricomycetidae (Nagy et al. 2016; Chen et al. 2020; Liu et al. 2017a; Zhao et al. 2017; Varga et al. 2019). In the order Amylocorticiales, the resupinate species predominate, suggesting that the great radiation of forms in the Agaricales could be derived from resupinate to pileate and stipitate forms (Virágh et al. 2021).

History

The order was circumscribed by Binder et al. (2010) in a study that tried to reflect the relationships between the different groups of Agaricomycetidae, mainly Agaricales and Boletales with the corticioid lineages containing mainly resupinate forms. Previously, species in the Amylocorticiales had been referred to as the Amylocorticiaceae (Larsson 2007) or Atheliaceae pro parte (Matheny et al. 2006). Several studies previously suggested that the Amylocorticiales should have considered in the Agaricomycetidae, but its precise placement was not been correctly set. As stated by Binder et al. (2010), analyses with nuc-lsu rRNA have placed the Amylocorticiales as the sister group of Agaricales or as the sister group of a clade containing Agaricales, Boletales and Atheliales (Binder et al. 2005; Hibbett and Binder 2002; Larsson et al. 2004; Larsson 2007). Analyses of a large dataset focused on Agaricales with nuc-lsu, nuc-ssu and 5.8S rRNA genes, and genes that encode two subunits of RNA polymerase II (rpb1, rpb2) suggested that the Amylocorticiales is the sister group of Agaricales, possibly along with a clade containing certain clavarioid (*Clavaria, Clavulinopsis*) and pileate-stipitate agaricoid forms (*Camarophyllopsis*) (Matheny et al. 2006).

Characters that define the taxa in the order

Amylocorticiales contains mostly resupinate forms with effused, effused-reflexed to almost pileate (*Irpicodon, Plicaturopsis*), or rarely multitiered pileate-stipitate (*Podoserpula*) basidiomes. The hymenial configuration varies from smooth to merulioid (*Podosperula*, *Plicaturopsis,* and some species in *Ceraceomyces*), irpicoid (*Irpicodon*) or poroid (*Anomoloma* and *Anomoporia*). The hyphal system is monomitic with clamped generative hyphae. Cystidial elements are rarely present. Basidia are generally terminal to more rarely lateral (*Amyloxenasma*), invariably producing four smooth, thin- or thick-walled, ellipsoid, cylindrical or allantoid, in mostly amyloid basidiospores. An amyloid reaction of the basidiospore wall is present in most Amylocorticiales species but lacking in *Ceraceomyces*, *Podoserpula*, and *Serpulomyces*, and recently a dextrinoid basidiospore reaction was detected in *Podoserpula aliweni* Garnica et al. (2021). Amyloidity of spores is not unique to Amylocorticiales and is a widespread phenomenon in both Russulales and Agaricales (Binder et al. 2010; Matheny et al. 2006; Bernicchia and Gorjón 2010).

Species live saprotrophically on decaying wood or as plant parasites. The species in Amylocorticiales are normally associated with a brown rot or more rarely with a white rot (*Anomoloma, Plicaturopsis*, Zhou et al. 2022b) and one species is thought to be ectomycorrhizal (*Podoserpula miranda*) (Buyck et al. 2012).

Plates

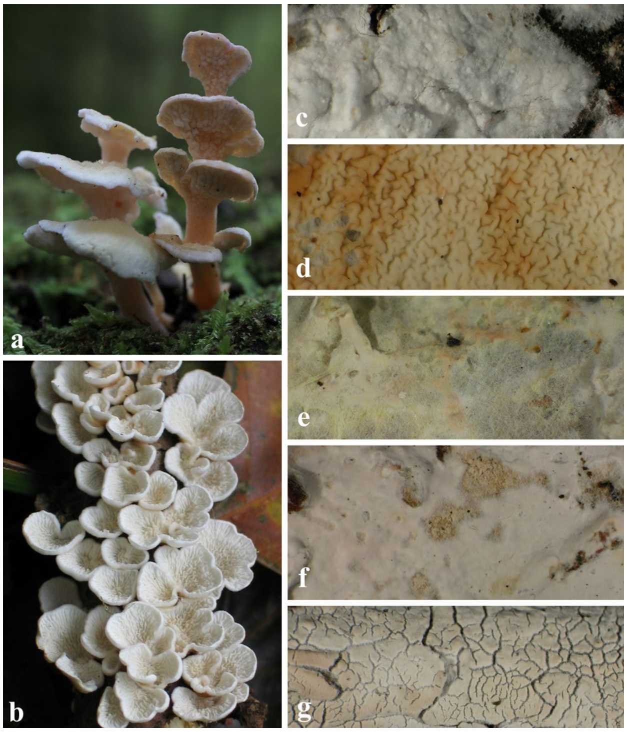


Fig. 5 Diversity of basidiome configuration in Amylocorticiales. **a** *Podoserpula pusio* (SPG 6153, New Zealand); **b** *Plicaturopsis crispa* (SPG 7017, Spain); **c** *Amylocorticium cebennense* (SPG 422, Spain); **d** *Ceraceomyces eludens* (SPG 1062, Spain); **e** *Ceraceomyces sulphurinus* (SPG 745, Spain); **f** *Ceraceomyces tessulatus* (SPG 762, Spain); **g** *Amyloathelia amylacea* (SPG 785, Spain)

Genera included

Family Amylocorticiaceae Jülich 1982

Agroathelia Redhead & Mullineux 2023
Amyloathelia Hjortstam & Ryvarden 1979
Amyloceraceomyces S.H. He 2020
Amylocorticiellum Spirin & Zmitr. 2002
Amylocorticium Pouzar 1959
Amyloxenasma (Oberw.) Hjortstam & Ryvarden 2005
Anomoloma Niemelä & K.H. Larss. 2007
Anomoporia Pouzar 1966
Ceraceomyces Jülich 1972
Irpicodon Pouzar 1966
Plicatura Peck 1872
Plicaturopsis D.A. Reid 1964
Podoserpula D.A. Reid 1963
Serpulomyces (Zmitr.) Zmitr. 2002

Evolution

The relationship between Atheliales and Amylocorticiales, another order in Agaricomycetidae dominated by corticioid species, is still unclear. Based on phylogenomic studies (Li et al. 2021c; Nagy et al. 2016), Atheliales is closely related with Amylocorticiales. However, large-scale multigene phylogenies inferred from nuclear ribosomal SSU and LSU, 5.8S, rpb1, rpb2, and tef1 (Chen et al. 2020; Zhao et al. 2017) showed that Amylocorticiales is most closely related to Agaricales, while Atheliales is closely related to Lepidostromatales, for which no genomes are currently available (Sulistyo et al. 2021). However, the order is well defined by gene and genomic analyses, although more genomes should be included to define the relationships of the different groups within Amylocorticiales.

Justification of order and problems

The position of *Athelia rolfsii* is controversial; it already appears distant from other *Athelia* representatives and in the present phylogenomic analyses it comes close to Amylocorticiales. *Athelia rolfsii* constitutes the sexual state of *Sclerotium rolfsii*, a facultative plant pathogen, that causes leaf and stem blights in a large number of plants (Bernicchia and Gorjón 2010).

At the moment, due to the few genomes available, the relationships between the different groups of species belonging to Amylocorticiales are based on the analysis of few genes (Binder et al. 2010). It would be desirable to incorporate more genomes into the phylogenies or perform phylogenomic analyses.

Significance

Ecological and economical roles

Amylocorticiales is a small group of fungi, with mostly wood-decaying species. It is necessary to clarify the supposed ectomycorrhizal way of life for some species of *Podoserpula*. Regarding its ecological role, although it is important, it is relative given its abundance and diversity without pathogenic crop species or other plants or animals parasites. As a curiosity, some species of *Podoserpula*, the pagoda mushroom, are used as handicrafts and in merchandising as art dolls, given the spectacular nature of their basidiomes, sometimes known as the 'Barbie pagoda fungi'. Some species, e.g. *Anomoporia* spp., were considered as rare and threatened species, and treated as indicator of old growth forests (Kotiranta and Niemelä 1996).

Atheliales Jülich 1982

Contributed by: Danny Haelewaters, Bobby Sulistyo

Introduction

Atheliales Jülich (1981) is an order in Agaricomycetidae composed of species producing resupinate and pellicular basidiomes with smooth hymenium. At present, it consists of over 120 described species in 17 genera, distributed among five families. Members of this order exhibit remarkably diverse ecological strategies ranging from saprotrophic to ectomycorrhizal to lichenicolous to symbiotic with termites. Some members may also be symbiotic with algae, orchid mycorrhizal, or fungicolous. The order includes a number of notable economically important species that damage fruits and vegetables in cold storage, while others produce enzymes for industrial, bioremediation, and therapeutic purposes. Nevertheless, molecular data are lacking for most species and the order still harbors several unresolved taxonomic issues.

History

The foundation of Atheliales can be traced back to *Corticium* sect. *Pellicularia* Bourdot and Galzin (1911), which consisted of resupinate fungi with pellicular or arachnoid basidiome and smooth hymenium, adhering loosely to the substrate. Members of this section clustered around *C. arachnoideum* Berk. and *C. centrifugum* (Lév.) Bres. Donk (1949) then re-examined Persoon's collection of *Athelia*, chose *A. epiphylla* as the generic type, placed *Corticium centrifugum* as its synonym, and emended *Athelia* using most species of *Corticium* sect. *Pellicularia* (Donk 1957). Meanwhile, closely related species of sect. *Pellicularia* would form other core genera of Atheliales: *Byssocorticium* (Singer 1944) and *Tylospora* (Donk 1957, 1960). In an effort to subdivide Corticiaceae s.l. into natural groups, Eriksson (1958) described 15 subfamilies. One of them was Athelioideae consisting of *Athelia*, *Byssocorticium*, and *Tylospora*. Parmasto (1968) then expanded Athelioideae to also accommodate fungi with pellicular effused-reflexed basidiomes and almost merulioid-poroid hymenium, and assigned species to tribes: Athelieae, Amylocorticieae, and Byssomerulieae. Athelieae Parm. is similar to Athelioideae sensu Eriksson (1958) with two extra genera: *Athelidium* and *Atheloderma*. Parmasto (1968) also subdivided *Athelia* into subgenera and sections, one of them being *Athelia* sect. *Byssina*. Jülich (1969) noted the complete absence of clamp connections and texture of the subiculum among members of sect. *Byssina*, and moved its members into a new genus, *Piloderma*. Jülich (1972) later emended the tribe Athelieae in his important monograph, adding *Piloderma* as well as several new genera including *Fibulomyces*, and *Leptosporomyces*. In his classification of basidiomycetes, Jülich (1981) introduced the order Atheliales consisting of four families: Atheliaceae, Byssocorticiaceae, Pilodermataceae, and Tylosporaceae. With the advent of molecular phylogenetics, Atheliales was accepted as a natural group (Binder et al. 2005; Boidin et al. 1998; Larsson et al. 2004), but only Atheliaceae was widely accepted as a family therein (Hibbett et al. 2007; Larsson 2007). In a molecular phylogenetic study focusing on the order, Sulistyo et al. (2021) restored and emended the families from Jülich (1981) and added a new, monotypic family: Lobuliciaceae.

Characters that define the taxa in the order

Atheliales members produce soft, pellicular, and corticioid basidiomes with smooth hymenium. This combination of characteristics gave rise to the term athelioid, referring to the fragile texture and thin, easily detachable basidiomes. Nevertheless, several unrelated taxa may be athelioid, as exemplified by genera that were previously part of Atheliales but are now placed in other orders based on molecular phylogeny—e.g., *Lyothelia* and *Pteridomyces*. At least one member of Atheliales, *Stereopsis vitellina*, is non-corticioid, producing stipitate stereoid basidiomes with soft and brittle texture upon drying (Sjökvist et al. 2012; Sulistyo et al. 2021). Basidiomes are generally light colored but can be bluish in *Byssocorticium* or olivaceous brown in *Piloderma*. All Atheliales members have monomitic hyphal system, sometimes producing hyphal strands. Clamps may be absent or present on the septa, while cystidia are always absent except in *Amphinema*. Basidia may be clavate to pedunculate with 2 to 4 sterigmata, and spores are never amyloid or dextrinoid but can be cyanophilous in Pilodermataceae and Tylosporaceae. Spore shape varies from subglobose to elliptic in Atheliaceae, Byssocorticiaceae, and Pilodermataceae, to triangular in *Tylospora* or seven-lobed in *Lobulicium*. Production of sclerotia is found in *Athelia*, notably in *A. arachnoidea* (Eriksson and Ryvarden 1973) and *A. termitophila* (Maekawa et al. 2020). Sclerotia are globose to subglobose, pale brown to orange brown or brown in maturity, with a diameter of 0.1–0.2 mm in *A. arachnoidea* (Yurchenko and Olubkov 2003) and 0.24–0.41 mm in *A. termitophila* (Maekawa et al. 2020).

Plates

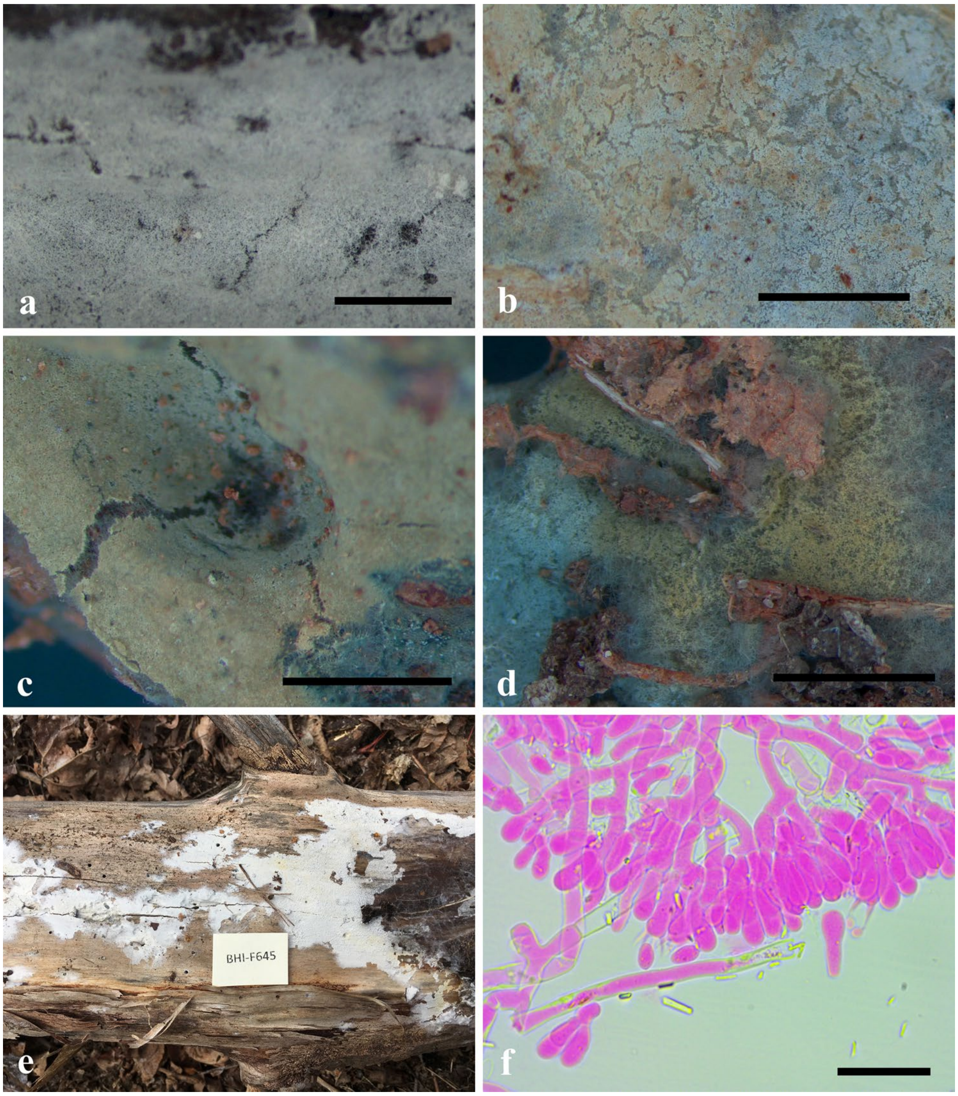


Fig. 6 Typical characteristics of Atheliales. **a** basidiome of *Athelia epiphylla*; **b** basidiome of *Amphinema byssoides*; **c**, **d** basidiome of *Byssocorticium atrovirens*; **e** basidiome of *Athelia* sp. sensu Haelewaters et al. (2018); **f** candelabra-like basidia clusters in *Athelia* sp. sensu. Scale Bars: a–d = 2 mm, f = 20 µm

Genera included

- Family Atheliaceae Jülich 1982
  - *Athelia* Pers. 1822
  - = *Fibularhizoctonia* G.C. Adams & Kropp 1996
  - *Athelicium* K.H. Larss. & Hjortstam 1986
  - *Athelocystis* Hjortstam & Ryvarden 2010
  - *Butlerelfia* Weresub & Illman 1980
  - *Elaphocephala* Pouzar 1983
  - *Hypochnella* J. Schröt. 1888
  - *Fibulomyces* Jülich 1972
  - *Hypochniciellum* Hjortstam & Ryvarden 1980
  - *Melzericium* Hauerslev 1975
  - *Mycostigma* Jülich 1976
  - *Taeniospora* Marvanová 1977
- Family Byssocorticiaceae Jülich 1982
  - *Athelopsis* Oberw. ex Parmasto 1968
  - *Byssocorticium* Bondartsev & Singer 1944
  - = *Byssocorticium* Bondartsev & Singer 1941
  - = *Caerulicium* Jülich 1982
  - *Leptosporomyces* Jülich 1972
- Family Lobuliciaceae Sulistyo, K.H. Larss. & M. Ryberg 2020
  - *Lobulicium* K.H. Larss. & Hjortstam 1982
- Family Pilodermataceae Jülich 1982
  - *Piloderma* Jülich 1969
  - *Tretomyces* K.H. Larss., Kotir. & Saaren. 2011
- Family Tylosporaceae Jülich 1982
  - *Amphinema* P. Karst. 1892
  - = *Diplonema* P. Karst. 1889
  - *Tylospora* Donk 1960
  - = *Tylosperma* Donk 1957

Evolution

Estimates of the origin of Atheliales range from the Early to the Late Cretaceous (this study; Varga et al. 2019; Sánchez-García et al. 2020). The ancestor to Atheliales was inferred to be saprotrophic white rot (Nagy et al. 2017), and the ectomycorrhizal strategy evolved independently in the *Byssocorticium*, *Amphinema–Tylospora*, and *Piloderma–Tretomyces* clades (Sánchez-García et al. 2020). Reynolds et al. (2018) found evidence suggesting horizontal gene transfer of psilocybin-related genes in *Athelia*, possibly due to overlapping ecological niches between some *Athelia* and psilocybin-producing species. Evolutionary studies focusing on Atheliales are lacking, but there is an increasing interest due to its enigmatic diversity of ecological strategies. Character evolution in Atheliales would also be an interesting subject to study, not only to improve its systematics, but also because of its eclectic mixture in several clades. For instance, the close relationships between *Tylospora* and *Amphinema*: the former has three-lobed spores while the latter has smooth spores and cystidia, unlike other Atheliales.

Justification of order and problems

Atheliales is firmly placed in Agaricomycetidae and most closely related with Lepidostromatales and Boletales (Sánchez-García et al. 2020; Varga et al. 2019). However, due to the uncertain placement of Lepidostromatales in this clade, the relationships are unresolved based on current data. Subsequently, the placements of several genera within Atheliales are still not supported by molecular data, including *Athelocystis*, *Butlerelfia*, *Elaphocephala*, *Hypochnicielllum*, *Melzericium*, and *Mycostigma*. All of these genera are monotypic except *Melzericium* (3 spp.), while *Hypochnicielllum* used to contain six members until most were transferred to *Amylocorticiellum*, leaving only the type species (Gorjón et al. 2011). In Sulistyo et al. (2021), *Athelia*, *Athelopsis* and *Leptosporomyces* were found to be non-monophyletic and the monophyly of *Amphinema* and *Piloderma* was unsupported. Meanwhile, only the type species of *Fibulomyces* and *Tylospora* have been included in molecular phylogenetic studies and their generic limits have yet to be tested.

A more in-depth study of these genera is necessary, especially for *Athelia* as well as its type species, *A. epiphylla*. Jülich (1972) introduced several *Athelia* species based on differences in spore shape and size. Eriksson and Ryvarden (1973) noted that these characteristics are considerably variable, even within the same basidioma, and provided a wider definition of *A. epiphylla*, which was later reinforced by Larsson and Ryvarden (2021). In a molecular phylogenetic study focusing on *Athelia*, Goyette et al. (2023) showed that this complex has a cosmopolitan distribution and is composed of *A. epiphylla*, *A. bombacina*, *A. neuhoffi*, and *A.* sp. sensu Haelewaters et al. (2018). Other complexes also exist within *Athelia* (Goyette et al. 2023), and disentangling relationships within the genus may require a more comprehensive sampling strategy with specimens from different geographical regions occurring on different substrates, as well as looking into underexplored characteristics such as fatty acid composition (Melhuish and Hacskaylo 1980).

Significance

Ecological and economical roles

Atheliales members show remarkably diverse ecological strategies. Most members are white rot saprotrophs (*Athelia*, *Athelopsis*, *Butlerelfia*; Tedersoo et al. 2014a) or ectomycorrhizal symbionts (*Amphinema*, *Byssocorticium*, *Piloderma*, *Tretomyces*, and *Tylospora*; Tedersoo et al. 2010; Aučina et al. 2019), while some are lichenicolous (*A. abscondita*, *A. alnicola*, *A. epiphylla*, and *A. salicum*, (Goyette et al. 2023; Jülich 1972). Ectomycorrhizal species of Atheliales form a major part of many ectomycorrhizal communities (Peter et al. 2008; Rosenthal et al. 2017; Southam et al. 2022) and are potentially diverse in the tropics (Tedersoo and Smith 2013), especially in Oceania and South East Asia (Corrales et al. 2022). Metabarcoding studies suggest that some Atheliales are fungicolous (Maurice et al. 2021) or endophytic (Daghino et al. 2022).

At least one species has been described to be symbiotic with termites from the genus *Reticulitermes* (*A. termitophila*, *Fibulorhizoctonia* sp.; Maekawa et al. 2020). Termite symbiotic species produce sclerotia that mimic termite eggs morphologically and chemically, which are stored and tended by termite workers (Matsuura et al. 2000). The sclerotia are provided with a protective environment with few competitors, while the termites might gain protection from antibacterial and antifungal substances secreted by the fungi (Matsuura et al. 2009a; Mitaka et al. 2019). Sequences obtained from the roots of achlorophyllous orchids (*Lecanorchis* spp. and *Erythrorchis altissima*) also suggest some Atheliales members are associated with mycoheterothrophy (Okayama et al. 2012; Ogura-Tsujita et al. 2018). In addition to this, some species of *Athelia* (*A. andina*, *A. phycophila*, and *A. poeltii*) and *Athelopsis* were reported to form symbiotic relationships with epiphytic algae (Jülich 1978, 1972; Oberwinkler 1970), which might be close to the alcobiosis concept of Vondrák et al. (2023), a trophic stage on the verge of lichenization. However, these algal-symbiotic species of Atheliales have never been collected since their description and no molecular data are available, hence the nature of their symbiosis as well as their allegiance to Atheliales is to be determined.

Several species of Atheliales are economically important as they cause spoilage of vegetables and fruits in cold storage. *Athelia arachnoidea* damages carrots (Adams and Kropp

1996) and optimally grows between 18 and 21 °C. Likewise, *A. psychrophila* also causes spoilage of carrots (de Vries et al. 2008) but also apples and pears (Wenneker et al. 2017) with optimal mycelium growth between 9 and 12 °C. Another cold-tolerant species is *A. termitophila*, which is shown to outcompete other wood decay fungi that normally exist within termite nest, especially during winter when the termites are less active (Komagata et al. 2022). Cold-tolerant fungi such as *A. psychrophila* and *A. termitophila* may be a potential source of cold-active enzymes with industrial applications.

Chemical diversity

The genome of *A. psychrophile*, commonly referred to as *Fibulorhizoctonia* sp. CBS 109695, suggests that it may be capable of producing enzymes with industrial, bioremediation, and therapeutic applications. On the fungal peroxidase database fPoxDB (http://peroxidase.riceblast.snu.ac.kr/; accessed 12 May 2023; Choi et al. 2014), *A. psychrophila* possesses 63 peroxidase genes covering 14 classes, with a distinct expansion of the heme-thiolate peroxidase (HTP) genes (35 copies). As a white rot saprotrophic species, *A. psychrophila* also possesses diverse genes for ligninolytic activities, with a relatively high proportion of genes being unique to the species (Nagy et al. 2017). Psilocybin-related genes are present in high copy number in *A. psychrophila* (Reynolds et al. 2018) and an unidentified termite-associated *Athelia* species (Konkel et al. 2021), suggesting their broader distribution in Atheliales.

Atractiellales Oberw. & Bandoni 1982

Contributed by: Nathan Schoutteten, Teun Boekhout, Andrey Yurkov

Introduction

Despite several detailed morphological studies on the biodiversity of basidiomycetous fungi that form minute, synnematous to stilboid basidiomes, our understanding of their phylogenetic relationships and, hence, their proper taxonomic placement strongly improved when molecular phylogenetic studies were introduced (Oberwinkler and Bandoni 1982; Oberwinkler and Bauer 1989; Bauer et al. 2006). Only these latter studies made it unequivocally possible to assess the extent of their diversity and evolutionary relationships. Atractiellales is the only described order in Atractiellomycetes and is one of the lineages in Pucciniomycotina that seem to have lost the ontogenetic yeast stage (Oberwinkler 2017). The order comprises not only stilboid species, but also species producing pycnidioid, corticioid and coralloid basidiomes with various textures exist. Several species are known to have distinct sexual and/or asexual morphs, with the asexual morph often producing sporodochia. These asexual morphs were formerly classified in separate genera (e.g., *Leucogloea*, *Infundibura*) which were later synonymised (Kirschner 2004). Most species are believed to be saprotrophic, although endophytic and mycorrhizal representatives are also known.

History

Atractiellales was introduced by Oberwinkler and Bandoni (1982) to include 'heterobasidiomycetes' with transversely septate or one-celled (holobasidia) basidia that form sessile basidiospores, and mostly germinate by budding, but also by the formation of hyphae. Hyphae contain so-called 'simple' septa with a diaphragm-like septum with a central pore towards which the septum gradually tapers. In a later work, Oberwinkler and Bauer (1989) recognized Agaricostilbales next to Atractiellales based on some observations, including ultrastructural features, but this order was mainly based on features of the 5.8S rRNA nucleotide sequences. Atractiellales possess curious organelles called symplechosomes, have the SPB (spindle pole body) during metaphase in the nuclear envelope, and have so-called SPB-endoplasmic reticulum caps (Weiss et al. 2004a, b; Bauer et al. 2006). Such ultrastructural features are, however, impossible to utilize for practical taxonomy. Using combined SSU and LSU rDNA sequence analysis, two new genera that formed pycnidia-shaped basidiomes, *Basidiopycnis* and *Proceropycnis*, were added to the order and this increased the morphological diversity known for the order (Oberwinkler et al. 2006). More recently, Aime et al. (2018d) introduced the monotypic genus *Atractidochium* for a species abundantly isolated as endophytes from *Pinus* needles and which produces sporodochia-like structures in culture. In a treatment of Atractiellomycetes with corticioid basidiomes, Spirin et al. (2018b) delineated the three genera *Bourdotigloea*, *Helicogloea* and *Saccosoma* based on rDNA phylogenetic reconstructions and detailed morphological comparisons.

Characters that define the taxa in the order

Atractiellales is mainly defined by its phylogenetic position in rDNA-based and multiple gene-based gene trees. Basidiome morphology in this order is highly variable, and ranges from corticioid to stilboid to pycnidioid (Oberwinkler et al. 2006; Schoutteten et al. 2018; Spirin et al. 2018b; Malysheva et al. 2020). One species is known to produce corraloid structures which bear pycnidioid basidiomes at terminal branches (Zhuang and He 2007). Basidia are in general transversely three-septate, and in *Bourdotigloea*, *Helicogloea*, and *Saccosoma* basidia bear a lateral appendage called the 'probasidial sac' in which karyogamy takes place (Baker 1936). Basidiospores are either sessile and not actively discharged (= gastroid or statismosporic) or produced on sterigmata and actively discharged (= ballistosporic), and they germinate by forming hyphae or microconidia. No ontogenetic yeast stages are reported from this group. At the ultrastructural level, the members of this order have symplechosomes, which can be described as stacked plate-like cisternae, which are interconnected by hexagonally arranged filaments. Symplechosomes are seemingly connected to mitochondria, but their function remains unknown to date (Oberwinkler and Bauer 1989; Weiss et al. 2004a, b; Bauer et al. 2006). After the discovery of symplechosomes by Bauer and Oberwinkler (1991), these structures were also reported by McLaughlin (1990), who indicated them as microscala. Septal pores of Atractiellales are either surrounded by microbodies or atractosomes, a character that was preliminary used by Bauer et al. (2006) to separate the different families in this order. However, only few species are investigated by TEM (transmission electron microscopy) for their septal pore complexes. The SPB occurs in the nuclear membrane during metaphase, and an SPB-endoplasmic reticulum cap exist (Bauer et al. 2006).

Plates

Fig. 7 Selected morphological characteristics of Atractiellales. **a** *Helicogloea sebacea* (NS 19-417, Netherlands); **b** moniliform cystidia of *Bourdotigloea* sp. (ND 19-195, Netherlands). More figures see in Oberwinkler et al. (2006), Zhuang and He (2007), Spirin et al. (2018a, b), and Schoutteten et al. (2018)

Genera included

- Family Atractogloeaceae Oberw. & R. Bauer 1989
  - *Atractogloea* Oberw. & Bandoni 1982
- Family Hoehnelomycetaceae Jülich 1982
  - *Basidiopycnis* Oberw., R. Kirschner, R. Bauer, Begerow & Arenal 2006
  - = *Basidiopycnides* J. Reid, Eyjólfsd. & Georg Hausner 2008
  - *Proceropycnis* M. Villarreal, Arenal, V. Rubio, Begerow, R. Bauer, R. Kirschner & Oberw. 2006
- Family Mycogelidiaceae W.Y. Zhuang 2007
  - *Mycogelidium* W.Y. Zhuang 2007
- Family Phleogenaceae Weese 1920
  - *Atractidochium* Oono, Urbina & Aime 2018
  - *Atractiella* Sacc. 1886
  - = *Hoehnelomyces* Weese 1920
  - = *Pilacrella* J. Schröt. 1887
  - *Bourdotigloea* Aime 2018
  - *Helicogloea* Pat. 1892
  - = *Exobasidiellum* Donk 1931
  - = *Infundibura* Nag Raj & W.B. Kendr. 1981
  - = *Leucogloea* R. Kirschner 2004
  - = *Neogloea* Aime 2018
  - = *Saccoblastia* Möller 1895
  - *Hobsonia* Berk. ex Massee 1891
  - *Phleogena* Link 1833
  - = *Botryochaete* Corda 1854
  - = *Ecchyna* Fr. ex Boud. 1885
  - = *Martindalia* Sacc. & Ellis 1885
  - *Saccosoma* Spirin 2018

Evolution

Not much is known about the evolutionary history of Atractiellales, but the group is recovered as monophyletic in various multilocus phylogenetic reconstructions (Weiss et al. 2004a, b; Aime et al. 2006; Bauer et al. 2006; Wang et al. 2015a). The molecular phylogeny suggests a considerable distance from basidiomycetes that have a similar macromorphology, such as Agaricostilbales (Agaricostilbomycetes) and Pachnocybales (Pucciniomycetes) with stilboid basidiomes and Heterogastridiales (Microbotryomycetes) with pycnidioid basidiomes. In contrast to these other groups, Atractiellales does not have an ontogenetic yeast stage, and species isolated in culture grow filamentously. The phylogenetic relationship of this order with respect to other groups in Pucciniomycotina remains to be resolved, and genome-wide DNA sequence data may help to resolve the relationships of this group. Interestingly, the origin and function of the symplechosomes remain enigmatic and this structure most likely represents a synapomorphy for this clade, although its presence has only been assessed in a limited number of species. The order is estimated to have originated about 330 million years ago (Zhao et al. 2017).

Justification of order and problems

Molecular phylogenetic rDNA-based studies clearly demarcated the order. Unfortunately, molecular sequence data for most species is restricted to nuclear rDNA loci, and the commonly used nuclear coding genes are not available for most species. Living cultures are available only for a few representatives. Given the minute basidiomes and the endophytic lifestyle of some species it can be expected that more taxa remain to be discovered.

Significance

Ecological and economical roles

Most species are believed to be saprotrophic, although endophytic (Bonito et al. 2017; Aime et al. 2018d) and mycorrhizal (Kottke et al. 2010) representatives are also known. The endophytic *Atractiella rhizophila* has been shown to enhance growth of *Quercus rubra* seedlings (Bonito et al. 2017).

Chemical diversity

As far as is known, these fungi have not been studied for their biochemical characteristics.

Auriculariales Bromhead 1840

Contributed by: Fang Wu

Introduction

Auriculariales is an order mainly composed of wood-inhabiting fungi with highly diverse basidiomes and complicated micro-structures (Weiss and Oberwinkler 2001; Wei and Dai 2008; Zhou and Dai 2013; Spirin et al. 2019a; Liu et al. 2022b). The genus *Auricularia* belonging to Auriculariaceae is the type genus of this order. It is characterized by gelatinous basidiomes, and transversely septate, clavate basidia (Wu et al. 2014a, 2015a, 2015b, 2021). However, some other gelatinous genera, e.g. *Exidia*, *Myxarium*, and *Stypella,* together with some poroid, lamellate and corticiod genera, e.g. *Elmerina*, *Eichleriella*, *Heterochaete*, have longitudinally or obliquely septate, ellipsoid, ovoid or subglobose basidia (Spirin et al. 2018a, 2019b; Ye et al. 2020). These characteristics lead to some families or genera of this order being classified into the Tremellales (Bandoni 1984; Lowy 1971). Based on molecular analysis, these are found to be members in Auriculariales (Weiss and Oberwinkler 2001). Some new genera were described with molecular data, e.g. *Grammatus*, *Adustochaete*, *Proterochaete* (Yuan et al. 2018; Alvarenga et al. 2019). However, the generic placement of some species cannot be determined and the generic delimitation in Auriculariales should be further clarified because some genera, e.g. *Exidia*, *Exidiopsis*, are polyphyletic (Liu et al. 2022b). Currently, the order includes two families and 57 genera, but the taxonomic status of genera and species within this order may undergo significant changes with further research.

History

Auriculariales was established by Bromhead (1840) to accommodate species with transversely septate basidia, known as auricularioid basidia. When ultra-structure of the septal pore and the spindle pole body were used in basidiomycetes systematics, Auriculariales was redefined to accommodate all heterobasidiomycetes with continuous parenthesomes, transversely or longitudinally septate basidia and hyphal haploid stages (Bandoni 1984). Bandoni (1984) recognized five families in the order, including Auriculariaceae, Aporpiaceae, Exidiaceae, Hyaloriaceae, Sebacinaceae. Wells (1994) merged Aporpiaceae into Hyaloriaceae, added Patouillardinaceae for species with obliquely septate basidia, and introduced Tremellodendropsidaceae for species of *Tremellodendropsis* with occasionally partially septate basidia. Weiss and Oberwinkler (2001) constructed phylogenetic relationships in Auriculariales and related groups based on nrLSU sequences, and resulted in a polyphyletic Auriculariales. The Sebacinaceae was confirmed as a monophyletic group, which appeared distant from other taxa ascribed to the Auriculariales (Weiss and Oberwinkler 2001). A group of closely related species containing members of the genera *Auricularia*, *Exidia*, *Exidiopsis*, *Eichleriella*, and *Heterochaete*, a group that included the members of the genus *Myxarium* and *Hyaloria pilacre* Möller, and a group consisting of species of the genera *Heterochaetella*, *Protodontia*, *Protomerulius*, and *Tremellodendropsis*, were significantly supported (Weiss and Oberwinkler 2001).

Weiss et al. (2004a, b) established Sebacinales to accommodate the closely related species of Sebacinaceae, and the order was widely accepted and supported by multigenes phylogenetic analysis (Riess et al. 2013; Zhao et al. 2017; Malysheva et al. 2019). Wells et al. (2004) reconsidered Auriculariaceae and Hyaloriaceae, and considered Exidiaceae as a synonym of Auriculariaceae. *Exidia* species were classified into Auriculariaceae (Kirk et al. 2008; Zhou and Dai 2013; Yuan et al. 2018; Spirin et al. 2019a). *Aporium* species of Aporpiaceae, were closely related to *Auricularia*, *Exidia* species of Auriculariaceae, and formed one clade in the phylogenies (Zhou and Dai 2013; Sotome et al. 2014; Yuan et al. 2018), so *Aporium* species were also classified into Auriculariaceae and the position of Aporpiaceae was abandoned (Kirk et al. 2008; Zhao et al. 2017). Hyaloriaceae was rarely mentioned and even abandoned (Kirk et al. 2008). However, the phylogenetic clade that included *Myxarium* species and *Hyaloria pilacre* was distant from other core taxa of Auriculariaceae (Weiss and Oberwinkler 2001; Yuan et al. 2018; Spirin et al. 2018a). Therefore, the family was accepted by some researchers (Wells et al. 2004; Tohtirjap et al. 2023). The family Patouillardinaceae was established by Jülich (1981) to accommodate the only genus *Patouillardina*, but the family was considered as a synonym of Exidiaceae and not accepted in Auriculariales in later studies (Kirk et al. 2008; Zhao et al. 2017). The family Tremellodendropsidaceae was established by Jülich (1981) to accommodate the species within Tremellales with richly branched basidiomes, and basidia which are only at the apex partially (incompletely) septate. Vizzini (2014) established Tremellodendropsidales to accommodate the family, which was confirmed by Berbee et al. (2016) based on phylogenetic analysis. Currently, two families, Auriculariaceae and Hyaloriaceae, are accepted in the order.

The number of genera is rapidly increasing in Auriculariales. Kirk et al. (2008) reported 32 genera in the order, and nearly 20 new genera were established in the first ten years (Malysheva and Spirin 2017; Yuan et al. 2018; Malysheva et al. 2018; Alvarenga et al. 2019; Alvarenga and Gibertoni 2021; Liu et al. 2022b). Fifty-seven genera are accepted in the order here.

Characters that define the taxa in the order

Auriculariales includes species with resupinate, effused-reflexed, hydnoid, cerebriform, coraloid and pileate basidiomes; thin or thick-walled basidia globose to cylindrical, cystidia present or absent, and thin-walled basidiospores that germinate by tubes or producing conidia (Bodman 1952; Lowy 1971).

Auriculariales is a higly diverse order with gelatinous, poroid, lamellate, corticoid and hydnoid basidiomes; transversely or longitudinally septate, cylindrical to clavate or subglobose to ovoid basidia; cystidia and hyphidia present or absent; and ovoid, subglobose, oblong-ellipsoid, cylindrical, or allantoid, thin-walled basidiospores (Malysheva et al. 2018; Yuan et al. 2018; Alvarenga et al. 2019; Wu et al. 2021). Most known species of Auriculariales are saprotrophs on wood causing white rot (Wu et al. 2022a; Tohtirjap et al. 2023).

Plates

Fig. 8 Basidiomes of genera *Auricularia* and *Exidia*. **a** *Auricularia heimuer* (Dai13782, Jilin province of China); **b** *Exidia glandulosa* (FYMF0049, Zhejiang province of China). Also see Figs. 2–5 in Malysheva et al. (2018), Figs. 1–2 in Spirin et al. (2019b), and Figs. 3–4 in Wu et al. (2021)

Genera included

Family Auriculariaceae Fr. 1838
=Exidiaceae R.T. Moore 1978
  Alloexidiopsis L.W. Zhou & S.L. Liu 2022
  Amphistereum Spirin & Malysheva 2017
  Aporpium Bondartsev & Singer 1944
  Auricularia Bull. 1780
  =*Auriculariella* (Sacc.) Clem. 1909
  =*Conchites* Paulet 1793
  =*Oncomyces* Klotzsch 1843
  =*Patila* Adans. 1763
  =*Seismosarca* Cooke 1889
  Eichleriella Bres. 1903
  Elmerina Bres. 1912
  Exidia Fr. 1822
  =*Spicularia* Chevall. 1826
  =*Ulocolla* Bref. 1888
  Exidiopsis (Bref.) Möller 1895
  Fibulosebacea K. Wells & Raitv. 1987
  Heterochaete Pat. 1892
  Heteroradulum Lloyd ex Spirin & Malysheva 2017
  Protodaedalea Imazeki 1955
  Pseudostypella McNabb 1969
  Sclerotrema Spirin & Malysheva 2017
  Tremellochaete Raitv. 1964
Family Hyaloriaceae Lindau 1897
  Helicomyxa R. Kirschner & Chee J. Chen 2004
  Hyaloria Möller 1895
  Myxarium Wallr. 1833
Auriculariales genera *incertae sedis*
  Adustochaete Alvarenga & K.H. Larss. 2019
  Atractobasidium G.W. Martin 1935
  Basidiodendron Rick 1938
  Bourdotia (Bres.) Bres. & Torrend 1913
  Ceratosebacina P. Roberts 1993
  Collyria Fr. 1849
  Crystallodon Alvarenga 2021
  Dendrogloeon Spirin & Miettinen 2015
  Ductifera Lloyd 1917
  =*Gloeotromera* Ervin 1956
  Endoperplexa P. Roberts 1993
  Gelacantha V. Malysheva & Spirin 2019
  Grammatus H.S. Yuan & C. Decock 2018
  Guepinia Fr. 1825
  =*Phlogiotis* Quél. 1886
  Hauerslevia P. Roberts 1998
  Heterorepetobasidium Chee J. Chen & Oberw. 2002
  Heteroscypha Oberw. & Agerer 1979
  Hyalodon V. Malysheva & Spirin 2018
  Hydrophana V. Malysheva & Spirin 2019
  Metabourdotia L.S. Olive 1957
  Metulochaete R.L.M. Alavarenga 2019
  Microsebacina P. Roberts 1993
  Mycostilla Spirin & V. Malysheva 2018
  Myxariellum Spirin & V. Malysheva 2019
  Ofella Spirin & V. Malysheva 2019
  Ovipoculum Zhu L. Yang & R. Kirschner 2010
  Porpopycnis R. Kirschner 2012
  Proterochaete Spirin & V. Malysheva 2019
  Protoacia Spirin & V. Malysheva 2019
  Protodontia Höhn. 1907
  Protograndinia Rick 1933
  Protohydnum Möller 1895
  Protomerulius Möller 1895
  Protoradulum Rick 1933
  Pseudohydnum P. Karst. 1868
  =*Hydnogloea* Curr., Berk. & Broome 1871
  Psilochaete V. Spirin & V. Malysheva 2019
  Renatobasidium Hauerslev 1993
  Stypella Möller 1895
  =*Gloeosebacina* Neuhoff 1924
  =*Heterochaetella* (Bourdot) Bourdot & Galzin 1928
  Stypellopsis Spirin & V. Malysheva 2018
  Tremellacantha Jülich 1980

Justification of order and problems

During the last seven years, several genera and species have been described and proposed in Auriculariales. The classification of this order has been amended through the revisions of types and newly collected material of species earlier unavailable for morphological and phylogenetic analysis, thus, old genera were restored, and new genera, combinations, and species were proposed (Malysheva and Spirin 2017; Malysheva et al. 2018; Alvarenga et al. 2019; Spirin et al. 2019a). However, the classification at the family level within this order is still unclear and requires better delimitation.

Significance

Ecological and economical roles

Some species in the Auriculariales are important edible and medicinal mushrooms, e.g., *Auricularia heimuer* F. Wu, B.K. Cui & Y.C. Dai and *A. cornea* Ehrenb. are widely cultivated in China. The former species is the second most important edible mushroom in China, and both species have properties of antitumor, antioxidant, and immunity enhancement (Li et al. 2013a; Wu et al. 2021). Recntly, some new cultivars have been domesticated (Yao et al. 2022; Zhang et al. 2022c; Li et al. 2023d). In addition, *Exidia yadongensis* F. Wu, Qi Zhao, Zhu L. Yang & Y.C. Dai is also an edible and medicinal mushroom with high economic value (4000 RMB/kg) in Tibet, Southwestern China, but it is not artificially cultivated (Wu et al. 2020b). Many edible species in Auriculariales are worth studying in the future.

Bartheletiales Thines 2017

Contributed by: Xiang-Yu Zeng

Introduction

Phylogeny of *Bartheletia paradoxa*, which was discovered on ginkgo leaf litter, remained unknown for a long time. Recently, its phylogeny was studied using genomic data by Mishra et al. (2018), revealing that *Bartheletia paradoxa* represents a new order, Bartheletiales. It is the most basal member of Agaricomycotina, forming a distinct lineage sister to all other taxa.

History

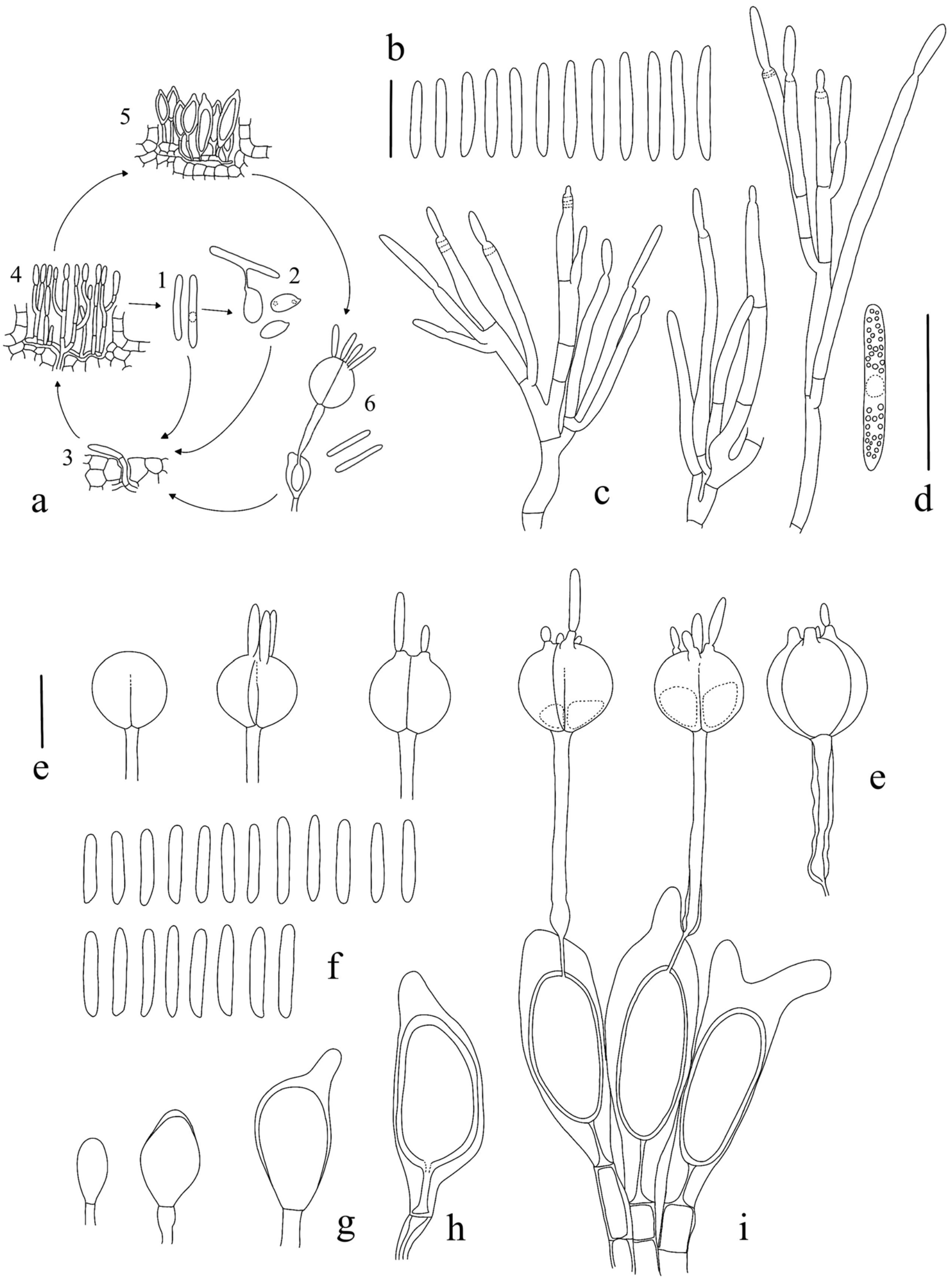
Bartheletia was monotypic described by Scheuer et al. (2008) and accommodates a new type of septal architecture for Basidiomycota. It is characterized by thick-walled teliospores, stipitate, longitudinally septate, statismosporic phragmobasidia and plasmodesma-like septal perforations. Its taxonomic position remained unclear until a recent molecular phylogenetic study revealed that it forms an order on its own in Agaricomycotina, Basidiomycota (Mishra et al. (2018).

Characters that define the taxa in the order

Bartheletiales is mainly characterized by plasmodesma-like septal perforations and the combination of sympodial and percurrent proliferation (Scheuer et al. 2008). It forms a phylogenetically distinct lineage sister to all other lineages of Agaricomycotina. Since the order is only known from one monotypic genus, it remains to be seen whether the peculiar morphology holds for the whole order.

Plates

Fig. 9 *Bartheletia paradoxa*. **a** tentative life cycle: 1, conidia; 2, secondary conidia; 3, mycelium; 4, conidioma with conidiophores; 5, sorus with resting spores; 6, septate basidium and basidiospores. **b** conidia; **c** conidiophores; **d** conidium from living material; **e** basidia; **f** basidiospores; **g** young teliospores; **h** mature teliospore; **i** mature teliospores, two of them with basidia. Scale bars = 20 µm. Redraw from Scheuer et al. (2008) and Koukol and Lotz-Winter (2016) by Mao-Qiang He



Genera included Family Bartheletiaceae R. Bauer, Scheuer, M. Lutz & Grube 2008

Bartheletia G. Arnaud ex Scheuer, R. Bauer, M. Lutz, Stabenth., Melnik & Grube 2008
= *Bartheletia* G. Arnaud 1954

Evolution

Bartheletiales occupies the most basal member of Agaricomycotina, but with low support. Its septal morphology is unique among Basidiomycota.

Justification of order and problems

Molecular phylogeny and phylogenomic analysis clearly showed that *Bartheletia paradoxa* occupies an isolated basal position within Agaricomycotina. However, its lifecycle remains unclear. Further research with additional specimens is needed to understand the full morphological, biological, ecological, and phylogenetic range of the representatives of the yet monotypic order.

Significance

Ecological and economical roles

Bartheletia paradoxa only sexually reproduces on leaves of *Ginkgo biloba*, and might be persisting as asymptomatic infection in some tissues of ginkgo trees (Scheuer et al. 2008). Further studies of additional species in this order are needed to clarify its lifecycle and ecological roles.

Chemical diversity

Unknown.

Other relevant data and future recommendations

It is interesting to study the origin and evolution of *Bartheletia paradoxa* to understand the early divergence of Basidiomycota, as it is the most basal clade in Agaricomycotina and possesses unique septal structures.

Boletales E.-J. Gilbert 1931

Contributed by: Naveed Davoodian, Takamichi Orihara

Introduction

Boletales currently comprises 16 families, 162 genera, and over 1300 species. Boletales is best known for its stipitate-pileate, fleshy, poroid taxa (i.e. boletes), however the order also contains taxa displaying different fruitbody morphologies, including gilled mushrooms, false truffles, crust-like species, and other forms. The majority of species are ectomycorrhizal with members are various plant families including but not limited to Pinaceae, Fagaceae, Myrtaceae, Phyllanthaceae, Fabaceae and Dipterocarpaceae (Agerer 1999; Raidl et al. 2006; Brearley 2012; Orihara and Smith 2017; Davoodian et al. 2019). Boletales also harbors species which engage in ecological lifestyles besides mycorrhizal relationships including saprotrophs (e.g., *Coniophora* spp.), mycoparasites (e.g., *Pseudoboletus parasiticus*), and others (e.g., *Boletinellus merulioides*). Many taxa in this order are of major ecological, cultural, and economic importance as ectomycorrhizal fungi and edible mushrooms (Bougher 1995; Sitta and Floriani 2008).

History

Boletales was established by Gilbert (1931). Binder and Hibbett (2006) made significant impacts on understanding of the order and the status and relationships of its suborders. Boletaceae was erected by Chevallier (1826) to accommodate *Boletus* as circumscribed at that time (incorporating bolete taxa from the essential works of Bulliard, Fries, and others) along with a number of other taxa since excluded from Boletales. Over the years, many workers have made major contributions to elucidating and describing the diversity of Boletaceae from Europe (e.g., Quélet, Šutara), Africa (e.g., Heinemann, Watling), Asia (e.g., Chiu, Corner, Hongo, Nagasawa), Australasia (e.g., Cleland, McNabb, Halling), Central and South America (e.g., Singer, Magnago, Henkel), and North America (e.g., Murrill, Thiers, Snell, Both). Nuhn et al. (2013) and Wu et al. (2014b) are critically important modern studies which provided a phylogenetic framework for Boletaceae taxonomy. Paxillaceae was validly described by Lotsy (1907) and is known to be sister to Boletaceae.

Sclerodermataceae was described by Corda (1842) though the name of the family was spelled incorrectly; it was spelled correctly by Fischer (1899). The family was later emended by Guzmán (1971). Sclerodermataceae along with Boletinellaceae, Calostomataceae, Diplocystidiaceae, and Gyroporaceae together constituted the Sclerodermatineae, a suborder of Boletales notable for its morphological and ecological diversity (Binder 1999; Binder and Bresinsky 2002; Louzan et al. 2007; Wilson et al. 2012). However, the present article provides evidence that Boletinellaceae is outside of Sclerodermatineae (Fig. 2). Since the turn of the century, a substantial amount of research has been done on these groups (Nagasawa 2001; Moyersoen et al. 2003; Phosri et al. 2007; Wilson et al. 2007; Gurgel et al. 2008; Fangfuk et al. 2010; Davoodian and Halling 2013; Magnago et al. 2018; Mei et al. 2021; Raghoonundon et al. 2021; Kasuya et al. 2022).

Suillaceae was described by Besl and Bresinsky (1997) and contains the genus *Suillus* Gray and other taxa. Rhizopogonaceae Gäum. & C.W. Dodge and Gomphidiaceae Maire ex Jülich accommodate two gasteroid genera and a group of mostly lamellate taxa, respectively. These three families are closely related as members of the suborder Suillineae Besl & Bresinsky. Some major works on the taxonomy of members of Suillineae include Zeller (1939), Miller (1964), Smith and Thiers (1964), Smith and Zeller (1966), Kretzer et al. (1996), Miller (2003), Mujic et al. (2014), Nguyen et al. (2016), and Wu et al. (2020c).

Hygrophoropsidaceae was established by Kühner (1980), and currently accommodates *Hygrophoropsis* and *Leucogyrophana*. The present study places the family as sister to the clade unifying the Boletales families mentioned in the above (Fig. 2). Together with Coniophoraceae, Serpulaceae, and Tapinellaceae, different studies over the years (including the present one) have more or less supported these families as forming an evolutionary grade along the base of Boletales, with Hygrophoropsidaceae in the position mentioned earlier in this paragraph, though studies drawing more definite conclusions about this situation are needed (Jarosch 2001; Binder and Hibbett 2006; Skrede et al. 2011). Fruitbody morphologies displayed by Coniophoraceae, Hygrophoropsidaceae, Serpulaceae, and Tapinellaceae include agaricoid, gasteroid, secotioid, crust-like, and polypore-like forms.

Characters that define the taxa in the order

Boletales is delineated by phylogeny, as there is no clear, useful set of homologous morphological features to define the order beyond relatively general ones applicable to many other Agaricomycetidae. Ecologically, most taxa are ectomycorrhizal, a number of species are wood decayers or other types of saprobes, some are mycoparasitic, and a small number of species engage in unusual tri-kingdom symbioses (i.e. members of the Boletinellaceae such as *Boletinellus merulioides*, *Phlebopus roseus*, and others; e.g., see Mei et al. 2021).

Boletaceae consists mostly of epigeous, stipitate-pileate taxa with pores (i.e. the hymenophore being tubular in these cases), though some taxa are lamellate. Boletaceae also contains numerous gasteroid lineages that are hypogeous, erumpent, or epigeous. Generally, gasteroid taxa in Boletaceae have truffle-like and secotioid basidiomes and do not forcibly discharge their basidiospores. In the non-gasteroid taxa, the pileipellis is usually a trichodermium (tangled or palisadal, sometimes gelatinized) though this can vary and intergrade e.g., it can be hymeniform, an epithelium, cuticular, or combinations/gradations of the different pileipellis types. Paxillaceae contains gilled mushrooms, truffle-like taxa (e.g., *Melanogaster* Corda, *Alpova* C.W. Dodge), more or less boletoid taxa e.g. *Gyrodon lividus* (Bull.) Sacc. and *Paragyrodon sphaerosporus* (Peck) Singer, and *Meiorganum* R. Heim, a wood-inhabiting genus with reduced stalk and more or less boletinoid hymenophore. *Hydnomerulius pinastri* (Fr.) Jarosch & Besl, which should be classified outside of Paxillaceae, is a resupinate fungus with wrinkled to toothed hymenophore. Boletinellaceae contains mushroom taxa with boletinoid to essentially poroid hymenophores.

Sclerodermatineae exhibit a diverse array of morphologies, including gasteroid forms and boletoid mushrooms. The suborder contains the familiar puffball genus Scleroderma. It also contains gasteroid taxa with more unusual morphologies e.g. gasteroid fungi with extended stalks covered in an outer layer that is often gelatinous (Calostoma spp.) or compound, stroma-bearing species (Diplocystis wrightii Berk. & M.A. Curtis). Gasteroid Sclerodermatineae often have ornamented spores. The bolete genus Gyroporus is easily distinguishable by the combination of a yellow spore print, clamp connections, and circumferential to variously arranged (i.e. not longitudinal) stipe hyphae.

Suillineae contains boletoid mushrooms, gilled mushrooms, and truffle-like taxa. With very few exceptions they are ectomycorrhizal with Pinaceae. The genus *Suillus* (Suillaceae) often exhibits one or more of the following: slimy to tacky caps, glandular dots (clusters of cystidia) on the stipe, and partial veils or remnant evidence of them. *Gomphidius* (Gomphidiaceae) can also have slimy to tacky caps; this is also observed in *Chroogomphus* (Gomphidiaceae) but to a lesser degree. *The genus Rhizopogon Fr. contains truffle-like species that form ectomycorrhizae almost exclusively with Pinaceae.*

Tapinellaceae comprises taxa with gilled mushroom (with well-developed to reduced stipes), resupinate/effused-reflexed, and polypore-like morphologies. Hygrophoropsidaceae contains *Hygrophoropsis* (J. Schröt.) Maire ex Martin-Sans and *Leucogyrophana* Pouzar, an agaricoid genus and a corticioid genus, respectively. Coniophoraceae contains taxa displaying a few different overall morphologies, however the family is dominated by crust-like species. Serpulaceae contains gilled mushrooms (*Austropaxillus* spp.), gasteroid taxa (*Gymnopaxillus*), and resupinate species (*Serpula* spp.). Tapinellaceae, Hygrophoropsidaceae, Coniophoraceae, and Serpulaceae are notable when considered together because they all contain some taxa that are resupinate/corticioid (i.e. crust-like); these taxa are morphologically diverse within the limits of their reduced, crust-like forms (e.g. hymenophores can range from smooth to merulioid).

Plates

Fig. 10 Morphological examples of Boletales. **a** *Boletus reticuloceps* (Boletaceae) from Sichuan province of China showing boletoid hymenophore i.e. pores/tubes (scale bar: 2 cm); **b** *Scleroderma* sp. from Sichuan province of China showing epigeous puffball basidiomes (scale bar: 1 cm); **c** *Tapinella atrotomentosa* (Tapinellaceae) from southeastern USA, gilled hymenophore clearly visible (credit: Naveed Davoodian, scale bar: 1 cm); **d** *Austropaxillus* sp. (Serpulaceae) from New Zealand, a gilled ectomycorrhizal mushroom presumably evolved from saprotrophic resupinate mushrooms (credit: Takamichi Orihara; scale bar: 2 cm); **e** *Calostoma fuscum* (Sclerodermatineae) from New Zealand, gasteroid basidiomes with gelatinous stalks (credit: Takamichi Orihara; scale bar: 1 cm); **f** *Turmalinea persicina* (Boletaceae) from Japan, a sequestrate, truffle-like species belonging to subfamily *Leccinoideae* (credit: Takamichi Orihara; scale bar: 1 cm); **g** *Rossbeevera* sp. basidiomes from Australia, outer basidiomes in cross section exposing gleba, basidiome on far right showing mature brown spores in gleba (credit: Michael A. Castellano, scale bar: approx. 1 cm); **h** *Melanogaster utriculatus* (Paxilliaceae) from Japan, a sequestrate, truffle-like species phylogenetically related to pileate-stipitate fungi *Paxillus* spp. (credit: Takamichi Orihara; scale bar: 1 cm)

Genera included

Family Boletaceae Chevall. 1826

- *Abtylopilus* Yan C. Li & Zhu L. Yang 2021
- *Acyanoboletus* G. Wu & Zhu L. Yang 2023
- *Afroboletus* Pegler & T.W.K. Young 1981
- *Afrocastellanoa* M.E. Sm. & Orihara 2017
- *Alessioporus* Gelardi, Vizzini & Simonini 2014
- *Amoenoboletus* G. Wu, E. Horak & Zhu L. Yang 2021
- *Amylotrama* Bloomfield, Davoodian, Trappe & T. Lebel 2022
- *Anthracoporus* Yan C. Li & Zhu L. Yang 2021
- *Aureoboletus* Pouzar 1957
- = *Sinoboletus* M. Zang 1992
- *Australopilus* Halling & N.A. Fechner 2012
- *Austroboletus* (Corner) Wolfe 1980
- *Baorangia* G. Wu & Zhu L. Yang 2015
- *Binderoboletus* T.W. Henkel & M.E. Sm. 2016

Boletellus Murrill 1909
=*Boletogaster* Lohwag 1926
=*Strobilofungus* McGinty 1915
Boletochaete Singer 1944
Boletus L. 1753
=*Ceriomyces* Murrill 1909
=*Dictyopus* Quél. 1886
=*Notholepiota* E. Horak 1971
=*Oedipus* Bataille 1908
=*Tubiporus* P. Karst. 1881
=*Xerocomopsis* Reichert 1940
Borofutus Hosen & Zhu L. Yang 2012
Bothia Halling, T.J. Baroni & Manfr. Binder 2007
Brasilioporus A.C. Magnago, Alves-Silva & T.W Henkel 2022
Buchwaldoboletus Pilát 1969
Butyriboletus Arora & J.L. Frank 2014
Cacaoporus Raspé & Vadthanarat 2019
Caloboletus Vizzini 2014
Carolinigaster M.E. Sm. & S. Cruz 2018
Castellanea T.W. Henkel & M.E. Sm. 2015
Chalciporus Bataille 1908
=*Rubinoboletus* Pilát & Dermek 1969
Chamonixia Rolland 1899
Chiua Y.C. Li & Zhu L. Yang 2016
Costatisporus T.W. Henkel & M.E. Sm. 2015
Crocinoboletus N.K. Zeng, Zhu L. Yang & G. Wu 2014
Cupreoboletus Simonini, Gelardi & Vizzini 2015
Cyanoboletus Gelardi, Vizzini & Simonini 2014
Durianella Desjardin, A.W. Wilson & Manfr. Binder 2008
Erythrophylloporus Ming Zhang & T.H. Li 2018
Exsudoporus Vizzini, Simonini & Gelardi 2014
Fistulinella Henn. 1901
=*Gastrotylopilus* T.H. Li & Watling 1999
=*Ixechinus* R. Heim 1968
Gastroboletus Lohwag 1926
Gastroleccinum Thiers 1989
Guyanaporus T.W. Henkel & M.E. Sm. 2016
Gymnogaster J.W. Cribb 1956
Harrya Halling, Nuhn & Osmundson 2012
Heimioporus E. Horak 2004
Heliogaster Orihara & K. Iwase 2010
Hemiaustroboletus Ayala-Vásquez, García-Jiménez & Garibay-Orijel 2022
Hemilanmaoa Yang Wang, Bo Zhang & Y. Li 2023
Hemileccinum Šutara 2008
=*Corneroboletus* N.K. Zeng & Zhu L. Yang 2012
Hongoboletus G. Wu & Zhu L. Yang 2023
Hortiboletus Simonini, Vizzini & Gelardi 2015
Hourangia Xue T. Zhu & Zhu L. Yang 2015
Hymenoboletus Y.C. Li & Zhu L. Yang 2016
Imleria Vizzini 2014
Imperator G. Koller, Assyov, Bellanger, Bertéa, Loizides, G. Marques, P.-A. Moreau, J.A. Muñoz, Oppicelli, Puddu & F. Richard 2015
Indoporus A. Parihar, K. Das, Hembrom & Vizzini 2018
Ionosporus O. Khmelnitsky 2019
Jimtrappea T.W. Henkel, M.E. Sm. & Aime 2015
Kaziboletus Hosen & Zhu L. Yang 2021
Kombocles Castellano, T.W. Henkel & Dentinger 2016
Lanmaoa G. Wu & Zhu L. Yang 2015
Leccinellum Bresinsky & Manfr. Binder 2003
Leccinum Gray 1821
=*Krombholziella* Maire 1937
=*Trachypus* Bataille 1908
Longistriata Sulzbacher, Orihara, Grebenc, M.P. Martín & Baseia 2020
Mackintoshia Pacioni & Sharp 2000
Mucilopilus Wolfe 1979
Mycoamaranthus Castellano, Trappe & Malajczuk 1992
Neoboletus Gelardi, Simonini & Vizzini 2014
Neotropicomus A.C. Magnago, Alves-Silva & T.W Henkel 2022
Nevesoporus A.C. Magnago & T.W. Henkel 2022
Nigroboletus Gelardi, Vizzini, E. Horak, T.H. Li & Ming Zhang 2015
Octaviania Vittad. 1831
=*Maccagnea* Zeller & C.W. Dodge 1928
Parvixerocomus G. Wu & Zhu L. Yang 2015
Paxilloboletus Furneaux, De Kesel & F.K. Khan 2022
Paxillogaster E. Horak 1966
Phylloboletellus Singer 1952
Phyllobolites Singer 1942
Phylloporopsis Angelini, A. Farid, Gelardi, M.E. Sm., Costanzo & Vizzini 2018
Phylloporus Quél. 1888
Porphyrellus E.-J. Gilbert 1931
Pseudoaustroboletus Y.C. Li & Zhu L. Yang 2014
Pseudoboletus Šutara 1991
Pulchroboletus Gelardi, Vizzini & Simonini 2014
Pulveroboletus Murrill 1909
Retiboletus Manfr. Binder & Bresinsky 2002
Rheubarbariboletus Vizzini, Simonini & Gelardi 2015
Rhodactina Pegler & T.W.K. Young 1989
Rossbeevera T. Lebel, Orihara & N. Maek. 2012
Royoungia Castellano, Trappe & Malajczuk 1992
Rubinosporus Vadthanarat, Raspé & Lumyong 2022
Rubroboletus Kuan Zhao & Zhu L. Yang 2014
Rugiboletus G. Wu & Zhu L. Yang 2015
Setogyroporus Heinem. & Rammeloo 1982
Singerocomus T.W. Henkel & M.E. Sm. 2016

Singeromyces M.M. Moser 1966
Solioccasus Trappe, Osmundson, Manfr. Binder, Castellano & Halling 2013
Spongiforma Desjardin, Manfr. Binder, Roekring & Flegel 2009
Spongispora G. Wu, S.M.L. Lee, E. Horak & Zhu L. Yang 2018
Strobilomyces Berk. 1851
= *Eriocorys* Quél. 1886
Suillellus Murrill 1909
Sutorius Halling, Nuhn & N.A. Fechner 2012
Tengioboletus G. Wu & Zhu L. Yang 2016
Tropicoboletus Angelini, Gelardi & Vizzini 2023
Tubosaeta E. Horak 1967
Turmalinea Orihara & N. Maek. 2015
Tylocinum Y.C. Li & Zhu L. Yang 2016
Tylopilus P. Karst. 1881
= *Leucogyroporus* Snell 1942
= *Phaeoporus* Bataille 1908
= *Rhodobolites* Beck 1923
= *Rhodoporus* Quél. ex Bataille 1908
Veloboletus Fechner & Halling 2020
Veloporphyrellus L.D. Gómez & Singer 1984
Villoboletus L. Fan & N. Mao 2023
Wakefieldia Corner & Hawker 1953
Xanthoconium Singer 1944
Xerocomellus Šutara 2008
Xerocomus Quél. 1887
= *Versipellis* Quél. 1886
Zangia Y.C. Li & Zhu L. Yang 2011

Family Boletinellaceae P.M. Kirk, P.F. Cannon & J.C. David 2001
Boletinellus Murrill 1909
Phlebopus (R. Heim) Singer 1936
= *Phaeogyroporus* Singer 1944

Family Calostomataceae E. Fisch. 1900
Calostoma Desv. 1809
= *Gyropodium* E. Hitchc. 1825
= *Husseia* Berk. 1847
= *Mitremyces* Nees 1816

Family Coniophoraceae Ulbr. 1928
Chrysoconia McCabe & G.A. Escobar 1979
Coniophora DC. 1815
= *Coniophorella* P. Karst. 1889
Coniophoropsis Hjortstam & Ryvarden 1986
Gyrodontium Pat. 1900
= *Boninohydnum* S. Ito & S. Imai 1940
Penttilamyces Zmitr., Kalinovskaya & Myasnikov 2019
Sedecula Zeller 1941

Family Diplocystidiaceae Kreisel 1974
Astraeus Morgan 1889
= *Diploderma* Link 1816
Diplocystis Berk. & M.A. Curtis 1868
Endogonopsis R. Heim 1966
Tremellogaster E. Fisch. 1924

Family Gasterellaceae Zeller 1948
Gasterella Zeller & L.B. Walker 1935

Family Gomphidiaceae Maire ex Jülich 1982
Chroogomphus (Singer) O.K. Mill. 1964
= *Brauniellula* A.H. Sm. & Singer 1959
Cystogomphus Singer 1942
Gomphidius Fr. 1836
= *Leucogomphidius* Kotl. & Pouzar 1972
Gomphogaster O.K. Mill. 1973

Family Gyroporaceae (Singer) Manfr. Binder & Bresinsky 2002
Gyroporus Quél. 1886
= *Coelopus* Bataille 1908
= *Leucobolites* Beck 1923
= *Leucoconius* Beck 1923

Family Hygrophoropsidaceae Kühner 1980
Hygrophoropsis (J. Schröt.) Maire ex Martin-Sans 1929
Leucogyrophana Pouzar 1958

Family Paxillaceae Lotsy 1907
Alpova C.W. Dodge 1931
Austrogaster Singer 1962
Gyrodon Opat. 1836
= *Anastomaria* Raf. 1820
= *Campbellia* Cooke & Massee 1890
= *Gilbertina* R. Heim 1966
= *Pseudogyrodon* Heinem. & Rammeloo 1983
= *Rodwaya* Syd. & P. Syd. 1901
= *Uloporus* Quél. 1886
Hoehnelogaster Lohwag 1926
Hydnomerulius Jarosch & Besl 2001
Meiorganum R. Heim 1966
Melanogaster Corda 1831
= *Argylium* Wallr. 1833
= *Bulliardia* Jungh. 1830
= *Hyperrhiza* Bosc ex Spreng. 1827
Neoalpova Vizzini 2014
Paragyrodon (Singer) Singer 1942
Paralpova Cabero & P. Alvarado 2020
Paxillus Fr. 1836
= *Paxillopsis* E.-J. Gilbert 1931
= *Rhymovis* Pers. ex Rabenh. 1844
= *Ruthea* Opat. 1836

Family Protogastraceae Zeller 1934
Protogaster Thaxt. 1934

Family Rhizopogonaceae Gäum. & C.W. Dodge 1928
Fevansia Trappe & Castellano 2000
Rhizopogon Fr. 1817
= *Anthracophlous* Mattir. ex Lloyd 1913
= *Hysteromyces* Vittad. 1844

=*Splanchnomyces* Corda 1831
=*Trappeindia* Castellano, S.L. Mill., L. Singh bis & T.N. Lakh. 2012
Rhopalogaster J.R. Johnst. 1902
Family Sclerodermataceae Corda 1842
Chlorogaster Læssøe & Jalink 2004
Favillea Fr. 1849
Horakiella Castellano & Trappe 1992
Pisolithus Alb. & Schwein. 1805
=*Durosaccum* Lloyd 1924
=*Endacinus* Raf. 1814
=*Lycoperdodes* Haller ex Kuntze 1891
=*Pisocarpium* Link 1808
=*Pisolithus* Alb. & Schwein. 1805
=*Polypera* Pers. 1818
=*Polysaccum* F. Desp. & DC. 1807
Scleroderma Pers. 1801
=*Actigea* Raf. 1814
=*Actinodermium* Nees 1816
=*Caloderma* Petri 1900
=*Goupilia* Mérat 1834
=*Mycastrum* Raf. 1813
=*Neosaccardia* Mattir. 1921
=*Nepotatus* Lloyd 1925
=*Phlyctospora* Corda 1841
=*Pirogaster* Henn. 1901
=*Pompholyx* Corda 1834
=*Sclerangium* Lév. 1848
=*Stella* Massee 1889
=*Sterrebekia* Link 1816
=*Veligaster* Guzmán 1970
Family Serpulaceae Jarosch & Bresinsky 2001
Austropaxillus Bresinsky & Jarosch 1999
Gymnopaxillus E. Horak 1966
Serpula (Pers.) Gray 1821
=*Gyrophana* Pat. 1897
=*Plicaturella* Murrill 1910
=*Xylomyzon* Pers. 1825
=*Xylophagus* Link 1809
Family Suillaceae Besl & Bresinsky 1997
Psiloboletinus Singer 1945
Suillus Gray 1821
=*Boletinus* Kalchbr. 1867
=*Boletopsis* Henn. 1898
=*Cricunopus* P. Karst. 1881
=*Euryporus* Quél. 1886
=*Fuscoboletinus* Pomerl. & A.H. Sm. 1962
=*Gastrosuillus* Thiers 1989
=*Ixocomus* Quél. 1888
=*Mariaella* Šutara 1987
=*Peplopus* (Quél.) Quél. ex Moug. & Ferry 1887
=*Pinuzza* Gray 1821
=*Rostkovites* P. Karst. 1881
=*Solenia* Hill ex Kuntze 1898
=*Viscipellis* (Fr.) Quél. 1886
Truncocolumella Zeller 1939
=*Dodgea* Malençon 1939
Family Tapinellaceae C. Hahn 1999
Bondarcevomyces Parmasto 1999
Pseudomerulius Jülich 1979
Tapinella E.-J. Gilbert 1931
=*Sarcopaxillus* Zmitr., Malysheva & E.F. Malysheva 2004
=*Tapinia* (Fr.) P. Karst. 1879
Boletales genera *incertae sedis*
Corditubera Henn. 1897
Corneromyces Ginns 1976
Marthanella States & Fogel 1999
Phaeoradulum Pat. 1900

Evolution

Bolete morphology (stipitate-pileate mushrooms with essentially poroid hymenophores) occurs in the crown group of Boletales: Boletineae (including Paxillaceae), Boletinellaceae, Sclerodermatineae, and Suillineae. Other morphologies also occur in most of these groups (e.g. gilled and gasteroid forms); gasteroid lineages have been derived multiple times (Binder and Bresinsky 2002; Wilson et al. 2012; Smith et al. 2015; Orihara and Smith 2017; Orihara et al. 2021; Lebel et al. 2022).

Findings presented here show Boletinellaceae is outside the suborder Sclerodermatineae, which was previously thought to be within. The results presented here suggest Boletinellaceae can be included in the suborder Boletineae, in a basal position. Also, *Hydnomerulius pinastri* is shown to be outside Paxillaceae, instead inferred to be sister to the clade unifying Paxillaceae and Boletaceae. The earliest diverged clades in the order, starting from the earliest, are inferred to be Serpulaceae, Coniophoraceae, and Hygrophoropsidaceae (Fig. 2). Further study of Tapinellaceae is needed to pinpoint its phylogenetic position and subsequent evolutionary implications.

Ecologically, the early diverging families in Boletales tend to be saprotrophic while more recently diverging families such as Boleataceae and Paxilliaceae tend to include a significantly higher proportion of ectomycorrhizal taxa. Recent multi-gene phylogenetic studies support that ectomycorrhizal symbiosis have independently evolved at least five times within the order (Sato and Toju 2019).

Justification of order and problems

Boletales and many of its constituent families have been consistently highly supported by numerous studies over the years, including the present one (Fig. 2). However, many problems remain to be addressed, including resolving the relationships between many taxa at and above the species level.

Two monotypic families described by Zeller in the previous century, Gasterellaceae and Protogastraceae, are in need of rediscovery and molecular study. The genera *incertae sedis Corditubera* Henn., *Corneromyces* Ginns, *Marthanella* States & Fogel, and *Phaeoradulum* Pat. need further study to confirm or disconfirm placement in Boletales.

Significance

Ecological and economical roles

Boletales is found worldwide in forest ecosystems and serve key roles in the cycling of nutrients. Most species are ectomycorrhizal, though some are saprotrophic or mycoparasitic. Boletales include both edible and toxic species, and some taxa are of importance to agriculture and forestry (Bougher 1995; Castro and Freire 1995; Cao et al. 2015). Many Boletales are important wild food sources for invertebrates and mammals, and the animals in turn contribute to spore dispersal (Fogel and Trappe 1978; Elliott 1922; Kitabayashi et al. 2022). Some Boletales are prized culinary mushrooms e.g., porcini (Sitta and Floriani 2008). An estimated 20–100 tons of porcini are sold globally each year (Rivas-Ferreiro et al. 2023). Recently one bolet, *Phlebopus portentosus* (Berk. & Broome) Boedijn, is successfully cultivated in China (Luo et al. 2022).

Chemical diversity

The chemistry of Boletales has been relatively well-studied (e.g., Kämmerer et al. 1985; Besl et al. 1986; Gill and Steglich 1987; Besl and Bresinsky 1997; Aulinger et al. 2001). Various atromentin derivatives, such as variegatic acid and gyroporin, cause the bluing oxidation reactions that are well-known in many stipitate-pileate Boletales. Chemical investigations of Boletales for medical and other biotechnological applications is a fairly active area of research (e.g., Morel et al. 2018; Kumla et al. 2021; Ringel et al. 2022).

Other relevant data and future recommendations

In the light of current phylogenetic knowledge, careful studies of existing collections in herbaria are needed both to resolve taxonomic issues and to aid in annotating historic collections. Given that the Boletales contains many conspicuous macrofungi often sought by amateur mycologists and mushroom hunters, results from Boletales research should be disseminated in ways that are readily accessible to the public. Increased synergy between professional mycologists and citizen scientists will continue to propel the study of boletes and relatives forward.

Buckleyzymales R.L. Zhao & K.D. Hyde 2017

Contributed by: Teun Boekhout, Andrey Yurkov

Introduction

Taxonomy of basidiomycetous yeasts for a long time accepted large, polyphyletic, but phenotypically rather well circumscribed genera. A multigene-based phylogenetic study marked the beginning of an extensive reclassification of many of such genera (Wang et al. 2015a, b). As a result, the genus *Buckleyzyma* was introduced for what has been referred to as aurantia-clade before and comprised species of *Rhodotorula* and *Sporobolomyces* (Wang et al. 2015b).

History

In a major revision of the classification of basidiomyctous yeasts based on multigene phylogenies, many new genera were introduced for species of *Rhodotorula* and *Sporobolomyces* from clades outside Sporidiobolales, amongst them *Buckleyzyma*. Due to its phylogenetic distance from other lineages, a family Buckleyzymaceaea was also introduced but considered *incertae sedis* in Cystobasidiomycetes (Wang et al. 2015b). More recently, a new order Buckleyzymales was introduced for this lineage (Zhao et al. 2017).

Characters that define the taxa in the order

Five species reclassified in *Buckleyzyma* have reddish-brownish colonies and were previously classified in the traditional red yeast genera, either *Sporobolomyces* or *Rhodotorula*. A sexual state has not been reported for any of these species. Reproduction is by polar budding, and pseudohyphae and true hyphae may be present. Ballistoconidia may occur in some species. Major CoQ system Q10 (Wang et al. 2015b).

Plates

See Fig. 3 in Wang et al. (2015b).

Genera included

Family Buckleyzymaceae Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout 2015

Buckleyzyma Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout 2015

Evolution

Buckleyzymales belongs to Cystobasidiomycetes with a sister relationship to *Symmetrospora, Hasegawazyma, Erythrobasidium*, and *Bannoa* (Wang et al. 2015a, b). They are estimated to have emerged 136 million years ago (Zhao et al. 2017).

Justification of order and problems

To date, most species of the order have been identified based on the combination of ribosomal ITS and LSU nucleotide sequences. Based on some molecular phylogenetic studies the order seems well circumscribed. Future studies will include more species to this taxon, which might reveal their sexual characteristics.

Significance

Ecological and economical roles

Unknown.

Chemical diversity

Unknown.

Cantharellales Gäum. 1926.
= Botryobasidiales Jülich 1982
= Ceratobasidiales Jülich auct. plur.
= Sistotrematales Jülich 1982
= Tulasnellales Rea

Contributed by: Ibai Olariaga, Rodrigo Márquez, Sergio P. Gorjón, Isabel Salcedo

Introduction

Cantharellales currently comprises about 725 recognized species, but its diversity is considered to be significantly higher, with a worldwide distribution. The order contains economically important fungi (Watling 1997), such as some genera of Hydnaceae that produce edible basidiomes (e.g., *Cantharellus*, *Craterellus*, *Hydnum*), mycorrhizal symbionts of orchids known as "Rhizoctonia like fungi" (including some species of *Tulasnella*, *Ceratobasidium* and *Rhizoctonia*), and important plant pathogens that cause economic losses (Veldre et al. 2013, *Ceratobasidium* spp., and especially, species of *Rhizoctonia solani* complex). Cantharellales comprises a morphologically and ecologically heterogeneous assemblage of fungi recovered consistently as monophyletic in phylogenetic studies (Bruns et al. 1998; Hibbett et al. 1997; Pine et al. 1999). The diversity is extremely high in terms of basidiomes configuration, including cantharelloid, hydnoid, corticioid, polyporoid, clavarioid, cyphelloid forms. Additionally, nearly all known trophic strategies exist in the order: ectomycorrhizal, orchid-mycorrhizal, liverwort mycobionts (Preußing et al. 2010), saprotroph, parasitic, lichenicolous (Diederich et al. 2022b), endophytic (Dearnaley et al. 2016), lichenized (Masumoto and Degawa 2020).

Family delimitation and relationships among families are still debated within Cantharellales. Usually four families are recognized: Hydnaceae (within which Cantharellaceae, Clavulinaceae and Sistotremataceae are sometimes segregated), Botryobasidiaceae, Cejpomycetaceae (syn. Ceratobasidiaceae s. auct.) and Tulasnellaceae (Olariaga 2021). The unstable family and generic classifications, particularly in the polyphyletic *Sistotrema* and *Rhizoctonia*-*Ceratobasidium* are mostly due to an accelerated evolution rate of nuclear ribosomal genes (18S, 28S, ITS) that produce phylogenetic artifacts in phylogenetic analyses across Cantharellales (Moncalvo et al. 2006; Olariaga 2021). Preliminary data based on analyses of a 526 single-copy ortholog gene sequence matrix suggested that Botryobasidiaceae is sister to Hydnaceae both sharing stichobasidia *i.e.* basidia with longitudinal spindles in the second division of the diploid nucleus that often have more than 4-sterigmata, with Tulasnellaceae and Cejpomycetaceae progressively sister to it (Márquez et al., unpublished). On the contrary, the latter two families produce corticioid basidiomes, chiastic basidia and repetitive basidiospores. The basidia in Tulasnellaceae, sometimes called epibasidia (e.g. Neuhoff 1924, see also Donk 1956), are unique due to their swollen septate sterigmata. Hence, there is no known synapomorphy for the whole Cantharellales.

History

Aiming at constructing a natural classification based on the evolutionary relationships, Gäumann (1926) coined the order Cantharellales to accommodate three genera with stichic basidia, despite producing different basidiomes cantharelloid or clavarioid, namely *Cantharellus*, *Clavulina*, and *Craterellus*. Donk (1933) classified this taxon at the suborder level as Cantharelloideae and incorporated within it *Hydnum repandum* and *H. rufescens*, which also have stichic basidia. In subsequent years, the mode of nuclear division was not given much importance and, even, Donk (1964) segregated again Cantharellaceae and Clavulinaceae, despite both sharing stichic basidia. Hesler and Smith (1963) proposed that *Cantharellus* was related to *Hygrophorus*, a genus with chiastic basidia, and both Corner (1966a, 1970) and Petersen (1971) considered *Cantharellus* as related to the clavarioid *Clavariadelphus*. The latter genus is now accommodated in Gomphales. Later, Jülich (1981) broadened the circumscription of Cantharellales again, strongly influenced by the contemporary evolutionary hypotheses. He attributed 15 families to Cantharellales, the most remarkable of which are: Cantharellaceae, Clavariadelphaceae, Clavariaceae, Clavulinaceae, Craterellaceae, Hydnaceae, Pterulaceae, Sparassidaceae, and Typhulaceae. He furthermore treated the poroid family Scutigeraceae in Cantharellales, due to the fact that inflated hyphae are also present in *Cantharellus* and *Hydnum*. Jülich (1981) believed that cantharelloid and clavarioid fungi were basal Homobasidiomycetes from which many other groups had evolved.

With the advent of the molecular era, the first broad phylogenies using nuclear ribosomal genes and different taxon samplings, found that *Cantharellus*, *Clavulina*, *Hydnum*, *Multiclavula*, *Sistotrema*, *Thanatephorus* (= *Rhizoctonia*) and *Tulasnella* formed a monophyletic group (e.g., Hibbett et al. 1997; Pine et al. 1999; Hibbett and Binder 2002) and the circumscription of Cantharellales was progressively narrowed down and many taxa excluded from Cantharellales (Olariaga 2021).

Characters that define the taxa in the order

Cantharellales is a highly heterogeneous monophyletic assemblage of fungi that lacks shared characters across the order. The Hydnaceae are sometimes referred to as the core cantharelloid clade (Moncalvo et al. 2006). It is the only family with representatives that produce complex fleshy basidiomes (e.g. cantharelloid, hydnoid, polyporoid, clavarioid) that are usually slow growing and long-lived due to resistance against invertebrate predation (Pilz et al. 2003), and include genera such as *Cantharellus*, *Clavulina*, *Craterellus*, *Hydnum*, alongside the *Sistotrema confluens* and *S. muscicola* species aggregates. All those genera are predominantly ectomycorrhizal. *Sistotrema* s.l., the polyphyly of which remains unaddressed, is characterized by corticioid basidiomes and urniform basidia (Bernicchia and Gorjón 2010). Two genera that form clavarioid basidiomes are lichenized, namely *Multiclavula* and *Bryoclavula*. Some *Sistotrema* s.l. species form asexual bulbils that are often lichenicolous and cause bleaching on or even kill lichen thalli (Diederich et al. 2022b). Basidia in Hydnaceae are stichic in all species tested for it, have often more than 4 sterigmata except for in *Clavulina* and show tendency to be urniform or suburniform. Botryobasidiaceae, producing thin corticioid basidiomes, share with Hydnaceae stichobasidia with more than 4 sterigmata, with few exceptions. Species within Botryobasidiaceae are characterized by having broad subicular hyphae and cylindrical to subcylindrical seldom constricted in the middle basidia (Bernicchia and Gorjón 2010). Some species produce asexual morphs assigned to *Haplotrichum*.

Tulasnellaceae and Cejpomycetaceae are featured by resupinate basidiomes and the combination of chiastic (Rogers 1932; Langer 2001), aseptate basidia that produce spores germinating by repetition. The unique epibasidia of Tulasnellaceae are sometimes evolutionarily interpreted as phragmobasidia (Martin 1957). Sexual morphs in Tulasnellaceae are usually thin, sometimes slightly gelatinous and are found on very decayed wood. Asexual morphs, assigned to the genus *Epulorhiza* before the end of dual nomenclature, form monilioid hyphae and have been isolated from orchids roots of many species (Roberts 1999). Saprotrophs, orchid and liverwort symbionts (Preußing et al. 2010) and ectomycorrhizal (Tedersoo et al. 2010) trophic modes have been described for Tulasnellaceae.

Cejpomycetaceae differ from Tulasnellaceae in having holobasidia and septal pore morphology (perforate parenthesomes in Cejpomycetaceae, imperforate in Tulasnellaceae). Cejpomycetaceae stands out for comprising important plant pathogens of the genera *Rhizoctonia* and *Ceratobasidium* sensu auct. The type of *Ceratobasidium* belongs to Sebacinales and most species of *Ceratobasidium* were transferred to *Rhizoctonia* (Oberwinkler et al. 2013b). Pathogenic asexual morphs have been isolated from a vast array of plants (Andersen and Stalpers 1994). To undertake species delimitation, plant pathologists use a method founded on the number of nuclei per cell and a biological species recognition approach, i.e., the "anastomosis group concept" (Matsumoto et al. 1932), based on the ability of isolates of the same species to fuse with each other in co-culture. The match between anastomosis groups (AG) and molecular data is not perfect, i.e. strains assigned to the same AG do not form monophyletic groups (Sharon et al. 2008). Teleomorphs of pathogenic Cejpomycetaceae are found on decayed wood and plant debris (Roberts 1999; Bernicchia and Gorjón 2010). Interestingly, the trophic diversity of the Cejpomycetaceae is extremely high with saprotrophic, orchid and liverwort symbiont, ectomycorrhizal and parasitic members (also lichenicolous, Diederich et al. 2022b).

Evolution

Published phylogenies with Cantharellales either are based on nuclear ribosomal genes (e.g., Moncalvo et al. 2006; Cao et al. 2021a) and are unreliable due to phylogenetic artifacts or include few representatives (Nagy et al. 2017; Li et al. 2021c). A fully resolved phylogeny with an appropriate taxon sampling is therefore missing. In this scenario, reconstructing with certainty the evolution and shifts in trophic modes and basidioma configuration of Cantharellales remains impossible. The most feasible possibility appears that the common ancestor of the Cantharellales produced resupinate corticioid basidiomes and had saprotrophic abilities.

Justification of order and problems

Although Cantharellales, as circumscribed here, is monophyletic (Nagy et al. 2017; Li et al. 2021c), the lack of a well-supported phylogeny with a comprehensive taxon sampling is reflected at different levels. At higher levels, relationships among families usually included in Cantharellales remain uncertain, and thus, Tulasnellaceae is even sometimes considered as an order on its own, Tulasnellales (Begerow et al. 2018). Generic delimitation problems affect the Hydnaceae, especially *Sistotrema* s.l., and the Cejpomycetaceae. As for *Sistotrema*, reported to be polyphyletic (Moncalvo et al. 2006; Cao et al. 2021a), no attempt has been made to segregate it into smaller monophyletic genera due to phylogenetic conflicts derived from the use of nuclear ribosomal markers. The existence of several generic names based on asexual bulbils and the poor support of basal nodes or phylogenies based on ribosomal markers make the taxonomic scenario more intricate. Barcode-sequencing to connect sexual and asexual morphs and phylogenomic approaches using multiple single-copy protein coding genes is necessary to address a possible dual nomenclature and to apply correct names based on an integrated, fully supported phylogeny. At species level, many species complexes need attention. The *Rhizoctonia solani* complex is probably the group with issues that need to be addressed more urgently. Based on intercompatibility tests and their ability to fuse, at least 29 groups have been recognized, some of which have been divided into subgroups (Sharon et al. 2008), but most of which lack a binomial name. Andersen and Stalpers (1994) revised 117 epithets available in *Rhizoctonia* and kept 41 of these in *Rhizoctonia* s. str. based on morphological characters. Regrettably, morphological characters have been stated to be of limited value in delineating species limits (Roberts 1999; Vilgalys and Cubeta 1994). In this framework, the *R. solani* complex needs a multidisciplinary revision to integrate all available knowledge, to obtain a better insight on species boundaries and to propose an adequate binomial nomenclature. The actual diversity of Cantharellales is very likely to be considerably higher than known today. Olariaga (2021) estimated that the order might comprise of ca. 1500 species.

Plate

Fig. 11 Diversity of basidiomes configuration in Cantharellales. **a** *Cantharellus friesii* (ARAN-Fungi 16862, Spain); **b** *Craterellus tubaeformis* (ARAN-Fungi 19448, Spain); **c** *Clavulina coralloides* (ARAN-Fungi 19457, Spain); **d** *Sistotrema brinkmannii* (ARAN-Fungi 17914, Spain); **e** *Multiclavula corynoides* (ARAN-Fungi 15688); **f** *Burgoa anomala* (ARAN-Fungi); **g** *Botryobasidium asperulum* (ARAN-Fungi 17833); **h** *Rhizoctonia* cf. *Fusispora* (ARAN-Fungi 17836, Spain); **i** *Tulasnella eichleriana* [SPG5135 (SALA), Spain]

Genera included

- Family Botryobasidiaceae Jülich 1982
  - *Botryobasidium* Donk 1931
  - =*Acladium* Link 1809
  - =*Allescheriella* Henn. 1897
  - =*Alysidium* Kunze 1817
  - =*Botryohypochnus* Donk 1931
  - =*Cyanohypha* Jülich 1982
  - =*Haplotrichum* Link 1824
  - =*Neoacladium* P.N. Singh & S.K. Singh
  - =*Parahaplotrichum* W.A. Baker & Partr. 2001
  - =*Phaeoblastophora* Partr. & Morgan-Jones 2002
  - =*Physospora* Fr. 1836
  - =*Sporocephalium* Chevall. 1826
  - *Suillosporium* Pouzar 1958
- Family Cejpomycetaceae Jülich 1981
- =Ceratobasidiaceae G.W. Martin sensu auct. 1948
  - *Ceratoporia* Ryvarden & de Meijer 2002
  - *Ceratorhiza* R.T. Moore 1987
  - *Rhizoctonia* DC. 1805
  - =*Aquathanatephorus* C.C. Tu & Kimbr. 1978
  - =*Cejpomyces* Svrček & Pouzar 1970
  - =*Koleroga* Donk
  - =*Thanatephorus* Donk 1958
  - =*Uthatobasidium* Donk 1956
  - =*Ypsilonidium* Donk 1972
  - *Scotomyces* Jülich 1978
- Family Hydnaceae Chevall. 1826
  - =Cantharellaceae J. Schröt. 1888
  - =Clavulinaceae Donk 1970
  - =Sistotremataceae Jülich 1982
  - *Adamflakia* Diederich & Lawrey 2016
  - =*Bulbilla* Diederich, Flakus & Etayo 2014
  - *Bergerella* Diederich & Lawrey 2020
  - *Bryoclavula* H. Masumoto & Y. Degawa 2020
  - *Burgella* Diederich & Lawrey 2007
  - *Burgellopsis* Diederich & Lawrey 2014
  - *Burgoa* Goid. 1937
  - *Cantharellus* Adans. 1821
  - =*Afrocantharellus* (Eyssart. & Buyck) Tibuhwa 2012
  - =*Goossensia* Heinem. 1958
  - *Clavulina* J. Schrot. 1888
  - *Craterellus* Pers. 1825
  - =*Pseudocraterellus* Corner 1958
  - =*Pterygellus* Corner 1966
  - *Hydnum* L. 1753
  - *Membranomyces* Jülich 1975
  - *Minimedusa* Weresub & P.M. LeClair 1971
  - *Multiclavula* R.H. Petersen 1967
  - *Neoburgoa* Diederich, E. Zimm. & Lawrey 2016
  - *Parmeliicida* Diederich, F. Berger, Etayo & Lawrey 2022
  - *Rogersiomyces* J.L. Crane & Schokn. 1978
  - =*Hyphobasidiofera* K. Matsush. & Matsush. 1996
  - *Sistotrema* Fr. 1821
  - =*Hydnotrema* Link 1833
  - =*Ingoldiella* D.E. Shaw 1972
  - =*Urnobasidium* Parmasto 1969
  - *Sistotremella* Hjortstam 1984
- Family Tulasnellaceae Juel 1897
  - *Pseudotulasnella* Lowy 1964
  - *Tulasnella* J. Schröt. 1888
  - =*Gloeotulasnella* Höhn. & Litsch. 1908
  - *Stilbotulasnella* Oberw. & Bandoni 1982
- Cantharellales *incertae sedis*
  - *Ceratobasidium* D.P. Rogers 1935

Significance

Cantharellales comprises a number of economically important species because of their edibility, constituting important ectomycorrhizal partners or being plant pathogens that cause damage in crops. Edible species of Cantharellales belong to the genera *Cantharellus*, *Clavulina*, *Craterellus* and *Hydnum*. Of those, *Cantharellus* and *Craterellus*, popularly called chantherelles are of special significance as the commercially most important group of mushrooms harvested from wild populations (Danell 1999). Watling (1997) estimated global chanterelle commerce at ca. 200,000 metric tons, worth approximately 1.25–1.4 billion dollars annually. Basidiomes of *Hydnum* and *Clavulina* are not more locally marketed and picked up by mushroom hunters in areas in which there has been tradition to consume certain species. An Ectomycorrhizal nutrition mode has evolved in several genera of the Hydnaceae that produce mostly fleshy and complex basidiomes (cantharelloid, hynoid, poroid, clavarioid), namely *Cantharellus*, *Clavulina*, *Craterellus*, *Hydnum* and *Sistotrema* (especially the *S. confluens* complex and poroid species around *S. muscicola*). Most ectomycorrhizal Cantharellales occur in well-preserved mature forests and show broad host ranges (Olariaga 2021). Well-known cases of continental endemicity have been described (Buyck 2016). Species of *Clavulina* have been reported to quantitatively be very important in ectomycorrhizal communities, especially in temperate regions where *Clavulina* species are being detected in environmental sequencing and ectomycorrhizal community studies (Uehling et al. 2012; Argüelles-Moyao et al. 2017). The economically most significant group of Cantharellales is the one constituted by many species of *Rhizoctonia*, which are important plant pathogens on more than 500 species of plants (Farr and Rossman 2005). As indicator of its importance and ongoing research, 808 articles that contained the word "Rhizoctonia" have been published in the last 5 years (2017–2022). Another significant group are some species of Tulasnella that are symbionts in orchid roots, including important species in the industry of ornamental plants (De 2020) or with implications in food industry (Otero et al. 2017).

Ceraceosorales Begerow, M. Stoll & R. Bauer 2007

Contributed by: Teeratas Kijpornyongpan

Introduction

Ceraceosorales is a monotypic order, consisting of only one described genus named *Ceraceosorus*. Currently the order and the genus contain three described species: *Ceraceosorus bombacis*, *Ceraceosorus guamensis*, and *Ceraceosorus africanus* (Cunningham et al. 1976; Kijpornyongpan and Aime 2016; Piątek et al. 2016). Members of Ceraceosorales do not produce teliospores but do produce basidia and basidiospores from sori on infected host leaves (Begerow et al. 2006; Piątek et al. 2016). Ultrastructure studies reveal that species of Ceraceosorales have a "simple" septum with septal pore caps, produce local interaction zones and intracellular hyphae (or haustoria) inside host cells (Begerow et al. 2006). Anamorphs of Ceraceosorales are yeast-like, producing blastoconidia at hyphal branches (Kijpornyongpan and Aime 2016). Morphologically, two-sterigmate basidia and the presence of intracellular hyphae are key characters of Ceraceosorales that are distinct from other orders of Exobasidiomycetes (Begerow et al. 2014). Teleomorphs of Ceraceosorales are known as phytopathogens on *Bombax* (Malvaceae), while anamorphs are known as phylloplane fungi. A recent study revealed extreme intragenomic variation of the internal transcribed spacer (ITS) of ribosomal DNA region in *Ceraceosorus* (Kijpornyongpan and Aime 2016), which will be of interest for future studies on concerted evolution of ribosomal DNA sequences.

History

The first known species of Ceraceosorales was described as *Dicellomyces bombacis* B.K. Bakshi (Bakshi et al. 1972). It was found as a pathogen causing a leaf spot disease on *Bombax ceiba* (Malvaceae) in Dehra Dun, India. A subsequent study by Cunningham et al. (1976) found that *D. bombacis* differs from other species in *Dicellomyces* by having indeterminate growth of hymenium and lacking basidiome tissues. Therefore, the new genus name *Ceraceosorus* B.K. Bakshi was erected to accommodate the new combination *Ceraceosorus bombacis* B.K. Bakshi. The species was classified in Brachybasidiaceae (Exobasidiales, Basidiomycota) based on persistent probasidia, elongated two-sterigmate basidia, and ballistosporic basidiospores with hilar appendices (Cunningham et al. 1976).

Ceraceosorales was erected by Begerow et al. (2006) based on distinct phylogenetic placements of *C. bombacis* from other orders of Exobasidiomycetes: Entylomatales, Exobasidiales, Doassansiales, and Microstromatales. Despite having local interaction zones, Ceraceosorales differs from other Exobasidiomycetes orders by the presence of intracellular hyphae (haustoria) inside a host cell (Bauer et al. 1997; Begerow et al. 2006). Validation of the family name Ceraceosoraceae was subsequently done based on the description of Ceraceosorales (Denchev and Moore 2009). Until now, the descriptions of Ceraceosorales and Ceraceosoraceae are based on the single species *C. bombacis* (Begerow et al. 2014).

After the first discovery in 1976, two additional species of *Ceraceosorus* were described in 2016. The second described species, *Ceraceosorus guamensis*, was found as an anamorphic phylloplane fungus from a healthy dicot leaf, collected from the island of Guam (Kijpornyongpan and Aime 2016). This is also the first study that conducted physiological studies on the anamorphs of *C. bombacis* and *C. guamensis*. The other species, *Ceraceosorus africanus*, was found as a pathogen on *Bombax costatum* leaves from Western Africa: Benin, Ghana and Togo (Piątek et al. 2016). Another isolate of *Ceraceosorus* species, found as a phylloplane fungus from Louisiana, the United States, was found in recent studies (Albu 2012; Albu et al. 2015). Their phylogenetic analyses showed this isolate appeared to be an undescribed species (Albu et al. 2015).

Characters that define the taxa in the order

Teleomorph: Fructification developed on the lower surface of leaves. Sori erupted from host epidermis without any enclosed tissues. Infection apparatus having local interaction zone with intracellular hyphae (haustoria) present inside host cells. Hymenium indeterminate growth, dense with basidia and basidioles at varied developmental stages. Probasidia persistent and elongate. Metabasidia with two sterigmata. Basidiospores reniform or curved clavate, spore surface smooth, hilar appendices present.

Anamorph: Hyphae branched, simple septate with septal pore caps but no clamp connection. Conidia fusiform or curved clavate, one to few-celled, surface smooth. Culture morphology cerebriform and velvety on potato dextrose agar (PDA), slow growth rate (equal or less than 2.5 mm after incubation at room temperature for 7 days), cultures on PDA become buff and waxy when aged, yeast-like colony morphology observed when cultured on corn meal agar (CMA).

Plates

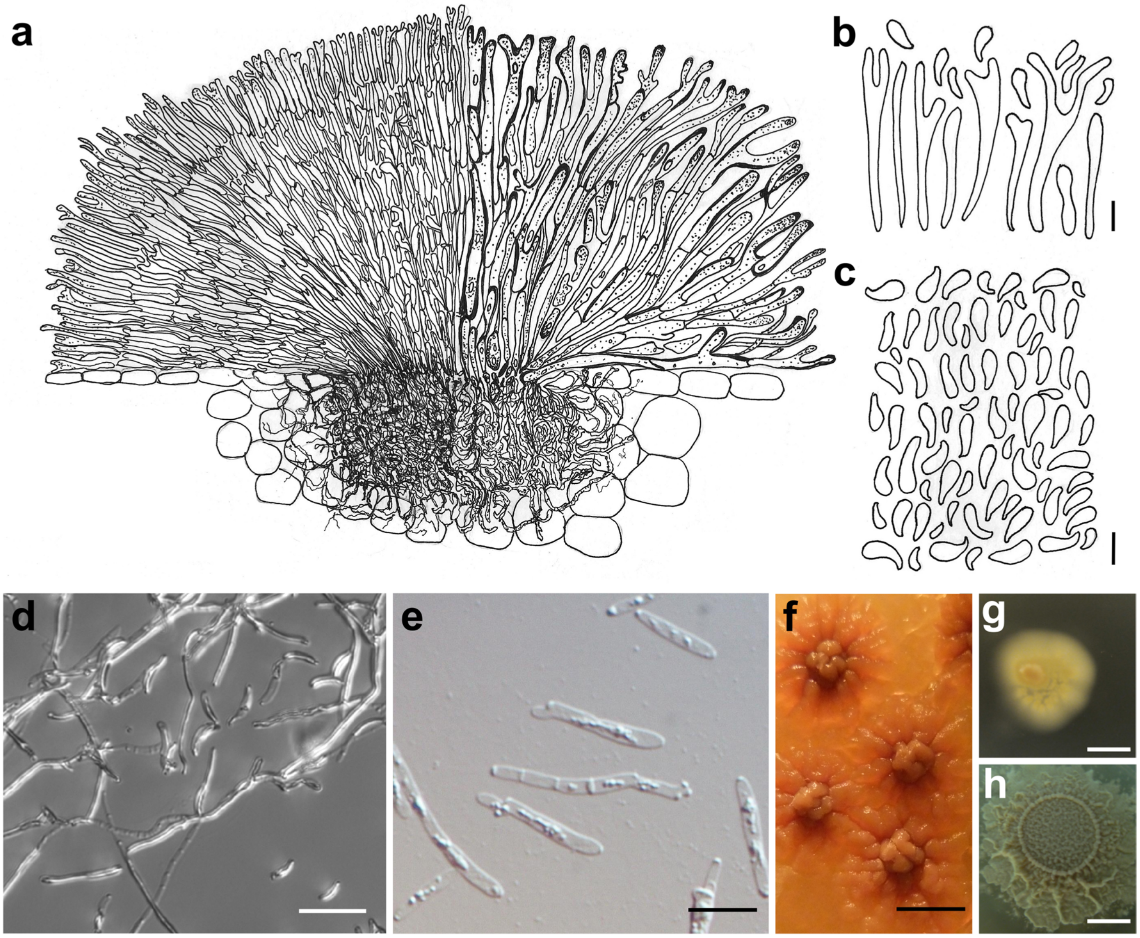


Fig. 12 Morphological characters of Ceraceosorales. **a** sorus on the lower surface of an infected leaf. The left panel depicts the overall structure of sorus fructification, while the right panel illustrates a closer look on a hymenial layer (top) and a contact zone with host tissues (bottom); **b** probasidium and two-sterigmate metabasidium; **c** basidiospores; **d** anamorphic hyphae with blastoconidia; **e** yeast-like micromorphology; **f** colony growing on potato dextrose agar; **g** colony growing on corn meal agar; **h** colony growing on nitrogen assimilation agar. Scale bars: a–c = 10 µm; d = 20 µm; e = 10 µm; f – h = 2.5 mm

Genera included

Family Ceraceosoraceae Denchev & R.T. Moore 2009

Ceraceosorus B.K. Bakshi 1976

Evolution

Originally, *Ceraceosorus* was classified in Brachybasidiaceae based on morphological similarities of basidia (Cunningham et al. 1976). Ultrastuctures of septal pores and local interaction zones are also similar to those described in Exobasidiales (Cunningham et al. 1976; Begerow et al. 2002a, 2006). However, Ceraceosorales is unique from Exobasidiales and other orders of Exobasidiomycetes by having haustoria, which are specialized structures for biotrophic pathogens (Begerow et al. 2006). Multi-locus gene phylogeny does not support a close relationship between Ceraceosorales and Exobasidiales, and the placement of Ceraceosorales is ambiguous (Begerow et al. 2006; Wang et al. 2015d). A recent phylogenomic study revealed Ceraceosorales as a sister order to Entylomatales, the order of smut fungi on herbaceous eudicots (Kijpornyongpan et al. 2018). Unlike smut fungi, the three orders of Exobasidiomycetes—Ceraceosorales, Exobasidiales, and Microstromatales—do not produce teliospores. Interestingly, pathogens in these orders have woody plants as hosts, and that may have a evolutionary connection to their parallel loss of teliospores (Begerow et al. 2014; Kijpornyongpan et al. 2018).

Justification of order and problems

The distinction of Ceraceosorales from other orders of Exobasidiomycetes is primarily demonstrated by phylogenetic studies (Begerow et al. 2006; Kijpornyongpan et al. 2018). Two-sterigmate metabasidia and the presence of intracellular hyphae are supporting morphological data for the establishment of the order (Begerow et al. 2014). One limitation for taxonomic study of Ceraceosorales is that currently there are only three described species in the order. Teleomorphs have been investigated from two of those, and *C. bombacis* is the only species with morphological data from anamorph and teleomorph (Cunningham et al. 1976; Kijpornyongpan and Aime 2016; Piątek et al. 2016). Ceraceosorales is likely rare to be detected and isolated through culture-dependent methods due to their very slow growth rate. In addition, their unique DNA sequences on the internal transcribed spacer (ITS) in the ribosomal DNA (rDNA) gene make them difficult to be captured by ITS primers commonly used in metagenomic studies (Kijpornyongpan and Aime 2016).

Significance

Ecological roles

Teleomorphs of Ceraceosorales are known as plant pathogens on leaves of *Bombax*: *C. bombacis* is a pathogen on *B. ceiba*, and *C. africanus* is a pathogen on *B. costatum* (Cunningham et al. 1976; Piątek et al. 2016). Anamorphs are thus far found as phylloplane fungi on healthy dicot leaves (Albu 2012; Kijpornyongpan and Aime 2016). Due to the scarcity of studies, a connection between the anamorph and teleomorph in a pathogenic life cycle is yet to be elucidated.

Other relevant data and future recommendations

Cloning-sequencing data of *C. bombacis* and *C. guamensis* revealed extreme intragenomic variation in the ITS region of the rDNA gene in Ceraceosorales (Kijpornyongpan and Aime 2016). The ITS variants do not overlap across different species. Therefore, *Ceraceosorus* will be a promising model to study on the concerted evolution of multicopy rDNA genes. Genomes have been sequenced for *C. bombacis* (Sharma et al. 2015) and *C. guamensis* (Kijpornyongpan et al. 2018). These reference genomic data will be useful for future studies in systematics, biotrophic pathology, and rDNA evolution of the genus.

Chionasterales N.A.T. Irwin, C.S. Twynstra, V. Mathur & P.J. Keeling 2021

Contributed by: Teun Boekhout

Introduction

The phylogeny of *Chionaster nivalis*, an enigmatic fungus that is part of snow communities, remained unknown for a long time. Recently, its phylogeny was studied using the ITS and the D1–D2 regions of the large subunit ribosomal DNA (LSU rDNA) (Irwin et al. 2021). This analysis revealed that it represents a new order, Chionasterales N.A.T. Irwin, C.S. Twynstra, V. Mathur & P.J. Keeling, positioned in Tremellomycetes, Agaricomycotina.

History

Chionaster was a monotypic genus described in 1903 (Wille 1903) and accommodates a unicellular fungus characterized by the presence of a central part with condensed cytoplasm with 3–5 radiating arms. Its taxonomic position remained unclear until recently when a molecular phylogenetic study revealed that it is part of Tremellomycetes, Agaricomycotina, Basidiomycota where it formed an order on its own (Irwin et al. 2021).

Characters that define the taxa in the order

Chionasterales is mainly characterized by its molecular phylogenetic position showing a sister relationship to Cystofilobasidiales. As the order is only known from one monotypic genus, it remains to be seen if the peculiar morphology (see above) will hold for the order.

Plates

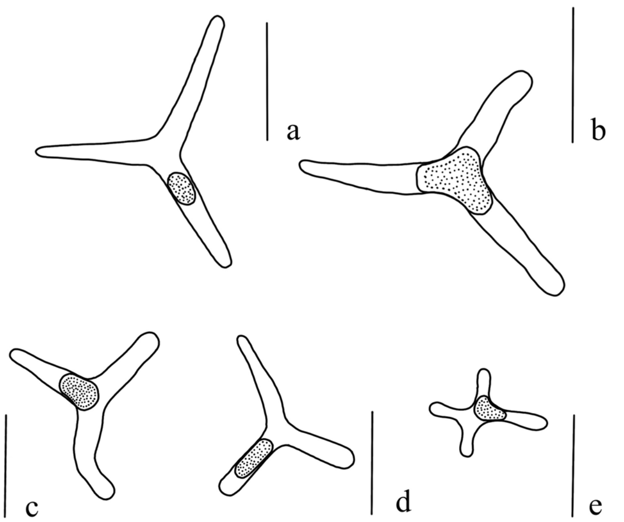


Fig. 13 The morphology of *Chionaster nivalis*. Scale bars = 30 µm. Redraw from Irwin et al. (2021) by Mao-Qiang He

Genera included

Family Chionasteraceae N.A.T. Irwin, C.S. Twynstra, V. Mathur & P.J. Keeling 2021
Chionaster Wille 1903

Evolution

Chionasterales occupies a basal position in Tremellomycetes with a sister relationship to Cystofilobasidiales. The cellular morphology of *Chionaster nivalis* is unique among Basidiomycota.

Justification of order and problems

Molecular phylogenetic data clearly showed that *Chionaster nivalis* occupies an isolated position within Tremellomycetes warranting recognition as an order. Further research is required to fully understand the morphological, biological, ecological, and phylogenetic range of this still monotypic order.

Significance

Ecological and economical roles

Chionaster nivalis is part of the so-called microbial snow communities and seems to have a global distribution where such communities occur. Hence it might be a psychrophilic species. Studies to further address this and other physiological characteristics of the species will need cultures of the species.

Chemical diversity

Unknown.

Other relevant data and future recommendations

As suggested by Irwin et al. (2021), *C. nivalis* might be an interesting species to study microbial adaptations to low temperatures.

Cintractiellales McTaggart & R.G. Shivas 2020

Contributed by: Teodor T. Denchev, Cvetomir M. Denchev, Dominik Begerow, Martin Kemler

Introduction

Cintractiellales consists of a single family, Cintractiellaceae, that was erected to accommodate the species of *Cintractiella* (Vánky 2003; McTaggart et al. 2020). *Cintractiella* is an unusual genus among the smut fungi. It produces sori in adventitious shoots clustered in groups on leaves, or in adventitious spikelets in the inflorescence, forming witches' brooms on sedges from Cyperaceae subfamily Mapanioideae, from the tropics and subtropics.

Cintractiellales is characterized by having intercellular hyphae forming coiled, lobed or branched haustoria into the host cells (Vánky 2003, 2013).

Characters that define the taxa in the order

Cintractiella includes four species. Type species, *C. lamii* Boedijn on *Hypolytrum* (from Indonesia and Thailand), as well as *C. kosraensis* Aime et al. on *Mapania* (from the Caroline Islands), and *C. scirpodendri* Prychid & J.J. Bruhl on *Scirpodendron* (from Queensland), possess sori in adventitious shoots clustered in groups on leaves. Sori develop around the upper part of each adventitious shoots, hidden by the narrow bracts of the adventitious shoots, but at the shoot apex, they are visible as a naked, curved column, ca. 5–6 mm long (in *C. lamii* up to 20 mm long), with a semi-agglutinated to granular spore mass on the column surface (Boedijn 1937; Aime et al. 2018c; McTaggart et al. 2020). Spores at maturity are single and minutely reticulate. Spore germination results in three-celled phragmobasidia with lateral and terminal basidiospores (McTaggart et al. 2020).

Cintractiella diplasiae (Henn.) M. Piepenbr. on *Diplasia* (from the Neotropics) develops sori in adventitious spikelets around the bases of peduncles, forming witches' brooms (Piepenbring 2001; Vánky 2013). The spores are single and verrucose.

Plates

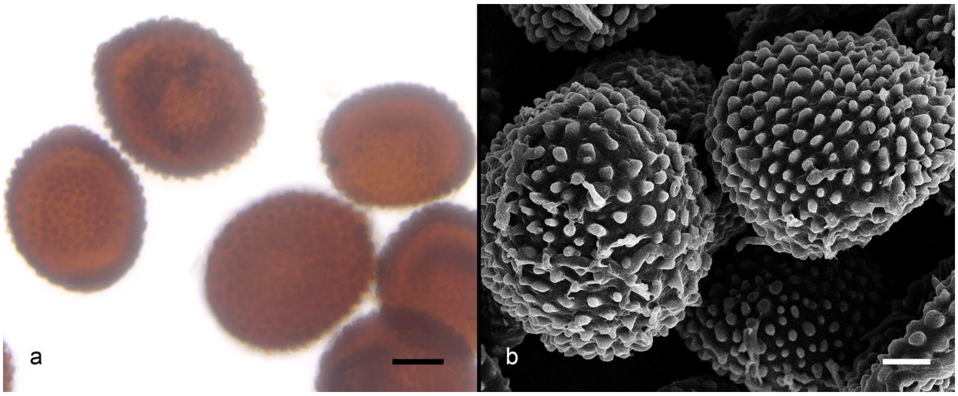


Fig. 14 Cintractiellales. **a**, **b** *Cintractiella diplasiae* on *Diplasia karataefolia* (isotype, Ule, Mycoth. Brasil. 2); **a** spores in LM; **b** spores in SEM. Scale bars: a = 10 µm; b = 5 µm

Genera included Family Cintractiellaceae Vánky 2003

Cintractiella Boedijn 1937

Evolution

Molecular study and phylogenetic analyses of *Cintractiella scirpodendri* demonstrated that *Cintractiella* did not share a most recent common ancestor with other orders of smut fungi and a new order, Cintractiellales, was introduced (McTaggart et al. 2020). It was suggested that the Cintractiellales may have shared a most recent common ancestor with the Malasseziomycetes (McTaggart et al. 2020).

Economic importance

None is known; no crop plants are affected.

Classiculales R. Bauer, Begerow, Oberw. & Marvanová 2003

Contributed by: Nathan Schoutteten, Teun Boekhout

Introduction

This small order currently only comprises three known species of aquatic hyphomycetous Basidiomycota and was initially proposed by Bauer et al. (2003) to accommodate *Jaculispora submersa* H.J. Huds. & Ingold and *Classicula fluitans* R. Bauer, Begerow, Oberw. & Marvanová. All known species have navicular conidia with attached setose branches, which is most likely an adaptation to an aquatic lifestyle. All species are characterized by clamped hyphae and basally clamped tremelloid haustoria, which indicate a possible mycoparasitic strategy. Molecular phylogenetic reconstructions indicated this clade is a member of Pucciniomycotina, and has an isolated position compared to other groups in this subphylum (Bauer et al. 2006). The peculiar ecology, morphology and phylogenetic position have led to the interpretation that this clade represents an order (Classiculales) and class (Classiculomycetes) on its own.

History

Jaculispora submersa was described by Hudson and Ingold (1960) from a water stream in Jamaica. This species is only known from the asexual conidial stage, but its basidiomycetous nature was recognised because of the presence of clamped hyphae. *Naiadella fluitans* was described to accommodate another asexual aquatic hyphomycete isolated from water streams in Canada and the Czech Republic, forming hyphae with clamp connections, binuclear navicular conidia, and tremelloid haustorial branches (Marvanová and Bandoni 1987). Only years later, Bauer et al. (2003) discovered the sexual stage of *N. fluitans* after submerging the culture in water. The sexual stage of this species is characterized by cylindrical, transversely three-septate basidia occurring singly or in clusters, with the sterigmata subapically swollen. Basidiospores are narrowly fusiform. Hyphae with clamp connections, but retraction septa without clamp connections. Tremelloid haustorial cells present and dikaryotic (Bauer et al. 2003). Conidia navicular with 2–3 setose branches. The genus *Classicula* was introduced to accommodate the sexual stage (Bauer et al. 2003). Aime et al. (2018b) proposed to protect the name *Classicula* over *Naiadella*. A third asexual aquatic hyphomycetous species in this group was described more recently by Qiao et al. (2018) from a water stream in China.

Characters that define the taxa in the order

Morphological description is indicated above. At the ultrastructural level, the hyphal septa have 'simple' septa that are associated with microbodies, and the spindle pole bodies (SPBs) occur inside the nucleus during metaphase (Bauer et al. 2003, 2006). Above all, the order is characterized by its isolated molecular phylogenetic position.

Plates

Fig. 15 *Classicula* sp. on Malt-Yeast-Peptone agar (MYP), also see Figs. 1–7 in Bauer et al. (2003) and Fig. 2 in Qiao et al. (2018)

Genera included Family Classiculaceae R. Bauer, Begerow, Oberw. & Marvanová 2003

Classicula R. Bauer, Begerow, Oberw. & Marvanová 2003
= *Naiadella* Marvanová & Bandoni 1987
Jaculispora H.J. Huds. & Ingold 1960

Evolution

Various molecular phylogenetic studies revealed different phylogenetic positions of the order. Bauer et al. (2006) found a sister group relation of Classiculomycetes to Pucciniomycetes, whereas other multi locus-based tree inferences placed the order sister to Microbotryomycetes (Wang et al. 2015a; Qiao et al. 2018), and a third multigene-based tree positioned it sister to Atractiellales (Bauer et al. 2003). The genome sequence of *Classicula sinensis* is available at MycoCosm (JGI), and their consensustree shows a sister relationship with Pucciniomycetes, like the findings of Bauer et al. (2006). Thus, the phylogenetic position of this group remains enigmatic and needs improved phylogenetic studies for which the use of whole genome-based orthologues and extended taxon sampling is recommended.

Justification of order and problems

Given the small size of the order it can be expected that new members will be identified in the future, which will undoubtedly enlarge our understanding of the limits of the order and its biological significance. To date, only genomic rDNA sequences are publicly available for *Classicula fluitans* and *Jaculispora submersa*.

Significance

Ecological and economical roles

Species occur in aquatic habitats (Hudson and Ingold 1960; Marvanová and Bandoni 1987; Bauer et al. 2003). The presence of tremelloid haustorial cells indicates a possible mycoparasitic strategy for these species.

Chemical diversity

Unknown.

Corticiales K.H. Larss. 2007
= Vuilleminiales Boidin, Mugnier & Canales 1998

Contributed by: Masoomeh Ghobad-Nejhad, Sergio P. Gorjón

Introduction

Corticiales K.H. Larss. was originally introduced by Hibbett et al. (2007) for the “corticioid clade” comprising a few taxa exclusively with a corticioid-type of basidiome (Binder et al. 2005; Larsson et al. 2004). Boidin et al. (1998) introduced Vuilleminiales with the family Vuilleminiaceae as its type. Justification towards synonymization of Vuilleminiales under Corticiales was already provided by Hibbett et al. (2007). Currently, Corticiales contains four families and about 29 genera. The order is one of the major lineages of Agaricomycetes with a corticioid type of basidiomes.

History

Hibbett et al. (2007) retained a single family Corticiaceae for Corticiales. Ghobad-Nejhad et al. (2010) recognized three distinct clades within Corticiales, each representing a family: (1) the clade containing the type species of *Corticium* and other species with diverse nutritional modes (the *Corticium* clade, family *Corticiaceae*). Recently, a thorough phylogeny revision for *Corticiaceae* s.s. has been provided (Ghobad-Nejhad et al. 2021); (2) the clade comprising *Vuilleminia*, *Cytidia* and *Australovuilleminia* (the *Vuilleminia* clade, family Vuilleminiaceae) with saprotrophic taxa growing on attached wood of angiosperms, with dendrohyphidia, mostly with gelatinous basidiomes, and almost all with allantoid basidiospores; and (3) the clade containing *Punctularia*, *Punctulariopsis*, and *Dendrocorticium* (the *Punctularia* clade, family Punctulariaceae) growing on fallen angiosperm wood and bearing ellipsoid spores. The fourth family Dendrominiaceae was recognized in Corticiales by Ariyawansa et al. (2015) with a single genus *Dendrominia*. There are also a number of genera traditionally speculated to be related to the Corticiales in the literature based on morphology only; as far as still no DNA is available from the type species of these genera, they still remain as *incertae sedis*. The family Corticiaceae is the largest family in the Corticiales and currently contains 12 genera (Ghobad-Nejhad et al. 2021).

Characters that define the taxa in the order

Corticiales taxa generally have simple, resupinate, smooth basidiomes, and a monomitic hyphal system with or without clamps, dendrohyphidia, and medium-sized to relatively large ellipsoid basidiospores. Many species develop probasidia and produce large basidia, usually with thick walls. Corticiales species are predominantly wood saprotrophs.

Plates

Fig. 16 Macromorphological diversity in Corticiaceae. **a** *Mycobernardia incrustans*; **b** *Corticium meridioroseum*; **c** asexual form of *Corticium roseum*; **d** *Corticium silviae*; **e** bulbils of *Erythricium aurantiacum*; **f** *Erythricium hypnophilum*; **g** *Erythricium laetum*; **h** *Laetisaria buckii*; **i** *Laetisaria lichenicola*; **j** *Marchandiomyces corallinus*; **k** *Marchandiomyces aurantioroseus*; **l** *Marchandiomyces* sp. From Ghobad-Nejhad et al. (2021). Copyright © 2021 Ghobad-Nejhad et al.

Genera included

Family Corticiaceae Herter 1910

- *Basidiodesertica* Maharachch., Wanas. & Al-Sadi 2021
- *Capillosclerotium* Prameela & Deeba 2013
- *Corticium* Pers. 1794
- =*Lyomyces* P. Karst. 1882
- =*Mycinema* C. Agardh 1824
- *Disporotrichum* Stalpers 1984
- *Erythricium* J. Erikss. & Hjortstam 1970
- =*Marchandiobasidium* Diederich & Schultheis 2003
- =*Necator* Massee 1898
- *Galzinia* Bourdot 1922
- *Giulia* Tassi 1904
- *Laetisaria* Burds. 1979
- =*Limonomyces* Stalpers & Loer. 1982
- *Lawreymyces* Lücking & Moncada 2017
- *Marchandiomyces* Diederich & D. Hawksw. 1990
- =*Marchandiopsis* Ghobad-Nejhad & Hallenb. 2010
- *Mycobernardia* Ghobad-Nejhad 2021
- *Tretopileus* B.O. Dodge 1946
- *Waitea* Warcup & P.H.B. Talbot 1962

  = *Chrysorhiza* T.F. Andersen & Stalpers 1996
- Family Dendrominiaceae Ghobad-Nejhad 2015
  - *Dendrominia* Ghobad-Nejhad & Duhem 2013
- Family Punctulariaceae Donk 1964
  - *Dendrocorticiopsis* Sheng H. Wu, C.L. Wei & S.H. He 2022
  - *Dendrocorticium* M.J. Larsen & Gilb. 1974
  - *Punctularia* Pat. 1895
  - = *Phaeophlebia* W.B. Cooke 1956
  - *Punctulariopsis* Ghobad-Nejhad 2010
- Family Vuilleminiaceae Höhn. 1904
  - *Australovuilleminia* Ghobad-Nejhad & Hallenb. 2010
  - *Cytidia* Quél. 1888
  - = *Lomatina* (Fr.) P. Karst. 1892
  - *Vuilleminia* Maire 1902
- Corticiales genera *incertae sedis*
  - *Ambivina* Katz 1974
  - *Amylobasidium* Ginns 1988
  - *Corticirama* Pilát 1957
  - *Hemmesomyces* Gilb. & Nakasone 2003
  - *Leptocorticium* Hjortstam & Ryvarden 2002
  - *Melzerodontia* Hjortstam & Ryvarden 1980
  - *Papyrodiscus* D.A. Reid 1979
  - *Ripexicium* Hjortstam 1995

Evolution

The remarkable family Corticiaceae is an iconic family of Basidiomycota with a long, controversial history. Corticiaceae has been largely used as a basket to hold diverse fungi that produce crust-like basidiomes. The bulk of these fungi have, however, found a home in other families and genera throughout the basidiomycete tree of life, leaving Corticiaceae as a poorly defined family with obscure boundaries. Because of its importance as a key family in understating the relationships of corticioid fungi and basidiomycetes at large, Ghobad-Nejhad et al. (2021) applied multigene phylogenetic analyses based on extensive original specimens to dig into the circumscription of genera in this family. As a result, a well-supported phylogenetic backbone for Corticiaceae was provided, and several ecologically and economically relevant plant pathogenic species were taxonomically disentangled. There are also asexually reproducing genera in Corticiaceae, namely the monotypic genera *Basidiodesertica, Giulia*, and *Disporotrichum* for which no sexual morph is yet known. The diverse nutritional lifestyles in Corticiaceae, including saprotrophic, plant pathogenic, lichenicolous, and endolichenic modes has been noteworthy. Ghobad-Nejhad et al. (2021) examined the evolution of nutritional habit and discovered that saprotrophy is the original lifestyle in this family.

Justification of order and problems

Corticiales and its four families are well-established and recovered in molecular phylogenetic studies. However, morphological delimitation of some genera and species especially *Laetisaria/Marchandiomyces* is still difficult (Ghobad-Nejhad et al. 2021). Several genera are known only by their asexual forms, leaving little evidence for morphological identification. A number of generic types await DNA data and so are still queued as *incertae sedis*. Full genome sequences are only available for two species (*Laetisaria culmigena, Punctularia strigosozonata*), while more candidates should be sequenced to enable phylogenomic studies in this order.

Significance

Ecological and economical roles

Corticiales taxa are widespread and inhabit woody plants, grasses, mosses, and lichen thalli. Most of the species are saprotrophic on hardwood plants. Economic aspects of Corticiales mostly relate to the phytopathogenic species in *Erythricium*, *Laetisaria,* and *Waitea* which cause diseases such as pink disease, brown ring patch, red thread sheath spot, and pink patch disease (Jayawardena et al. 2019). *Erythricium salmonicolor* is a devastating pathogen causing pink disease in several economically important trees such as citrus, cacao, coffee, *Eucalyptus*, and rubber. *Laetisaria fuciformis* and *L. roseipellis* are pathogens of turfgrasses. *Waitea circinata* infects cereals, legumes, and turfgrasses.

Chemical diversity

Corticiales taxa may be noted for producing lignin modifying enzymes. Morgenstern et al. (2008) detected partial sequences of manganese peroxidases in the Corticiales, reporting the first-class II fungal peroxidases from *Cytidia salicina*. *Punctularia* has been subject to numerous studies on its metabolites and bioactivity (e.g. Acero et al. 2022; Knijn et al. 2019).

Other relevant data and future recommendations

Future research is needed to: obtain whole nuclear and mitochondrial genome sequences from additional Corticiales species for better understanding of their ecology, evolution, and chemistry; run phylogenomics across the order; examine the metabolite profile and biological activity of the species.

Cryptomycocolacales Oberw. & R. Bauer 1990

Contributed by: Nathan Schoutteten, Teun Boekhout

Introduction

Cryptomycocolacales contains only one family with two monotypic genera and remains enigmatic due to its strongly deviating morphology and ecology compared to other known groups of Basidiomycota. Both representatives are presumed to be colacosome-interacting mycoparasites of ascomycetous hosts, similar to some mycoparasites in Microbotryomycetes. Based on interpretations of morphological, ultrastructural, and phylogenetic reconstructions, it is expected that Cryptomycocolacales diverged early in the evolution of Basidiomycota. Some molecular phylogenetic studies suggested that it occupies a basal position in Pucciniomycotina and Basidiomycota, although its position remains unresolved to date (Aime et al. 2006; Bauer et al. 2006; Weiss et al. 2004a, b).

History

Cryptomycocolax was proposed by Oberwinkler and Bauer (1990a, b) to accommodate *C. abnormis*, a peculiar species that was found as a gelatinous layer overgrowing a pyrenomycetous host fungus on *Circium* stems. This species is only known from the type locality, on the vulcanic Mount Irazú, Costa Rica, and has so far only been collected once. The second genus, *Colacosiphon*, was found in a few mixed cultures derived from bark beetles obtained from decaying *Pinus* logs in Germany (Kirschner et al. 2001). LSU-based phylogenetic reconstructions showed that these two genera cluster together, and potentially take a basal position in Pucciniomycotina and Basidiomycota (Bauer et al. 2006). These two genera comprise the order Cryptomycocolales in Cryptomycocolamycetes (Bauer et al. 2006).

Characters that define the taxa in the order

Cryptomycocolales accommodates filamentous, colacosome-interacting mycoparasitic species. Yeast-like budding of basidiospores was reported only for *Cryptomycocolax abnormis*, but no living cultures are available (Oberwinkler and Bauer 1990a). The reproductive structures of both species are highly specialised and are distinct from those known from other members of Basidiomycota. The sporogenesis of *Cryptomycocolax abnormis* was well-studied and is characterized by a short-lived transversally one-septate basidial stage. During basidium development, the upper cell is abscised, after which the basal cell elongates, and apically gives rise to a variable number of sessile spores in a successive way. Sporogenesis in *Colacosiphon filiformis* is more enigmatic and it is not clear whether the observed sporogenous structures involve mitotic or meiotic processes. The sporogenous cells are aseptate, elongate up to 870 µm long, and give rise to a variable number of sessile spores. Teliospores are absent. Dikaryotic chlamydospores or chlamydospore-like structures are described from both species. Septal pores of both species are 'simple' and have Woronin body-like structures. SPB (spindle pole body), as far as known, have large lateral discs that are connected by small middle pieces during interphase and prophase, and during metaphase they occur in the nuclear envelope (Bauer et al. 2006; Oberwinkler and Bauer 1990a). Both species use specialized structures, so-called colacosomes, to interact with their host fungus. *Cryptomycocolax abnormis* is reported to contain two distinct types of colacosomes, whereas *Colacosiphon filiformis* only contains one type.

Plates

See Figs. 1, 2, 3, 4, 5, 6, 7 in Oberwinkler and Bauer (1990a, b) and in Kirschner et al. (2001).

Genera included

Family Cryptomycocolacaceae Oberw. & R. Bauer 1990
  Colacosiphon R. Kirschner, R. Bauer & Oberw. 2001
  Cryptomycocolax Oberw. & R. Bauer 1990

Evolution

Both the Woronin body-like structures surrounding septal pores in *Colacosiphon* and *Cryptomycocolax* and the SPB structure of *Cryptomycocolax* display similarities with ascomycetous ultrastructure rather than the ultrastructure typical of Basidiomycota. This suggests that both genera may hold interesting phylogenetic positions, which has been investigated by Weiss et al. (2004a, b) and Bauer et al. (2006). Their phylogenetic reconstructions incorporating LSU rDNA sequence data strongly supported the clustering of both genera, but no supported relationship with any other known groups of Basidiomycota was obtained. Based on the limited available data, Cryptomycocolacales can be considered as an early diverging lineage in Basidiomycota, and Weiss et al. (2004a, b) even suggested this species could be the most ancient basidiomycete lineage known to date. However, this group is in serious need of more detailed investigation, and genome sequences of the two known species could help clarify their position regarding other lineages. The presence of colacosomes is shared with some species of Microbotryales, a distantly related order in Pucciniomycotina (Bauer 2004; Weiss et al. 2004a, b; Aime et al. 2006; Bauer et al. 2006). The possible homology of these structures was discussed by Bauer (2004) and Bauer et al. (2006). Isolation of these structures and studies of their biochemical content are needed to support this presumption or not.

Justification of order and problems

Cryptomycocolacales seems justified based on ultrastructural markers and various molecular phylogenetic studies based on LSU sequences. One of the major problems regarding this order is the unavailability of living cultures and the limited available DNA sequence data. Only the sequence of the D1/D2 region of the nuclear ribosomal DNA is known for both species, which proves to be insufficient to reconstruct their phylogenetic position and probably whole genome sequencing is necessary to resolve this.

Significance

Ecological and economical roles

Both species occur as colacosome-interacting mycoparasites in association with ascomycetous hosts. It is likely that *Colacosiphon filiformis* uses bark beetles as the dispersal agent.

Chemical diversity

Not known.

Cystobasidiales R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw. 2006

Contributed by: Nathan Schoutteten, Teun Boekhout, Andrey Yurkov

Introduction

Systematics of basidiomycetous yeasts and filamentous Basidiomycota (mainly so-called heterobasidiomycetes) has long been hampered by separate treatment of both groups of fungi and different established taxonomic approaches. Early molecular phylogenetic studies of basidiomycetous yeasts and heterobasidiomycetes showed a tremendous phylogenetic heterogeneity in both groups that has been conformed in later studies. The study of both groups in phylogenetic studies has resulted in integrated taxonomic treatments, which have been a major step forward (Weiss et al. 2004a, b; Bauer et al. 2006; Wang et al. 2015a, b). These studies have revealed the Cystobasidiales comprising both asexually reproducing basidiomycetous yeasts and sexually reproducing heterobasidiomycetous fungi. The vast majority of Cystobasidiales is only known from a yeast stage, and the sexual stage is currently known from a few species only.

History

Cystobasidium fimetarium, a dimorphic fungus with transversely septate basidia, a thick-walled probasidium and tremelloid haustorial cells in its sexual stage was placed in the family Cystobasidiaceae by Gäumann (1926). According to Kirk et al. (2008) this family contained two genera with nine species. Later, many molecular phylogenetic studies identified a strongly supported clade within Pucciniomycotina including *C. fimetarium* and several basidiomycetous yeasts that were previously found to be part of the Erythrobasidium clade (Fell et al. 2000; Aime et al. 2006; Bauer et al. 2006; Yurkov et al. 2015; Zhao et al. 2017). A total of eleven yeast species were accommodated in the genus *Cystobasidium* by Yurkov et al. (2015) and later, Wang et al. (2015b) listed 17 species in the genus, of which a sexual filamentous stage is only known from *C. fimetarium*. Various heterobasidiomycetes with transversally septate basidia and a thick-walled probasidium were assigned to the genus *Cystobasidium* based on morphological similarities such as the thick-walled probasidium, but no cultures or molecular data are available and it is likely these species belong to other groups in Pucciniomycotina (Martin 1939; Olive 1952). The genus *Occultifur* was proposed by Oberwinkler (1990) for *Occultifur internus*, an intrahymenial mycoparasite of a dacrymycetous host fungus. *O. internus* is characterized by transversally three-septate basidia, thick-walled ellipsoid conidia, clamped hyphae, and the presence of tremelloid haustorial cells. Later, Sampaio et al. (1999a) described *O. externus*, which was isolated as a yeast from leaf litter and of which the sexual stage was observed only in culture. This species was assigned to the genus *Occultifur* based on ultrastructural similarities of the septal pore complex, which is both in *O. internus* and *O. externus* characterized by the cystosome.

Characters that define the taxa in the order

Small gelatinous basidiomes present, pale violaceous to pinkish. Sexual state occurs only in connection with the coprophilous ascomycetous host. Hyphae septate with or without clamp connections, probasidia inflate, thick-walled, basidia elongate, transversely septate, with allantoid basidiospores that are actively discharged, and may germinate by secondary spores or yeast cells. Ballistoconidia are not known. Haustoria present. Cell walls do not contain fucose. Separation of spindle pole bodies (SPBs) occurs in the cytoplasm, and during metaphase, they are present inside the nucleus. Hyphal septa are so-called 'simple' and are occluded by cystosomes. Nanometer fusionpores occur at the host-parasite contact zone of haustorial apices (Bauer et al. 2006). Mycosporines may be present. Yeast colonies are whitish to pinkish. Budding is usually polar, and filaments or true hyphae may occur (Oberwinkler 2017). Yurkov and collaborators transferred the *Rhodotorula minuta* clade with nine species to *Cystobasidium* and emended the genus (Sampaio and Oberwinkler 2011a; Yurkov et al. 2015).

Plates

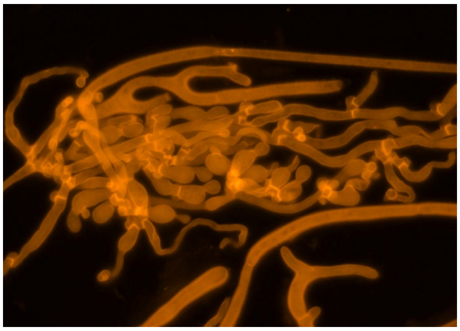


Fig. 17 *Occultifur internus* (NS 20-130B) growing intrahymenially in its host *Dacrymyces* sp. Note the haustorial cells with a widened base, slender middle part, and a globular apex. Also see figures of Sampaio et al. (1999a) and Fig. 8 of Oberwinkler (2017)

Genera included

Family Cystobasidiaceae Gäum. 1926
  Cystobasidium (Lagerh.) Neuhoff 1924
  Halobasidium Z. Guo, Y.R. Wang, Q.C. Hou, W.C. Li, H.J. Zhao, Z.H. Sun & Z.D. Zhang 2019
  Occultifur Oberw. 1990
Cystobasidiales genera *incertae sedis*
  Begerowomyces Q.M. Wang & F.Y. Bai 2020
  Robertozyma Q.M. Wang & F.Y. Bai 2020

Evolution

Cystobasidiales formed a coherent monophyletic clade in a multigene phylogenetic analysis, with two genera, *Cystobasidium* and *Kondoa*. As both dimorphic species and species only known from yeast stages do occur in this group, it may be expected that other sexual stages will be discovered in the future. The filamentous stage of *C. fimetarium* seems closely related to the yeasts *C. minutum* and *C. slooffiae* (Yurkov et al. 2015; Wang et al. 2015a, b). It is likely that the cystosome that occludes the septal pores in hyphae of multiple species is a synapomorphy of the class Cystobasidiomycetes, and hyphal stages of more species should be investigated for the presence of this structure.

Justification of order and problems

Cystobasidiales seems phylogenetically well circumscribed by phylogenetic reconstructions, but the extent of the phenotypic diversity is not fully understood. Several species in the genera *Cystobasidum* and *Occultifur* are known from filamentous stages only, and no living cultures or nucleotide sequence data are available for them. It is likely that various of these species belong to other orders of Basidiomycota, which may challenge circumscriptions of these groups.

Significance

Ecological and economical roles

Cystobasidium fimetarium is a mycoparasite occurring on dung, probably with ascomycetous coprophilous fungi as host. Whether the same lifestyle applies to all yeast morphs remains unknown (Oberwinkler 2017; Yurkov et al. 2015). Yeast morphs are known from diverse habitats such as phylloplane, soil, water, and deep-sea sediments. Some species are psychrophilic. *C. minutum* is occasionally reported as an opportunistic pathogen (Yurkov et al. 2015).

Chemical diversity

Mycosporines may be present, main carotenoid pigments are torulene and torularhodin. Nitrate is not assimilated, starch-like compounds are not produced, and D-glucuronate is utilized. Fermentative abilities are absent. (Yurkov et al. 2015).

Other relevant data and future recommendations

To date, most species of the order have been identified based on the combination of ribosomal ITS and LSU nucleotide sequences. Among these two markers, ITS is usually more variable than LSU. Additionally, partial sequences of the gene encoding translation elongation factor 1 alpha (TEF1) were employed in phylogenetic analyses.

Cystofilobasidiales Fell, Roeijmans & Boekhout 1999

Contributed by: Teun Boekhout, Andrey Yurkov

Introduction

For a long time, phylogenetic relationships among basidiomycetous yeasts were inferred from biochemical, morphological, and physiological data. However, the introduction of molecular phylogenetic studies could identify the relationships between yeasts, including basidiomycetous yeasts, more accurately. Cystofilobasidiales was recognized by D1/D2 LSU rDNA sequence analysis that corroborated earlier Small SubUnit (SSU) rDNA sequence analysis (Fell et al. 1999).

History

Assessing phylogenetic relationships between basidiomycetous yeasts has been notoriously difficult. Early SSU rDNA sequence analysis of Basidiomycota (Swann and Taylor 1993) revealed many clades that were later interpreted as genera, families, and orders. One of these clades, comprising species of the genera *Cystofilobasidium*, *Itersonilia*, *Krasilnikovozyma*, *Phaffia*, *Mrakia*, *Tausonia*, and *Udeniomyces* formed order Cystofilobasidiales (Fell et al. 1999; Liu et al. 2015a, b). Note that some of the species were previously classified in genera such as *Cryptococcus* and *Trichosporon*, genera that are now limited to Tremellales and Trichosporonales, respectively.

Characters that define the taxa in the order

Cystofilobasidiales is mainly characterized by its coherent phylogenetic clustering based on various molecular phylogenetic analyses. The order comprises species without basidiomes, and usually, with a yeast phase, with cell walls that contain xylose and that utilize d-glucuronate, nitrate and nitrite, and often myo-inositol. The Q-enzyme system is Q8 or Q10. Hyphal septa are dolipores, but without a parenthesome (or SPC). Teliospores are usually present in sexual species, that are heterothallic or self-sporulating. Basidia, if present, are holobasidiate (Fell et al. 1999).

Plates

See relevant pictures for genera in The Yeasts, a Taxonomic Study, 5th edition (Kurtzman et al. 2011).

Genera included

Family Cystofilobasidiaceae K. Wells & Bandoni 2001
  Cystofilobasidium Oberw. & Bandoni 1983
Family Mrakiaceae Xin Zhan Liu, F.Y. Bai, M. Groenew. & Boekhout 2015
  Itersonilia Derx 1948
  Krasilnikovozyma Xin Zhan Liu, F.Y. Bai, M. Groenew. & Boekhout 2015
  Mrakia Y. Yamada & Komag. 1987
  =*Mrakiella* Margesin & Fell 2008
  Phaffia M.W. Mill., Yoney. & Soneda 1976
  =*Rhodomyces* Wettst. 1885
  =*Xanthophyllomyces* Golubev 1995
  Tausonia Babeva 1998
  Udeniomyces Nakase & Takem. 1992
  Vustinia Kachalkin, Turchetti & Yurkov 2019

Evolution

Cystofilobasidiales forms the basal lineage in Tremellomycetes and, hence, it is the most basal lineage known of Agaricomycotina. This might imply that several phenotypic features, such as the presence of teliospores and fermentative capabilities of some species, are interesting starting points for comparative studies on evolutionary trends among Agaricomyctina. The mean time of origin of the order is estimated at 350 million years ago (Zhao et al. 2017). Among synapomorphies, remarkable physiological adaptations to cold habitats, psychrophily and psychrotolerance are shared between several genera of the order.

Justification of order and problems

Based on various molecular phylogenetic studies the circumscription of Cystofilobasidiales is well accepted (Swann and Taylor 1993; Fell et al. 1999; Liu et al. 2015a, b).

Significance

Ecological and economical roles

Many species of Cystofilobasidiales are psychrophilic and psychrotolerant, making them a source of low temperature enzymes. Species of the genus *Phaffia* are known to produce astaxanthin, a carotenoid pigment widely used as a colorant in aquaculture, especially of salmons (Schroeder and Johnson 1995; Fell and Johnson 2011; Luna-Flores et al. 2022; Nair et al. 2013). The pigment may also act as an antioxidant (Schroeder and Johnson 1995). Some species of *Cystofilobasidium* produce red carotenoid pigments (including high proportion of beta-carotene) and coenzyme Q10 that are potentially interesting from a biotechnological or health perspective (Herz et al. 2007; Yurkov et al. 2008; Moliné et al. 2009). Species of *Mrakia* are psychrophilic and fermentative; therefore, they can contaminate orange juice during transportation or storage at industrial-scale low temperatures. More recently, species of *Mrakia* got attention in the brewing of low alcohol beers (de Francesco et al. 2018; Linnakoski et al. 2023). *Tausonia pullulans* can produce β-galactosidase useful for the hydrolysis of lactose (Xu et al. 2012). The dimorphic fungus *Itersonilia perplexans* causes flower blight in anemone, dahlia, chrysanthemum, and globe artichoke, and is responsible for substantial post-harvest losses in cut flower production (Begerow et al. 2017).

Chemical diversity

Within the order variation exists in the number of isoprenologues of the co-enzyme Q system, quantities and diversity of carotenoid pigments, and fermentative capabilities.

Other relevant data and future recommendations

To date, most species of the order have been identified based on the combination of ribosomal ITS and LSU nucleotide sequences. However, this approach is not suitable for identification and delimitation of many species in genera *Mrakia* and *Phaffia*, which show high degree of similarity in the two markers (David-Palma et al. 2020; Yurkov et al. 2020). In the absence of other molecular markers, the delimitation of closely-related species and genera in the order requires solid support from a polyphasic approach (Figs. 8, 9, 10, 11, 12, 13, 14, 15, 16, 17).

Dacrymycetales Henn. 1897
=Calocerales Rea 1922
=Metatremellales Lowy 1968
=Unilacrymales Shirouzu, Tokum. & Oberw. 2013

Contributed by: Anton Savchenko

Introduction

Dacrymycetales is an order of basidial fungi inhabiting dead wood and developing predominantly yellow-tinted gelatinous basidiomes. The scope of the order is equal to the scope of its parental class Dacrymycetes, which represents a robustly supported clade and a sister to the Agaricomycetes. The order is comprised of four families: Dacrymycetaceae and Cerinomycetaceae include most taxa, while Unilacrymaceae and Dacryonaemataceae jointly contribute only five species. The families are well distinguished in phylogenetic trees, though morphologically they require combinations of multiple characters for unambiguous identification (Zamora and Ekman 2020; Savchenko et al. 2021). Altogether, 20 genera have been more or less directly linked to Dacrymycetales, of which 13 were used in modern literature (Savchenko 2023). The majority of the genera belong to Dacrymycetaceae, while the remaining three families are monotypic. It is estimated that there are ca. 120 species of Dacrymycetales (Shirouzu et al. 2020), but the actual number is likely to be much higher. All dacrymycete genera are polyphyletic and likely host vast semi-cryptic diversity. Indications for this can be found in the recent accelerated rate of species description and in the fact that at least 475 names at sub-generic ranks are associated with the order, most with never sequenced types (Savchenko 2023).

On a morphological level, Dacrymycetales is clearly identified by the bisterigmate Y-shaped basidia (Fig. 18h lower), with the only exception of *Unilacryma unispora* with unisterigmate basidia (Fig. 18h upper) (Wells 1994). This unique feature and a singular position of *U. unispora* in phylogeny prompted Shirouzu et al. (2013) to raise the family Unilacrymaceae and order Unilacrymales (the latter is not accepted in this treatment). Recently, a bisterigmate relative of *U. unispora* was found, and definition of Unilacrymaceae became more complex (Zamora and Ekman 2020). In the same work a small family Dacryonaemataceae was raised for three species of genus *Dacryonaema*, one of which, *Da. rufum*, develops distinctive synnematous basidiomes. Another family, Cerinomycetaceae, consists of the genus *Cerinomyces* that was historically defined by corticioid basidiomes. It was shown that this character evolved in the class at least three times independently, and the genus in traditional definition appeared to be polyphyletic. *Cerinomyces* was freshly redefined to cover the clade and scope of Cerinomycetaceae, and as a result species with gelatinous basidiomes were introduced to the genus alongside corticioid members (Savchenko et al. 2021). Currently *Cerinomyces* includes 33 formal and informal species. The last family, Dacrymycetaceae, is highly diverse and hosts the majority of dacrymycetes. In this family the largest numbers of species are accumulated in polyphyletic genera *Dacrymyces* (the family type), *Calocera*, *Ditiola*, and *Dacryopinax*.

History

Dacrymycetes were studied from the beginning of systematic mycology and were certainly known long before that. The earliest-described genera still associated with the group are *Dacrymyces* (Nees von Esenbeck 1817), *Ditiola* (Fries 1822; the name was first proposed by Browne 1756), and *Calocera* (Fries 1825). Initially dacrymycetes were treated together with other jelly fungi, often as a part of Tremellales. By the end of the nineteenth century, basidial typology became an essential part of the fungal taxonomy, and since then, dacrymycetes were usually singled out as a separate taxon in the rank of family or order. The family Dacrymycetaceae was proposed for gelatinous taxa by Brefeld (1888). Schröter (1889) is often cited as the name author, but Brefeld's work has precedence by a few months (Stafleu and Cowan 1976, 1985). The order Dacrymycetales was described a few years later, with a circumscription covering both gelatinous and corticioid taxa (Engler and Prantl 1900). In the twentieth century Dacrymycetales was expanded with several genera and one family, Cerinomycetaceae (Jülich 1981). During that time significant contributions to the taxonomy of the group were made by J. Rick, G.W. Martin, Y. Kobayashi, T.W. Brasfield, M.A. Donk, L.L. Kennedy, R.F.R. McNabb, B. Lowy, D.A. Reid, F. Oberwinkler, and others. The highest impact had a series of monographs by McNabb: it still remains to be the most comprehensive reference for many genera (McNabb 1964, 1965a, b, c, d, e, 1966, 1973).

Already the first phylogenetic tree that included Dacrymycetales clearly indicated monophyly of the order (Swann and Taylor 1993). Unity of Dacrymycetaceae and Cerinomycetaceae was first shown by Larsson et al. (2004) and Kirschner and Yang (2005); and lastly the position of Unilacrymaceae was established by Shirouzu et al. (2013). The latest advancements include description of a small family Dacryonaemataceae (Zamora and Ekman 2020), revision of Cerinomycetaceae (Savchenko et al. 2021), and establishment of *Dendrodacrys*, a new genus in Dacrymycetaceae (Zamora et al. 2022; Savchenko et al. 2022). Aside that, several new species and combinations were recently raised in *Calocera* and *Dacrymyces* (Phookamsak et al. 2019; Fan et al. 2021; Lian et al. 2022; Mendes-Alvarenga and Gibertoni 2022).

Characters that define the taxa in the order

Members of Dacrymycetales occur on dead wood and develop either of two principal types of basidiomes: gelatinous (Fig. 18a, c, d) or corticioid (Fig. 18b). The former type dominates in the order, and such basidiomes are known in a large variety of shapes (pustulate, pulvinate, resupinate, capitate, cerebriform, cupulate, spathulate, cylindrical-dendroid, Fig. 18e) and colors (depending on the presence and abundance of carotenoids and other pigments, from almost transparent to yellow, orange, brown, and black). Corticioid basidiomes are rarer and vary from almost arid and light-colored (*Cerinomyces*, Fig. 18b) to waxy gelatinous and yellow or orange (two clades in Dacrymycetaceae).

On the microscopical level the structure of basidiomes is relatively simple and almost universally includes two areas: internal and hymenial. Internal area, depending on the complexity and size of basidiome, can be either undifferentiated (*Dacrymyces, Cerinomyces*) or divided into zones. Most notably, cylindrical stems of *Calocera*, *Dacryopinax*, *Guepiniopsis* and several other taxa display densely packed thin cortex, wide sub-surficial zone of loosely interwoven hyphae, and tight internal core of concentrated parallel wide hyphae of presumably mechanical function. Conversely, some of the thinnest corticioid species can lack internal area almost completely. Regardless of overall basidiome complexity, sterile and marginal areas of many species are covered with a palisade layer of terminal hyphae, often with thickened walls. Hymenium is usually amphigenous and mainly composed of the almost cylindrical Y-shaped basidia with stout subcylindrical sterigmata (Fig. 18h) and, in certain species, includes diagnostic hyphidia (Fig. 18i). Basidiospores are important for identification and vary in shapes (from ovoid and ellipsoid to cylindrical, from slightly to strongly curved), septation (the most frequent septa numbers are 0, 1, 3, 7, > 7), and wall thickness (Fig. 18g). Basidiospores germinate by hyphae or microconidia, but never by repetition (Wells and Bandoni 2001). Hyphal septa can be either with or without clamp connection (Fig. 18f); in the species of Unilacryma a mix of these two types can be observed. On the ultrastructural level, Dacrymycetales share the composition of the septal pore apparatus with some groups of Agaricomycetes (mostly with "heterobasidial" fungi). Specifically, they are characterized by dolipores surrounded by parenthesomes without perforations (McLaughlin and Spatafora 2014).

Plates

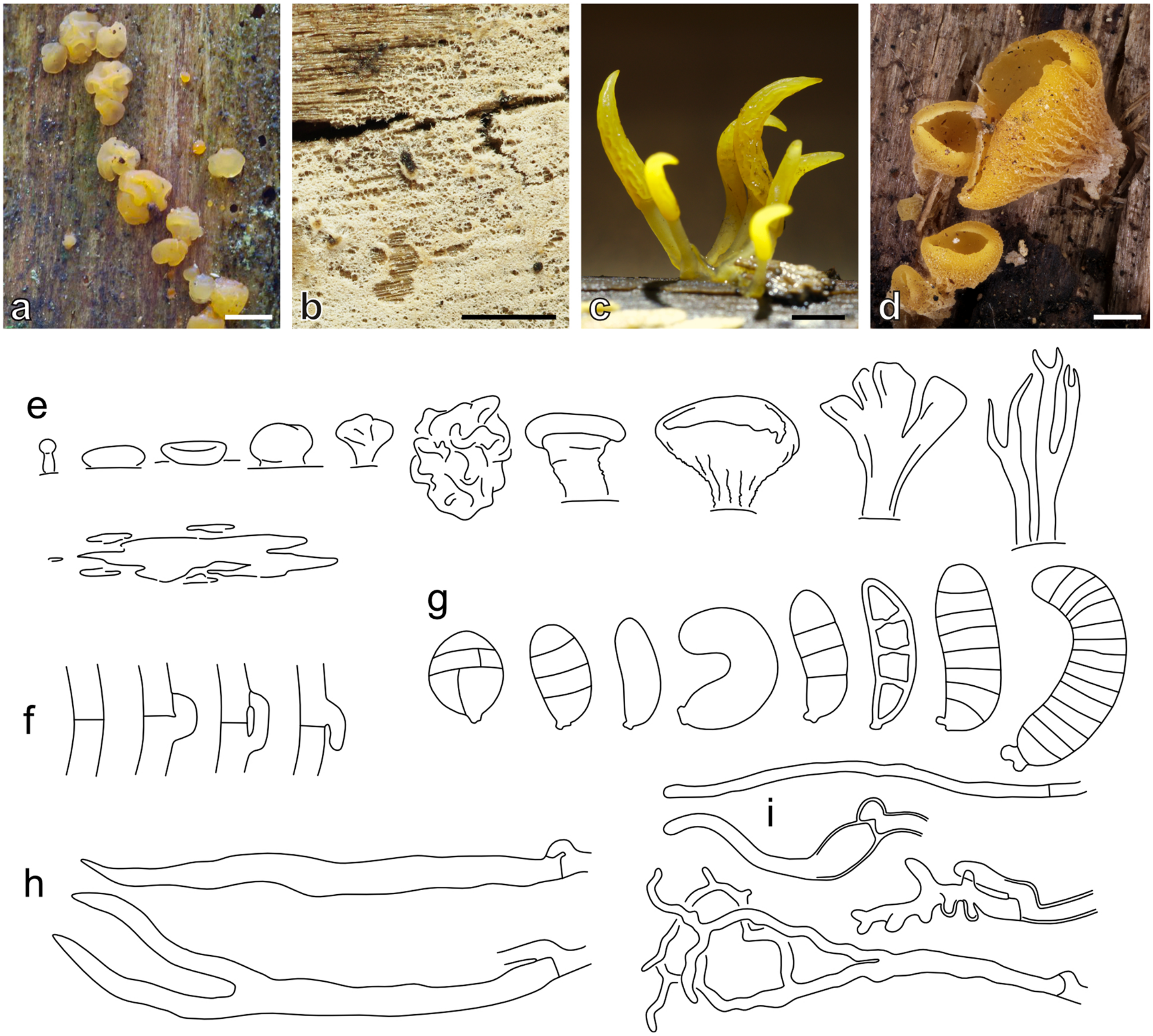


Fig. 18 Example members of Dacrymycetales and morphological characters commonly used in identification, modified after Savchenko (2023). **a** *Dacrymyces* sp. (TUF135036, Estonia); **b** *Cerinomyces borealis* (GB-0071203, Sweden); **c** *Calocera cornea* (TUF135043, Estonia); **d** *Guepiniopsis buccina* [CWU(MYC)7014, Ukraine]; **e** basidiome types, above: synnematous, pustulate, pustulate and centrally depressed, pulvinate, capitate with simple stem, cerebriform, capitate with distinguished stem, cupulate, spathulate, cylindrical-dendroid; below: resupinate or corticioid; **f** hyphal septa: simple, clamped, with medallion-shaped clamp, with unfinished clamp; **g** basidiospores: ovoid (muriform septation), ellipsoid (only transverse septation), cylindrical (from aseptate to > 7 transverse septa, slightly or strongly bent, thin- or thick-walled); **h** basidia: uni- and bisterigmate; **i** hyphidia: simple, simple with thickened base, weakly branched, strongly branched. Scale bars = 1 mm

Genera included

Family Cerinomycetaceae Jülich 1981
    Cerinomyces G.W. Martin 1949
Family Dacryonaemataceae J.C. Zamora & S. Ekman 2020
    Dacryonaema Nannf. 1947
Family Dacrymycetaceae Bref. 1888
    = Caloceraceae Pat. 1900
    Calocera (Fr.) Fr. 1828
    = *Calopposis* Lloyd 1925
    = *Corynoides* Gray 1821
    Dacrymyces Nees 1816
    = *Hydromycus* Raf. 1808
    = *Septocolla* Bonord. 1851
    Dacryomycetopsis Rick 1958
    Dacryomitra Tul. & C. Tul. 1872

Dacryopinax G.W. Martin 1948
Dacryoscyphus R. Kirschner & Zhu L. Yang 2005
Dendrodacrys J.C. Zamora, A. Savchenko, Á. Gonz.-Cruz, Prieto-García, Olariaga & Ekman 2022
Ditiola Fr. 1822
= *Dacryopsis* Massee 1891
Femsjonia Fr. 1849
= *Arrhytidia* Berk. & M.A. Curtis 1849
= *Cerinosterus* R.T. Moore 1987
Guepiniopsis Pat. 1883
Heterotextus Lloyd 1922
Family Unilacrymaceae Shirouzu, Tokum. & Oberw. 2013
Unilacryma Shirouzu, Tokum. & Oberw. 2013

Evolution

In the current work, the stem age of this group is estimated to be 346 million years, which generally agrees with previous studies (Floudas et al. 2012; Zhao et al. 2017; Varga et al. 2019; Zamora and Ekman 2020). According to Zamora and Ekman (2020), the ancestor of Dacrymycetales had bisterigmate basidia, hyphae with simple clamp connections at most septa, lack of carotenoids, conspicuous cytoplasmic lipid contents, and uninucleate young basidiospores. During evolution, complete loss of clamp connections occurred only in a few groups in Dacrymycetaceae, and reversions were uncommon. Another important trait, the presence of carotenoids, was acquired only once by the common ancestor of Dacrymycetales and then lost several times, in groups such as Unilacrymaceae, Dacryonaemataceae, and Cerinomycetaceae. The latter family is also marked with a unique change from one to two nuclei in young basidiospores.

Justification of order and problems

Circumscription of Dacrymycetales that covers all four families is deemed to be the most practical. An alternative approach—accepting Unilacrymales as a standalone order—raises a question of how to address the family Dacryonaemataceae. Two options were suggested: it can be assigned to a separate order, which action may even justify further division of Dacrymycetales into at least two orders (one for Dacrymycetaceae and another for Cerinomycetaceae), or it can be included in Unilacrymales, which will draw the latter hardly diagnosable. Therefore this treatment follows Zamora and Ekman (2020) and keeps Unilacrymales as a part of Dacrymycetales. Meanwhile, the most difficult challenges in taxonomy of Dacrymycetales are related to refinement of generic boundaries in Dacrymycetaceae and revision of old species names. Establishment of their identity and resolution of synonymy will facilitate species description without risk of creating superfluous names.

Significance

Ecological and economical roles

Dacrymycetales occurs worldwide in forested areas and develop basidiomes either directly on dead wood or, in rare cases, on the ground but connected to buried wood remnants (e.g., *Calocera viscosa*). The group members are known to cause a brown type of wood rot, which was confirmed in genomic studies (Floudas et al. 2012; Nagy et al. 2016). Dacrymycetales commonly occurs on man-made wooden structures, potentially causing damage to industrial and historical sites (Held et al. 2020; Flyen and Thuestad 2023).

Doassansiales R. Bauer & Oberw. 1997

Contributed by: Teodor T. Denchev, Cvetomir M. Denchev, Dominik Begerow, Martin Kemler

Introduction

Doassansiales was erected to accommodate an ecologically well-characterized group of smut fungi, which infect various aquatic or paludal plants (or at least plants growing in moist habitats). This group is united by a suite of morphological, ultrastructural, and molecular characteristics (Bauer et al. 1997; Begerow et al. 2014). The type genus, *Doassansia*, was introduced by Cornu (1883).

This group includes mainly sporeball-forming genera. Members of *Burrillia*, *Doassansia*, *Entylomaster*, *Heterodoassansia*, *Nannfeldtiomyces*, *Narasimhania*, *Pseudodermatosorus*, *Pseudodoassansia*, *Pseudotracya*, and *Tracya* produce scattered or gregarious, many-spored spore balls, embedded in the host tissue, and appearing on the surface of the infected organs (leaves and petioles, sometimes stems) as numerous, raised, minute, dark dots. Spore balls are rather permanent (with exception of *Nannfeldtiomyces*), composed of spores, sterile cells, and/or modified mycelial filaments, in different arrangements and proportions. Spore balls have an outer layer (cortex) of firmly adherent sterile cells (except *Burrillia* and *Nannfeldtiomyces*) or spores (*Tracya*). Spores are hyaline or poorly pigmented. Genera differ in the spore ball components and their arrangement (Vánky 1981, 2011, 2013). Spore germination, where it is known, is after *Tilletia*-type (Vánky 2013). This group of species is monographically studied by Setchell (1892) and Vánky (1981, 2011).

Molecular studies of another smut fungus on aquatic or paludal plants, *Entyloma callitriches* Liro on *Callitriche* spp., demonstrated that it should be assigned to the Doassansiaceae, although this fungus possesses single spores and other characteristics similar to that of typical species of *Entyloma* (Bauer et al. 1997; Vánky et al. 1998). As this species is not sporeball-forming, a new genus, *Doassinga*, was introduced for its accommodation (Vánky et al. 1998).

Molecular analyses of another former member of *Entyloma* on aquatic plants, *Entyloma nymphaeae* (D.D. Cunn.) Setch. (currently as *Rhamphospora nymphaeae* D.D. Cunn.), also resulted in an assignment of this species to the Doassansiales (Bauer et al. 1997; Vánky et al. 1998). Like '*Entyloma*' *callitriches*, *Rhamphospora nymphaeae* forms single, hyaline spores in the leaves of its hosts, but *Doassinga callitrichis* grows only intercellularly, whereas *R. nymphaeae* forms haustoria. For accommodation of the latter species, a new family, Rhamphosporaceae, was proposed in the Doassansiales (Bauer et al. 1997; Vánky et al. 1998; Begerow et al. 2014).

On the basis of morphological, ultrastructural, and molecular characteristics, two smut fungi on *Selaginella*, *Melanotaenium oreophilum* Syd. and *M. selaginellae* Henn. & E. Nyman, were considered as members of a new genus, *Melaniella*, and family, Melaniellaceae, in the Doassansiales (Bauer et al. 1999a). These species have intercellular hyphae, single and pigmented spores, and spore germination of *Exobasidium*-type, i.e. holobasidia with ballistosporic basidiospores (Bauer et al. 1999a).

Currently, three families, 13 genera, and 40 species are included in this order.

Characters that define the taxa in the order

Doassansiales is plant parasites that sporulate in vegetative parts of the hosts, predominantly on leaves or petioles. Host spectrum of Doassansiales is quite diverse: lycopods (Selaginella), monocots, and eudicots. Doassansiales is divided into three families: Melaniellaceae, Doassansiaceae, and Rhamphosporaceae.

Melaniellaceae species differ from the members of Doassansiaceae by having single and pigmented spores, and spore germination of *Exobasidium*-type, i.e. holobasidia with ballistosporic basidiospores. This family includes a single genus, *Melaniella*, which consists of two species on *Selaginella* (Lycopodiopsida). Yeast or yeast-like states are unknown.

Doassansiaceae includes sporeball-forming genera (except *Doassinga*). Spores are hyaline or poorly pigmented. Teliospores germinate with holobasidia, often with sigmoid basidiospores. Species have intercellular hyphae that form local interaction zones with complex interaction apparatus containing cytoplasmic compartments; haustoria absent. Septal pore is simple with two membrane caps, without inner plates (Bauer et al. 1997; Vánky 2013; Begerow and McTaggart 2018). Hosts are members of monocots—Alismataceae (incl. Limnocharitaceae), Araceae (incl. Lemnaceae), Butomaceae, Hydrocharitaceae, Pontederiaceae, and Typhaceae (incl. Sparganiaceae); basal eudicots (Ranunculaceae); rosids (Lythraceae and Onagraceae); and asterids—Acanthaceae, Primulaceae, Campanulaceae, Menyanthaceae, Plantaginaceae (incl. Callitrichaceae), and Scrophulariaceae. Yeast or yeast-like states are unknown (a note on *Savulescuella* is provided below).

Rhamphospora nymphaeae, the only species in the Rhamphosporaceae, has single and hyaline spores, with an apical papilla (0.5–2 µm high) formed by locally swollen exosporium, and a basal appendage from a remnant of the sporogenous hypha. *Rhamphospora nymphaeae* is characterized by the presence of haustoria. Teliospores germinate with holobasidia; basidiospores are filiform. On the basidiospores secondary sporidia are produced on short pedicels, perpendicular to the long axis of the basidiospores. Secondary sporidia may produce tertiary sporidia, or secondary sporidia conjugate in pairs by a conjugation bridge (Bauer et al. 1997; Vánky 2013; Begerow and McTaggart 2018). *Rhamphospora nymphaeae* parasitizes members of basal angiosperms (Nymphaeaceae). A yeast-like state is unknown.

Plates

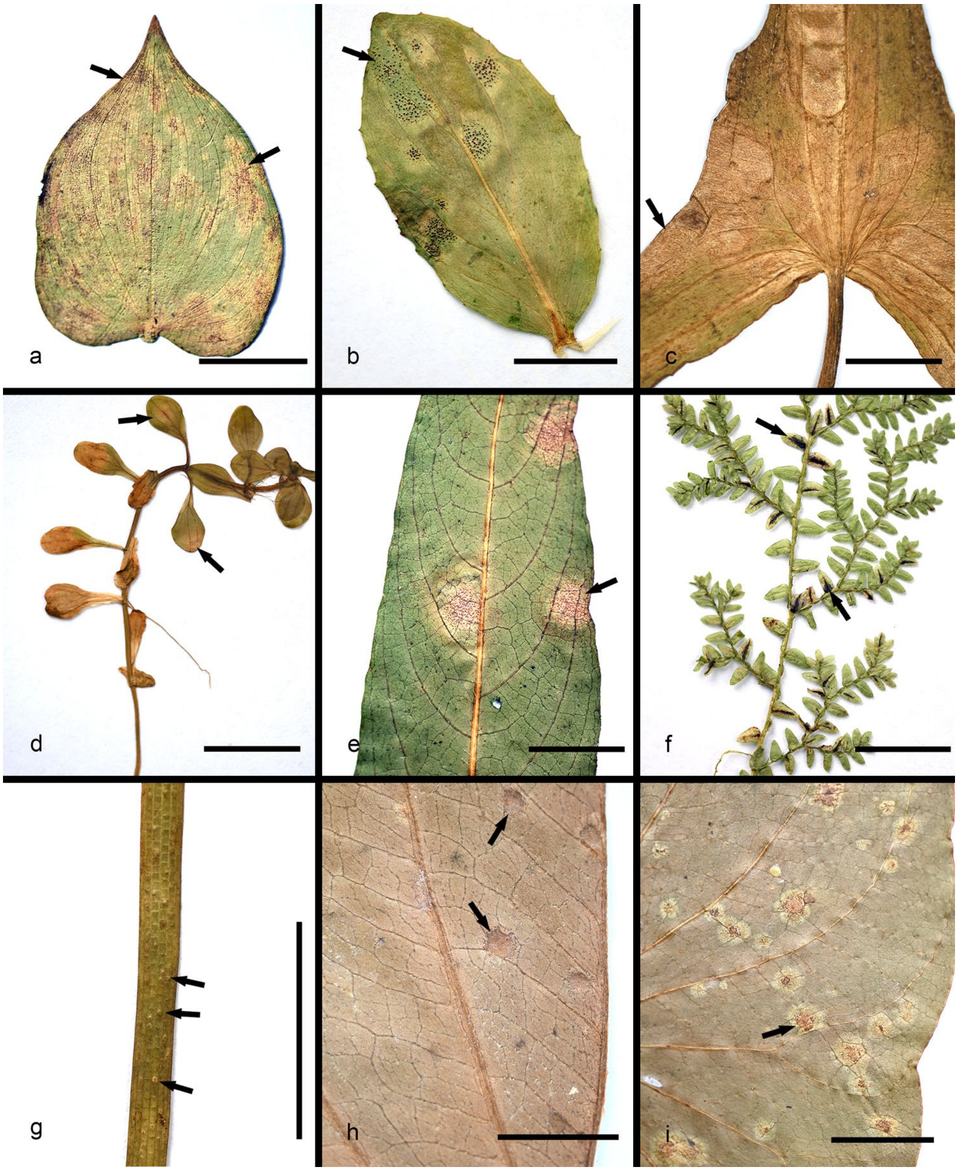


Fig. 19 Doassansiales. **a**–**i** habit. **a** *Burrillia ajrekarii* on *Pontederia vaginalis,* China (Vánky Ustil. Exs. 504); **b** *Doassansia epilobii* on *Epilobium alpestre,* Germany (Vánky Ustil. Exs. 666); **c** *Doassansia sagittariae* on *Sagittaria sagittifolia,* Romania (Vánky Ustil. Exs. 74); **d** *Doassinga callitrichis* on *Callitriche stagnalis,* Germany (Vánky Ustil. Exs. 560); **e** *Heterodoassansia hygrophilae* on *Hygrophila auriculata,* India (Vánky Ustil. Exs. 815); **f** *Melaniella oreophila* on *Selaginella goudotiana* var. *abyssinica,* Zimbabwe (Vánky Ustil. Exs. 1060); **g** *Nannfeldtiomyces anomalus* on *Sparganium natans,* Sweden (Vánky Ustil. Exs. 349); **h** *Pseudodermatosorus alismatis-oligococci* on *Albidella oligococca,* Sri Lanka (Vánky Ustil. Exs. 176); **i** *Pseudodermatosorus alismatis-oligococci* on *Limnophyton obtusifolium,* Zimbabwe (Vánky Ustil. Exs. 1061). Arrows in **a**–**i** indicate sori. Scale bars: a–i = 1 cm

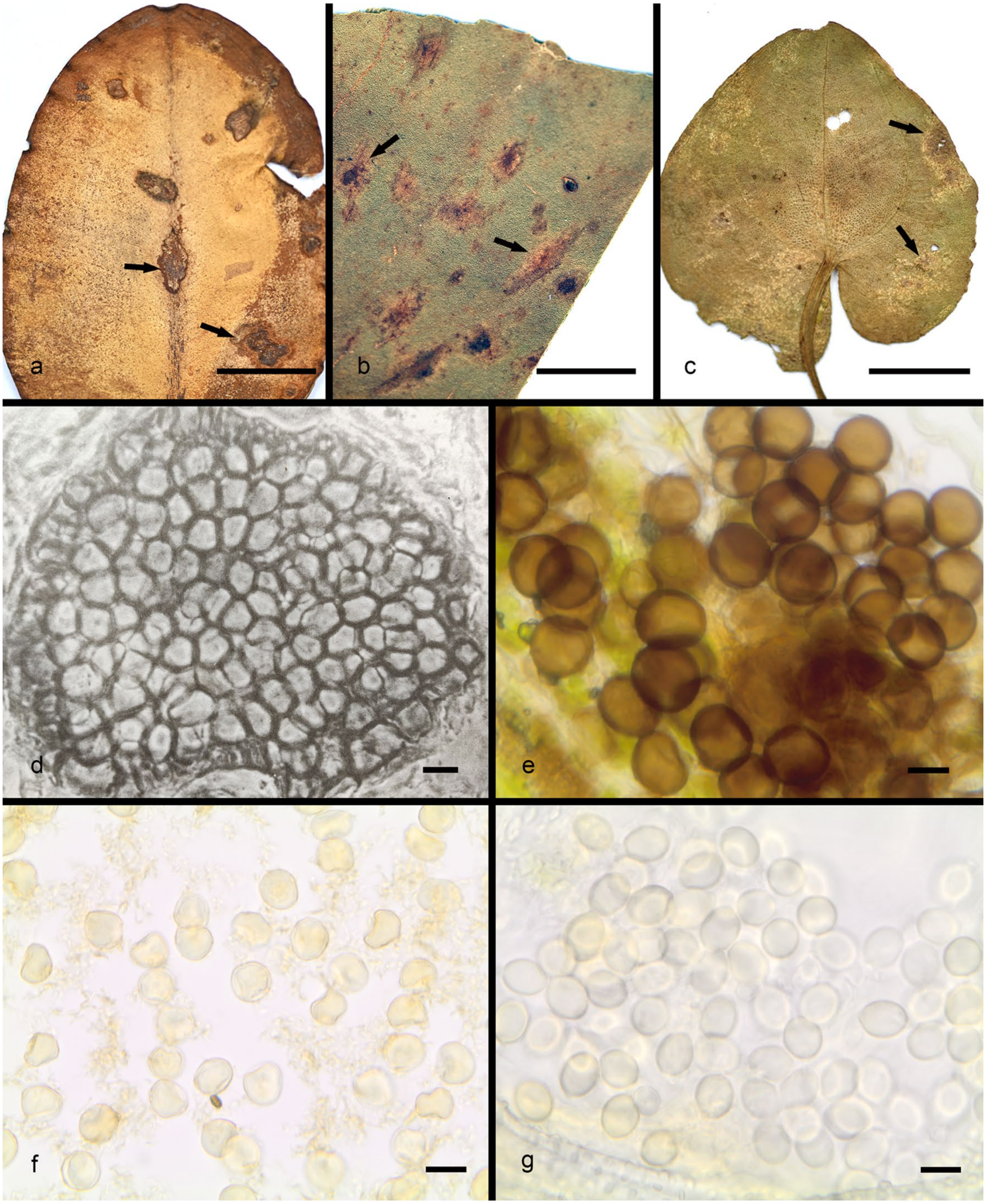


Fig. 20 Doassansiales. **a**–**c** habit. **a** *Pseudodoassansia hydrocleydis* on *Hydrocleys nymphoides,* Argentina (Vánky Ustil. Exs. 1079); **b** *Rhamphospora nymphaeae* on *Nymphaea alba,* Germany (Vánky Ustil. Exs. 519); **c** *Tracya hydrocharidis* on *Hydrocharis morsus-ranae,* Sweden (Vánky Ustil. Exs. 360); **d** spore ball of *Heterodoassansia punctiformis* on *Lythrum volgense,* Bulgaria (holotype of *Doassansia peplidis*, BPI; after Denchev 2001); **e** spores of *Melaniella oreophila* on *Selaginella goudotiana* var. *abyssinica,* Zimbabwe (Vánky Ustil. Exs. 1060); **f** spore ball of *Nannfeldtiomyces anomalus* on *Sparganium natans,* Sweden (Vánky Ustil. Exs. 349); **g** spores of *Rhamphospora nymphaeae* on *Nymphaea alba,* Germany (Vánky Ustil. Exs. 519). Arrows in **a**–**c** indicate sori. Scale bars: a–c = 1 cm; d–g = 10 µm

Genera included

Family Doassansiaceae R.T. Moore ex P.M. Kirk, P.F. Cannon & J.C. David 2001
  Burrillia Setch. 1891
  = *Stereosorus* Sawada 1943 (nom. inval., Art. 39.1)
  Doassansia Cornu 1883
  = *Setchellia* Magnus 1896
  = *Savulescuella* Cif. 1959
  Doassinga Vánky, R. Bauer & Begerow 1998
  Entylomaster Vánky & R.G. Shivas 2006
  Heterodoassansia Vánky 1993
  Nannfeldtiomyces Vánky 1981
  Narasimhania Thirum. & Pavgi 1952
  Pseudodermatosorus Vánky 1999
  Pseudodoassansia (Setch.) Vánky 1981
  Pseudotracya Vánky 1999
  Tracya Syd. & P. Syd. 1901
  = *Cornuella* Setch. 1891 (nom. illeg., Art. 53.1)
  = *Tracyella* Zambett. 1970 (nom. inval., Art. 39.1)
Family Melaniellaceae R. Bauer, Vánky, Begerow & Oberw. 1999
  Melaniella R. Bauer, Vánky, Begerow & Oberw. 1999
Family Rhamphosporaceae R. Bauer & Oberw. 1997
  Rhamphospora D.D. Cunn. 1888

Evolution

Doassansiales is among the orders of smut fungi that is morphologically and ultrastructurally well characterized and the molecular phylogeny is highly congruent with these data (Begerow et al. 2004). Members of this order are ecologically well characterized by their occurrence on paludal or aquatic plants, or at least on plants of moist habitats, and infect hosts in various plant families. They apparently evolved in the ecological niche of aquatic plants, developing complex spore balls (with numerous spores and sterile cells) that remain embedded in the host tissue until its decay. More or less sigmoid basidiospores are an adaptation to water dispersal (Begerow et al. 2014).

Justification of order and problems

Savulescuella, typified by *S. alismacearum* (Sacc.) Cif., was proposed by Ciferri (1959) for accommodation of the anamorphic species in the Doassansiaceae. *Savulescuella* consists of three species, including *S. aquatilis* (Peck) Cif. and *S. hydrocharidis* Cif.

Savulescuella alismacearum was originally described as *Cylindrosporium alismacearum* Sacc. on *Alisma plantago-aquatica* L. (Saccardo 1880b). Vánky (2011) assumed that this asexual morph is just "basidiospores of spores that germinated in situ". Currently, *S. alismacearum* is considered a synonym of *Doassansia alismatis* (Nees ex Fr.) Cornu.

Savulescuella hydrocharidis was described for the conidial stage of *Tracya hydrocharidis* Lagerh. (Ciferri 1959). Later, it was transferred by Zambettakis (1970) to a new genus, *Tracyella*. It is an invalidly published anamorphic generic name (without a description or diagnosis in Latin, Art. 39.1 Shenzhen Code) making the combination *Tracyella hydrocharidis* (Cif.) Zambett. also invalid (Art. 35.1). According to Vánky (2011), this anamorphic name "probably refers to basidiospores of in situ germinated spores".

The third species, *S. aquatilis*, was introduced for the conidial stage of *Doassansia occulta* (H. Hoffm.) Cornu (q.e. *Doassansiopsis occulta* (H. Hoffm.) Dietel) (Ciferri 1959) but the cited basionym was *Ramularia aquatilis* Peck, q.e. *Doassansiopsis hydrophila* (A. Dietr.) Lavrov. Thus, *S. aquatilis* is currently reduced to a synonym of *Doassansiopsis hydrophila* (Vánky 2011).

Economic importance

Rhamphospora nymphaeae, affecting cultivated *Nymphaea* species, causes yellowish-brown spots on the leaves that turn reddish-brown with age, eventually developing into necrotic lesions. This affects the quality of these ornamental plants.

Entylomatales R. Bauer & Oberw. 1997

Contributed by: Teodor T. Denchev, Cvetomir M. Denchev, Dominik Begerow, Martin Kemler

Introduction

Entylomatales consists of a single family, Entylomataceae, which was erected to accommodate the species of *Entyloma*. The type genus, *Entyloma*, was introduced by de Bary (1874) who characterized this genus by the formation of teliospores, their germination with *Tilletia*-like basidia, and the presence of characteristic white leaf spots.

Members of *Entyloma* are parasites on plants from many different lineages of eudicots. They develop sori in the vegetative organs of their hosts, mostly in leaves and petioles, rarely in stems or roots, usually forming few to numerous spots, sometimes swellings or galls formed by hypertrophic growth of host tissue. Spores are permanently embedded in the host tissue, singly or in irregular groups, hyaline, yellow or yellowish brown, and usually with a smooth, two-layered wall; very rarely the outer layer is tuberculate (e.g., *E. verruculosum* A.A. Fisch. Waldh.) or torn apart into prismatic, pyramidal or coarse and irregular pieces (e.g., *E. urocystoides* Bubák) (Vánky 2011, 2013; Denchev et al. 2021). In the case of *E. eranthidis* T. Denchev et al., the spore wall is initially smooth, at maturity cracking and rupturing irregularly, some ruptures reaching inner layer (Denchev et al. 2021). Spores are often with a hyaline gelatinous sheath. Spore germination is of *Tilletia*-type (Vánky 2013).

In the past, *Entyloma* was an extremely heterogeneous genus from which numerous species were excluded. Some species were transferred to the Peronosporales, Protomycetales, Chytridiales, Pucciniales or other taxonomic groups (see Vánky 1994). For species on Poaceae resembling *Entyloma* but with spore germination of *Ustilago*-type, Savile erected a new genus, *Ustilentyloma* (Savile & Parmelee 1964). *Entyloma sparganii* (Lagerh.) Cif. on *Sparganium* (Sparganiaceae, now reduced to Typhaceae), and *E. vignae* Bat. et al. on *Vigna* (Fabaceae) were transferred to *Nannfeldtiomyces* and *Erratomyces*, respectively (Vánky 1981; Piepenbring and Bauer 1997). For *Entyloma callitriches* Liro on *Callitriche* (Callitrichaceae, now reduced to Plantaginaceae), a new genus, *Doassinga*, was introduced (Vánky et al. 1998). The dark-spored '*Entyloma*' species were separated into new genera: *Eballistra*, *Jamesdicksonia*, *Phragmotaenium* (Bauer et al. 2001b), and *Melanustilospora* (Denchev 2003). Currently, *Entyloma* continues to be a large genus, with 189 recognized species (Denchev et al. 2021; He et al. 2022).

In the Entylomataceae, there is a second genus, *Tilletiopsis*, that consists of five anamorphic yeast species, often isolated from leaves, fruits, and other plant surfaces, sometimes associated with sori of plant parasites of different lineages, such as rusts, powdery or downy mildews (Begerow and McTaggart 2018; Li et al. 2022c). This generic name was first introduced by Derx (1930).

Characters that define the taxa in the order

Entyloma are plant parasites that sporulate in vegetative parts of the hosts, predominantly in leaves or petioles. The host spectrum of *Entyloma* is quite diverse and includes host plants belonging to 27 families of eudicots (mainly from Apiaceae, Asteraceae, and Ranunculaceae). Spores are permanently embedded in the host tissue, singly or in irregular groups, hyaline or poorly pigmented. Teliospores germinate with holobasidia. Species have intercellular hyphae that form local host-parasite interaction zones with simple interaction apparatus; haustoria absent; teliospores and interaction apparatus are with homogeneous contents; septal pore is simple with two membrane caps (Bauer et al. 1997; Begerow et al. 2014; Begerow and McTaggart 2018). The anamorphic stage, *Entylomella*, is often present on leaf surface as white, punctate elevations or whitish tufts within the spots (Ciferri 1959; Vánky 2011). Anamorph is mostly associated with the teleomorphic state and in the cases when an anamorph is known, both states usually occur together on the leaves (Braun 1995).

Members of *Tilletiopsis* are saprotrophic yeast-like fungi. Their yeast cells are ballistosporic, with colonies that are cream-colored, pinkish-cream, yellow–brown, or brown, tough or brittle to soft; hyphae are septate, hyaline, monokaryotic, regularly branched with retraction septae; chlamydospores and ballistoconidia may be present; Diazonium blue B and urease reactions positive, major ubichinon is CoQ-1 (Boekhout 1991a, 2011; Begerow and McTaggart 2018). Sexual reproduction is unknown.

Plates

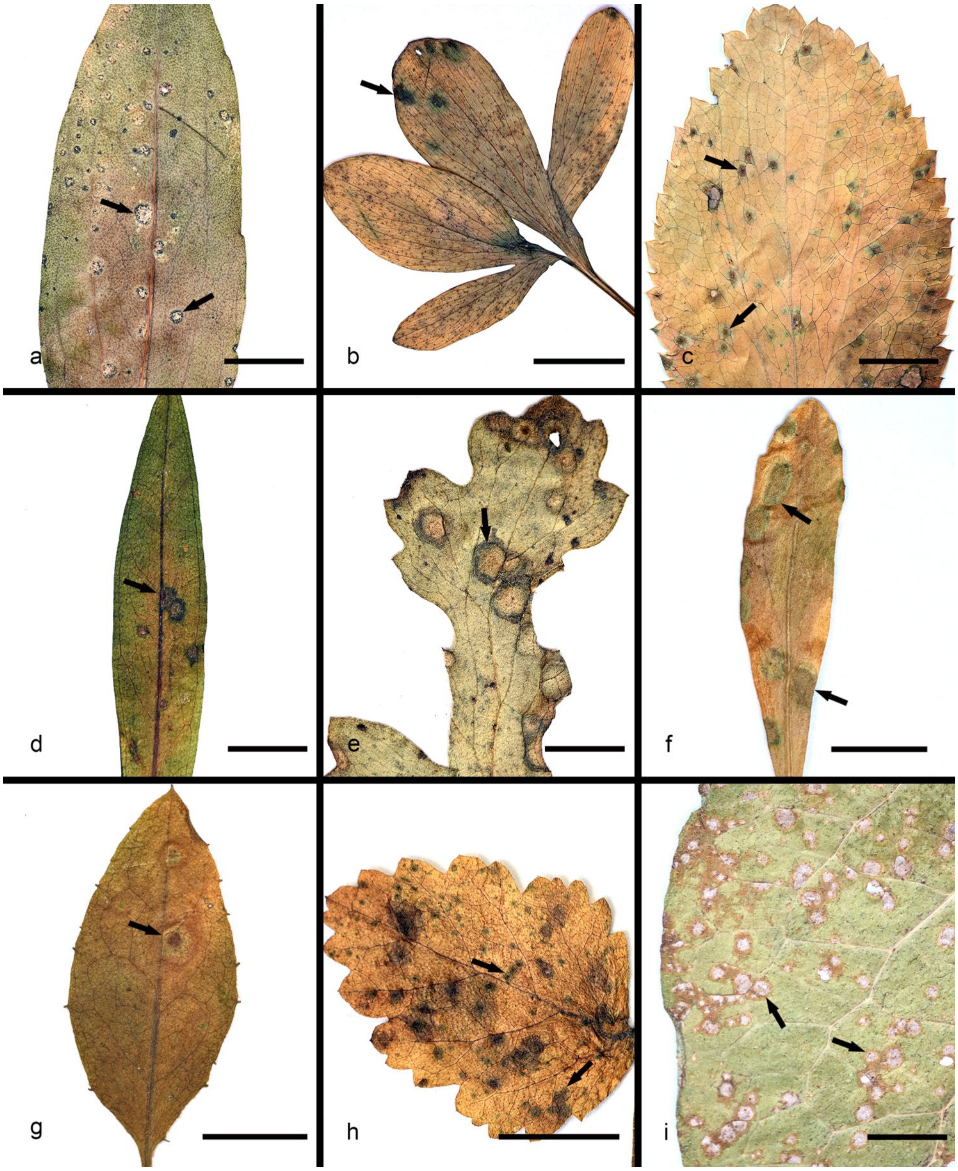


Fig. 21 Entylomatales. **a**–**i** habit. **a** *Entyloma arnicale* on *Arnica montana,* Switzerland (Vánky Ustil. Exs. 392); **b** *Entyloma corydalis* on *Corydalis solida,* Germany (Vánky Ustil. Exs. 670); **c** *Entyloma eryngii-plani* on *Eryngium planum,* Romania (Vánky Ustil. Exs. 507); **d** *Entyloma fergussonii* on *Myosotis scorpioides,* Romania (Vánky Ustil. Exs. 275); **e** *Entyloma fuscum* on *Glaucium flavum,* Greece (Vánky Ustil. Exs. 278); **f** *Entyloma gaillardianum* on *Gaillardia pulchella,* Hungary (Vánky Ustil. Exs. 397); **g** *Entyloma hieracii* on *Hieracium transsilvanicum,* Romania (Vánky Ustil. Exs. 73); **h** *Entyloma magocsyanum* on *Tordylium maximum,* Romania (Vánky Ustil. Exs. 83); **i** *Entyloma serotinum* on *Symphytum officinale,* Romania (Vánky Ustil. Exs. 2). Arrows in **a**–**i** indicate sori. Scale bars: a–i = 1 cm

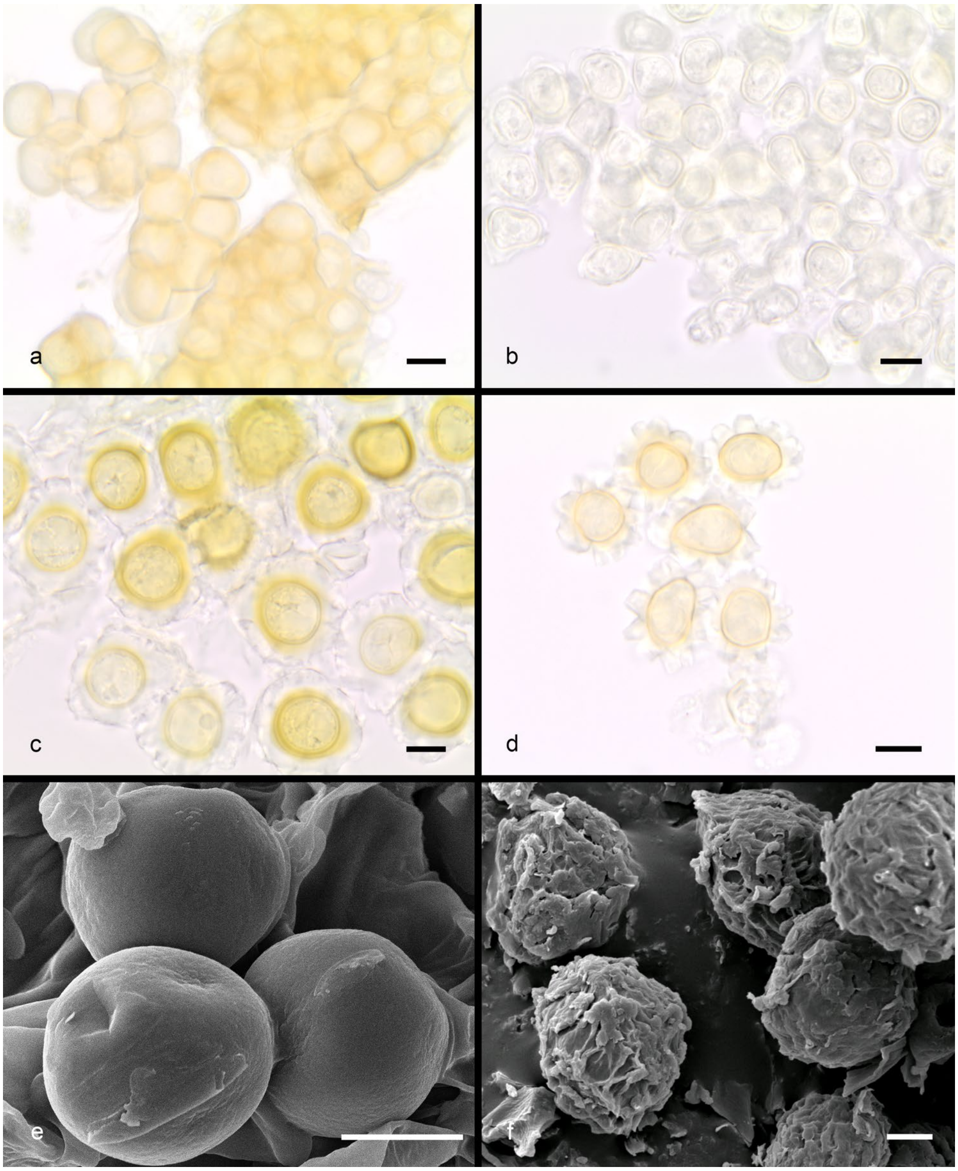


Fig. 22 Entylomatales. **a**–**d** spores in LM. **a** *Entyloma fuscum* on *Glaucium flavum,* Greece (Vánky Ustil. Exs. 278). **b** *Entyloma microsporum* on *Ranunculus repens,* Romania (Vánky Ustil. Exs. 63). **c** *Entyloma eranthidis* on *Eranthis longistipitata,* Uzbekistan (TUR 109345, holotype). **d** *Entyloma urocystoides* on *Corydalis cava,* Bulgaria (SOMF 15191). **e**, **f** spores in LM. **e** *Entyloma gaillardianum* on *Gaillardia* sp., Bulgaria (SOMF s.n.). **f** *Entyloma eranthidis* on *Eranthis longistipitata*, Uzbekistan (TUR 109345, holotype). Scale bars: a–d = 10 µm, e, f = 5 µm

Genera included

Family Entylomataceae R. Bauer & Oberw. 1997
Entyloma de Bary 1874
= *Entylomella* Höhn. 1924
Tilletiopsis Derx 1948

Evolution

Importance of host specificity in delimiting species within *Entyloma* has varied significantly during the last eight decades (Denchev et al. 2021). Savile (1947) applied a morphological species concept, based on spore sizes and asexual morph. He synonymized species with similar morphology, parasitizing host species on different genera from the same family. As a result of this broad species concept, Savile accepted only eight species of *Entyloma* on North American asteraceous hosts. Other authors (e.g. Liro 1938; Lindeberg 1959; Vánky 2011) applied narrower species concepts, considering *Entyloma* species as infecting one or more hosts from the same host genus or occasionally a few closely related host genera (Denchev et al. 2021). During the last two decades with the application of molecular methods, it became evident that members of *Entyloma* exhibit a far higher host specificity, parasitizing a single or only a few closely related host species (Begerow et al. 2002b; Savchenko et al. 2016; Kruse et al. 2018). It also became evident that much higher diversity than currently recognized in *Entyloma* should be expected (Kruse et al. 2018).

Most basal species of *Entyloma* parasitize hosts in the Ranunculales. The remarkable diversity of other host plant families was explained by jumps from ranunculaceous hosts to the distantly related Asteraceae and subsequent jumps from Asteraceae to distantly related hosts in the Apiaceae, Boraginaceae, Scrophulariaceae, Solanaceae, etc. (Begerow et al. 2004).

Justification of order and problems

Entylomella was first introduced by Höhnel (1916). There are differing opinions as to whether this is a validly published name. Although a description of a genus is lacking, there is information that the proposed genus *Entylomella* is separated from *Cylindrosporium* (as '*Cylindrosporium* Sacc. (non Grev.) pro parte') in order to accommodate the conidial forms of *Entyloma*, and Braun (1995) considered this sufficient for a valid publication. Later, this generic name was introduced again with morphological differences and discussion (Höhnel 1924). Type species is *Entylomella ranunculi* (Bonord.) Höhn. (q.e. *Entyloma ficariae* A.A. Fisch. Waldh.). Thus, this generic name is validly published but it is reduced to a synonym of *Entyloma*.

Tilletiopsis was first mentioned by Derx (1930) and chosen to reflect the morphological resemblance of his isolates to species of *Tilletia* (Richter et al. 2019). This name was validly published in 1948, but without designation of a type species (Derx 1948). Since the strain on which this generic name is based was not preserved, a morphologically similar strain was selected by Nyland (1950) to serve as a neotype of the type species of *Tilletiopsis*, which he named *T. washingtonensis* Nyland. Concept of *Tilletiopsis* was originally based on morphological characteristics but was changed and expanded along with the growing number of species discovered (Richter et al. 2019). Currently, the number is reduced to five species (He et al. 2022). For this lineage of anamorphic yeast species, it is still unclear whether they have an unknown plant parasitic teleomorph (Begerow and McTaggart 2018).

Economic importance

Entyloma species on cultivated ornamental plants (e.g., *E. calendulae* (Oudem.) de Bary on *Calendula*, *E. dahliae* Syd. & P. Syd. on *Dahlia*, *E. gaillardianum* Vánky on *Gaillardia*) causes yellowish green to brownish green spots on the leaves that become brown to dark brown with age, affecting the aesthetic value of these plants. Some species have been researched for their potential in biological control of weeds.

Tilletiopsis washingtonensis is involved in a postharvest disorder on apples, called white haze, that is caused by extensive mycelial growth over the surface of apple fruit, occurring most prominently in the apple harvest season during humid and colder periods and under low oxygen storage (Boekhout et al. 2006; Baric et al. 2010).

Erythrobasidiales R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw. 2006

= Cyphobasidiales T. Sprib. & H. Mayrhofer 2016

Contributed by: Teun Boekhout, Nathan Schoutteten, Andrey Yurkov

Introduction

Polyphyletic nature of the red yeast genus *Rhodotorula* became apparent soon after the introduction of molecular barcodes and the first phylogenetic studies (Fell 1995; Fell et al. 2000). As a result, Erythrobasidiales was introduced (Bauer et al. 2006). Recently, lichen-associated fungi started to receive much attention due to the launching of some ideas that strongly challenge our current, albeit limited, understanding of lichen biology. Next to the classically involved two partners, being the main fungal partner, and a green alga and/or cyanobacteria, basidiomycetous yeasts have been proposed as another intrinsic partner of the lichen ecosystem (Spribille et al. 2016). The authors suggested that *Cyphobasidium* species may play an important role in the lichen symbiosis and even proposed them as an essential third partner. However, there is only little evidence that supports such statements and the specific nature of the interaction between *Cyphobasidium* and lichen species remains elusive and is subject of ongoing debates. Several authors believe that a lichen parasitic strategy is a more plausible explanation for the ecology of Cyphobasidiales (Oberwinkler 2017; Diederich et al. 2022b). Furthermore, most of the clades referred to as the third lichen partner naturally persist in the environment as saprotrophic yeasts (Oberwinkler 2017).

History

In 1983, Yamada and Komagata described *Rhodotorula hasegawae* to accommodate a yeast with an orange reddish colony, without forming ballistoconida, and with coenzyme Q10(H_2). Based on peculiarities of the life cycle, a new teleomorphic genus, *Erythrobasidium*, was proposed with *Erythrobasidium hasegawianum* as only species (Hamamoto et al. 1988). Using molecular phylogenetic and morphological studies, including ultrastructural aspects, Erythrobasidiales was proposed by Bauer et al. (2006). Recent phylogenetic studies suggest that lichen parasites *Cyphobasidium* are likely to belong to Erythrobasidiales (Millanes et al. 2016; Kachalkin et al. 2019). Phylogenetic analyses showed that the parasitic lichen-inhabiting teleomorphic genus *Cystobasidium* is polyphyletic (Millanes et al. 2016) and distributed between two clades. The first clade contained the type species *C. fimentarium* and numerous *Rhodotorula* species from the minuta clade (Yurkov et al. 2015). The second clade, with *C. hypogymniicola* and *C. usneaicola*, was placed outside Cystobasidiales and close to *Cyrenella elegans* in the Erythrobasidiales. *Cyphobasidium* was described from lichen thalli by Millanes et al. (2016) to accommodate *C. hypogymniicola* and *C. usneaicola*, and soon this genus became the type of the newly proposed family Cyphobasidiaceaea and order Cyphobasidiales (Spribille et al. 2016). However, these interpretations were based on phylogenetic studies with poor taxon sampling, and it is highly likely that Cyphobasidiales is a part of Erythrobasidiales and should consequently be interpreted as a synonym as indicated by Kachalkin et al. (2019). Recently, seven additional *Cyphobasidium* species were described by Diederich et al. (2022b) based on morphological and phylogenetic data, bringing the total known diversity to nine species in this genus.

Characters that define the taxa in the order

Yeast colony color is usually orange to red. Asexual reproduction is by polar and multilateral budding. Ballistoconidia are absent or present. Hyphae are produced from single cells without mating or after mating. Clamp connections are present or absent. Septal pores are “simple”, cystosomes are absent. Teliospores are not present. Holobasidia are produced in culture, and form sessile, not forcibly discharged basidiospores. Major sugar components from whole-cell hydrolysates are mannose and glucose, xylose is absent. Major ubiquinone is Q-10(H2) or Q-9. SPBs during metaphase are in the nuclear envelope (Bauer et al. 2006; Hamamoto 2011a, b).

Species of *Cyphobasidium* occur as galls on lichens and are only known from the sexual stage. They are characterized by thick-walled probasidia that give rise to cylindrical, 1–3 transversely septate basidia, with ellipsoid to fusiform basidiospores that have a refractive apiculus and may germinate with an ontogenetic yeast stage.

Plates

See Figs. 112.2 and 112.3 in Hamamoto (2011a).

Genera included

Family Erythrobasidiaceae Denchev 2009
Family Erythrobasidiaceae Denchev 2009
Bannoa Hamam. 2002
Erythrobasidium Hamam., Sugiy. & Komag. 1988
genera *incertae sedis*
Cyphobasidium Millanes et al. 2016
Cyrenella Goch. 1981
Hasegawazyma Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout 2015

Evolution

Erythrobasidiales includes some yeast taxa, most of which have hydrogenated coenzyme Q systems. *Hasegawazyma*, however, has nine isoprenologous. *Cyrenella* and *Hasegawazyma* appear to be basal taxa in the order (Wang et al. 2015a, b). For a full understanding of the evolutionary trajectory of this order, comparative genomics approaches are needed. Zhao et al. (2017) estimated emergence of the order at 122 million years ago.

Justification of order and problems

Erythrobasidiales is justified based on molecular phylogenetic and ultrastructural considerations (Bauer et al. 2006; Wang et al. 2015a, b). The addition of new members may help us to better understand the limits of the order.

Significance

Ecological and economical roles

Many species are inhabitants of the phyllosphere. *Cyrenella elegans* is a dimorphic fungus of which the filamentous stage is characterized by conidia with setose branches, which is interpreted as an adaptation to live in aquatic habitats. Cyphobasidium species inhabit lichens, and seems to be widespread in term of both, geography and hosts, e.g., species of *Bryoria*, *Hypogymnea, Letharia*, and *Usnea* (Millanes et al. 2016; Spribille et al. 2016; Diederich et al. 2022b). Cystobasidiomycete specific FISH demonstrated the presence of *Cyphobasidium* species in lichen thalli and/or associated lichen biofilms (Spribille et al. 2016, 2020). Tagirdzhanova et al. (2021) attempted to investigate the genome structure of *Cyphobasidium* species associated in the thallus of *Alectoria sarmentosa*.

Chemical diversity

Erythrobasidiales shows heterogeneity in coenzyme Q systems. Most species have CoQ10(H2) but Q-9 is also present (Bauer et al. 2006; Hamamoto 2011a, b).

Other relevant data and future recommendations

To date, most species of the order have been identified based on the combination of ribosomal ITS and LSU nucleotide sequences. Among these two markers, ITS is usually more variable than LSU. The discovery of the presence of basidiomycetous yeasts in the cortex of many lichen species at a global scale has been one of the most interesting discoveries in lichenology lately. Possibly, these yeasts play an essential, yet unknown role in the lichen ecosystem, but their exact role and interaction capabilities remains to be determined. Unfortunately, no cultures were obtained to elucidate their biological role in laboratory experiments. Because the occurrence of yeasts related to genera *Cyphobasidium* and *Microsporomyces* in asymptotic lichens has been reported in the literature (Hawksworth and Grube 2020), attempts to get cultures need priority and are crucial to better understand the biology of these species and their role in lichen thalli.

Exobasidiales Henn. 1898

Contributed by: Vasiliy A. Dudka, Cvetomir M. Denchev, Virginia Ramírez-Cruz, Teodor T. Denchev

Introduction

Exobasidiales was introduced to accommodate species of the genus *Exobasidium* and two species of the genus *Microstroma, M. album* (Desm.) Sacc. and *M. juglandis* (Bérenger) Sacc. (Henning 1898), the latter being recently considered as a type species of a new genus, *Pseudomicrostroma* (Kijpornyongpan and Aime 2017). In the current systems, *Microstroma* and *Pseudomicrostroma* are placed in another order, Microstromatales (Bauer et al. 1997; Kijpornyongpan and Aime 2017).

In the system of the Exobasidiomycetes, Exobasidiales characterizes by having local interaction zones with complex interaction apparatus producing interaction rings in haustoria, presence of simple septal pores with membrane caps and with or without central tubes within the pore channels, and lack of teliospores (with the exception of Graphiolaceae) (Bauer et al. 1997; Begerow et al. 2014; Begerow and McTaggart 2018). All members of the order are holobasidiate and dimorphic (Begerow & McTaggart 2018).

Exobasidiales contains five families and 19 genera, with a total of 108 species. Species in this order are grouped together by ultrastructural and morphological characteristics and molecular data (Bauer et al. 1997; Begerow et al. 1998, 2002a, b).

Characters that define the taxa in the order

Representatives of Exobasidiales are either parasites of plants, sporulating in the above-ground parts of their hosts, or yeasts or yeast-like fungi inhabiting various substrates. Exobasidiales includes five families: Brachybasidiaceae, Cryptobasidiaceae, Exobasidiaceae Graphiolaceae, and Laurobasidiaceae.

Graphiolaceae is characterized by the presence of haustoria, constricted at the point of penetration through host cell wall and consisting of a clamped basal body with several lobes extending into the host cell (Bauer et al. 1997; Begerow et al. 2002a, 2014). Species of this family form small basidiomes (0.2–1 mm in diameter) of black or brown color on leaves of hosts in the Arecaceae (Piepenbring et al. 2012, 2020). Fructification of the Graphiolaceae starts between chlorenchyma and hypodermal tissue (Cole 1983). Basidioma is formed by a peridium and inner space filled with elaters (except *Stylina*), chains of basidia, and spores. These structures are developed on a basal layer of hyphae connected to intercellular hyphae which penetrate the walls of host cells and form ramified haustoria with globose branches (Oberwinkler et al. 1982; Piepenbring et al. 2012). Two to eight basidiospores arise laterally on basidia. A species known only in asexual, saprotrophic developmental stage, *Graphiola fimbriata* S. Nasr et al., was recently described for the first time in the Graphiolaceae (Nasr et al. 2019). The family includes two genera, *Graphiola* and *Stylina*.

Brachybasidiaceae is characterized by the formation of ballistosporic holobasidia with two sterigmata. The hilar appendages of the basidiospores are oriented adaxially at the basidium apex (Begerow et al. 2002a). Brachybasidiaceae species lack haustoria (Bauer et al. 1997; Begerow et al. 2002a) and infect monocots. Yeast or yeast-like states are present. Species sporulate on the surface of host organs: basidia may protrude through stomata (suprastomatal balls) or emerge from the disintegrated epidermis, being elongated in the latter case. Among the basidia there are paraphyses. Basidiospores are ellipsoid, smooth, thin-walled, hyaline, often septate. Almost all species form conidia. Eight genera are included: *Brachybasidium*, *Dicellomyces*, *Kordyana*, *Lelum*, *Marantokordyana*, *Meira*, *Proliferobasidium,* and *Yunzhangomyces* (Begerow et al. 2014; Piepenbring et al. 2020; Denchev and Denchev 2021; Li et al. 2022c). *Kordyana* comprises parasites on hosts in the Commelinaceae, Bignoniaceae, Burseraceae, and Poaceae. Basidia of *Kordyana* are cylindrical, 2-sterigmate (rarely three), sometimes protruding through stomata with paraphyses. Related genus *Marantokordyana* is similar in morphology to *Kordyana*, but its plant host is Marantaceae (Piepenbring et al. 2020). *Brachybasidium* is a monotypic genus infecting palms (Arecaceae), with basidia protrude through stomata without paraphyses; conidia are unknown. At the moment, *Dicellomyces* includes two species parasitizing on Poaceae and Arecaceae. The basidia are formed in discoid, gelatinous basidiomes breaking through epidermis. *Proliferobasidium* is a monotypic genus of which a single species parasitizes on the Heliconiaceae members. A distinctive feature of this species is the basidium formed in gelatinous pustules breaking through the epidermis or stomata and ornamented with repeated proliferations from within the probasidial wall. Position of *Lelum* is controversial due to the peculiarities of morphology and specificity of the host (Piepenbring et al. 2020). Based on molecular phylogenetic analyses, yeast genus *Meira* was placed in the Brachybasidiaceae family. *Meira* species have a wide ecological range (Boekhout et al. 2003; Tanaka et al. 2008; Rush and Aime 2013; Cao et al. 2018). A recently described genus *Yunzhangomyces* includes both sexual and asexual species (Li et al. 2022c).

Distinguishing characteristics of Exobasidiaceae are abaxial orientation of the hilar appendages of the ballistosporic basidiospores on the holobasidia (Begerow et al. 2002a, 2014). Depending on the species, haustoria are present or absent (Begerow et al. 2002a). Exobasidiaceae has similar morphological features to Brachybasidiaceae. They are parasites on dicots, mostly in the Ericaceae. Infection is systemic and develops as spots on the leaves or some of the shoots, galls and witches' brooms or affect the entire plant. Species sporulate on the surface of the host organs. Basidia may protrude through stomata (suprastomatal balls) or emerge from the disintegrated epidermis, being elongated in the latter case. Basidiospores are ellipsoidal, musiform, smooth, thin-walled, hyaline, often multicellular. Almost all species form conidia. Exobasidiaceae comprises four genera: *Arcticomyces*, *Austrobasidium*, *Exobasidium*, and *Muribasidiospora* of which *Exobasidium* has the highest species number. These species are parasites, mostly on hosts in the Ericaceae. The genus demonstrates the whole variety of infections characteristic to the family. Number of sterigmata per basidium is not fixed, varying from two to eight. Basidiospores are ellipsoid, musiform, smooth, thin-walled, hyaline, often with septum (Nannfeldt 1981). *Arcticomyces* is a monotypic genus causing systemic infection of the Saxifragaceae. Morphology of its basidia and basidiospores is similar to *Exobasidium*, but the basidia are developed on stroma-like structures (Savile 1959). *Muribasidiospora* includes parasites on plants in the Anacardiaceae, Cannabaceae, and Theaceae (Begerow et al. 2001). They form spots on the leaves or part of shoots. Basidia are two- to four-sterigmate, basidiospores are ellipsoidal, smooth, thin-walled, hyaline, becoming muriformly septate upon germination. The monotypic genus *Austrobasidium* forms large galls (up to 10 cm) on the stems of the Hydrangeaceae members. The basidia are four- to six-sterigmate; the basidiospores are subcylindrical, abaxially curved, hyaline, smooth (Palfner 2006).

Members of Laurobasidiaceae form gastroid, two- to four-sterigmate holobasidia with blastosporic basidiospores (Begerow et al. 2002a). This family has morphological features similar to Exobasidiaceae (e.g., basidium structure) and Cryptobasidiaceae (e.g., the gasteroid basidia, parasitism on Lauraceae) (Begerow et al. 2014). However, based on some morphological differences and molecular phylogeny, description of a distinct family was proposed (Somrithipol et al. 2018). Basidiospores are ellipsoidal, smooth-walled, hyaline, separating upon germination (Kakishima et al. 2017a). Laurobasidiaceae is monotypic with the only genus *Laurobasidium* parasitizes on Lauraceae and sporulates on the surface of the host organs causing large galls with root-like outgrowths (Somrithipol et al. 2018). This family includes the asexual species *Acaromyces ingoldii* Boekhout et al. ex Denchev & T. Denchev which was reduced to a synonym of *Laurobasidium hachijoense* (Y. Otani, Kakish. & Iijima) Kakish. et al. (Somrithipol et al. 2018).

Cryptobasidiaceae has a unique type of sporulation among the Exobasidiales. Basidiospores are formed on gasteroid holobasidia without sterigmata, in peripheral lacunae of the host galls. After maturation, the galls are destroyed, releasing the spore mass. Hosts are dicots mainly in Lauraceae. Species of Cryptobasidiaceae form galls in various organs. Paraphyses are present in basidial layer. Basidiospores are blastosporic, ornamented, slightly pigmented and thick-walled, often with septa. Formation of conidia is unknown. The family is composed of five genera: *Botryoconis*, *Clinoconidium*, *Coniodictyum*, *Drepanoconis*, and *Phacellula*. The *Clinoconidium* species are parasites on Lauraceae, forming galls of white or brown color on various host organs (Kakishima et al. 2017b, 2020). Basidiospores are unicellular, ellipsoidal, ornamented, thick-walled, hyaline or brown. *Drepanoconis* species are also parasites on Lauraceae. They cause infection of leaves, fruits, and branches; their basidiospores are curved, with slightly noticeable ornamentation and gelatinous wall and are formed on gastroid basidia (Hendrichs and Oberwinkler 2003). *Coniodictyum* is monotypic. *Coniodictyum chevalieri* Har. & Pat. has multicellular, ornamented spores and infect species in the Rhamnaceae, producing white galls on various organs (Maier et al. 2006). The monotypic genus *Botryoconis* includes parasitizes on Lauraceae. It causes severe deformation of wood, leaves, and fruits. Basidial layer comprising paraphyses and gasteroid holobasidia are formed in the infected part. Basidiospores are colorless, ornamented, formed in a group of eight spores per basidium (Hendrichs and Oberwinkler 2003). *Phacellula* is also a monotypic genus that infects Rhamnaceae, forming white, erect tufts, up to 2 mm high, on the leaves. Basidia with colorless, septate basidiospores are developed on the galls (Seifert and Bandoni 2001).

Plates

Fig. 23 Exobasidiales. **a–i** habit. **a** *Arcticomyces warmingii* on *Saxifraga oppositifolia* (LE F-38034, Murmansk Oblast, Russia); **b** *Exobasidium arescens* on *Vaccinium myrtillus* (LE F-332771, Saint Petersburg, Russia); **c** *Exobasidium cassiopes* on *Cassiope tetragona* (LE F-341370, Murmansk Oblast, Russia); **d** *Exobasidium japonicum* on *Rhododendron ledebourii* (LE F-341253, Krasnoyarsk Krai, Russia); **e** *Exobasidium myrtilli* on *Vaccinium myrtillus* (LE F-341361, Murmansk Oblast, Russia); **f** *Exobasidium pachysporum* on *Vaccinium uliginosum* (LE F-341360, Saint Petersburg, Russia); **g** *Exobasidium rostrupii* on *Vaccinium microcarpum* (LE F-332711, Khanty-Mansi Autonomous Okrug—Yugra, Russia); **h** *Exobasidium savilei* on *Chamaedaphne calyculata* (LE F-332726, Khanty-Mansi Autonomous Okrug—Yugra, Russia); **i** *Graphiola phoenicis* on *Phoenix dactylifera* (LE F-61882, the Botanical garden (BIN RAN), Saint Petersburg, Russia)

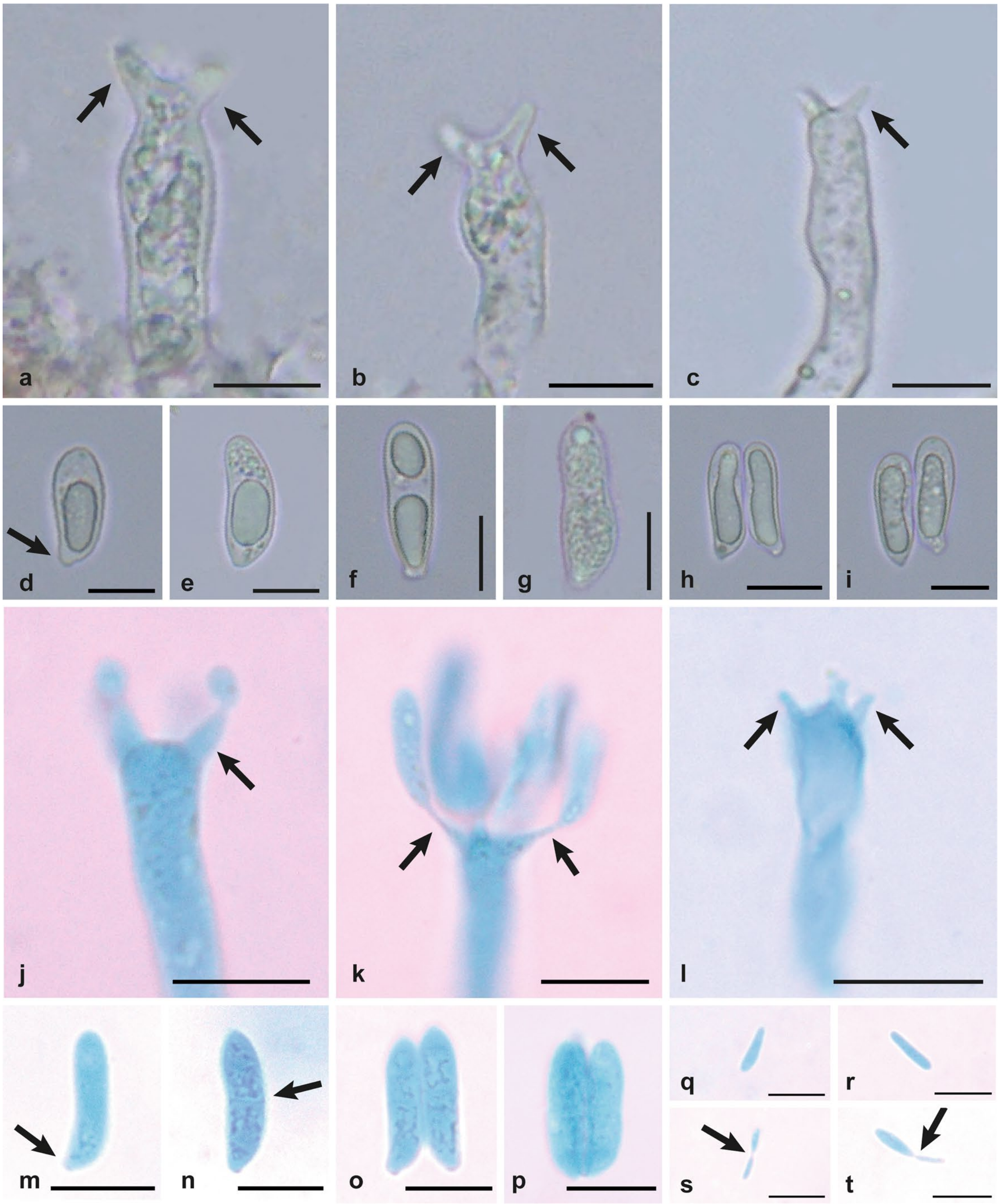


Fig. 24 Exobasidiales. **a**–**i** microstructures in LM of *Exobasidium aequale* on *Vaccinium myrtillus* (LE F-341368, Murmansk Oblast, Russia); **a**–**c** basidia with sterigmata (arrows); **d**–**g** basidiospores single, well-marked the hilar appendices (arrow); **h**, **i** basidiospores in pairs; **j**–**t** microstructures (colored in cotton blue) in LM of *Exobasidium ledi* on *Rhododendron tomentosum* (LE F-333043, Saint Petersburg, Russia); **j**–**l** basidia with sterigmata (arrows); **m** basidiospora with well-marked the hilar appendices (arrow); **n** basidiospore with septa (arrow); **o**, **p** basidiospores in pairs or group; **q**, **r** conidia single; **s**, **t** germinating conidia, place of separation (arrows). Scale bars: a–t = 10 µm

Genera included

Family Brachybasidiaceae Gäum. 1926
  Brachybasidium Gäum. 1922
  Dicellomyces L.S. Olive 1945
  Kordyana Racib. 1900
  Lelum Racib. 1900
  Marantokordyana M. Piepenbr., Maike Hartmann, T.A. Hofm. & M. Lutz 2020
  Meira Boekhout, Scorzetti, Gerson & Sztejnb. ex Denchev & T. Denchev 2021
  Proliferobasidium J.L. Cunn. 1976
  Yunzhangomyces Q.M. Wang, E. Tanaka, M. Groenew. & Begerow 2022
Family Cryptobasidiaceae Malençon ex Donk 1956
  Botryoconis Syd. & P. Syd. 1906
  Clinoconidium Pat. 1898
  Coniodictyum Har. & Pat. 1909
  Drepanoconis J. Schröt. & Henn. 1896
  Phacellula Syd. 1927
Family Exobasidiaceae J. Schröt. 1888
  Arcticomyces Savile 1959
  Austrobasidium Palfner 2006
  Exobasidium Woronin 1867
  Muribasidiospora Kamat & Rajendren 1968
Family Graphiolaceae Clem. & Shear 1931
  Graphiola Poit. 1824
  =*Elpidophora* Ehrenb. ex Link 1824
  =*Nigrocupula* Sawada 1944 (nom. inval.)
  =*Trichodesmium* Chevall. 1826
  Stylina Syd. & P. Syd. 1921
Family Laurobasidiaceae Pinruan, Sommai, Suetrong, Somrith. & E.B.G. Jones 2018
  Laurobasidium Jülich 1982
  =*Acaromyces* Boekhout, Scorzetti, Gerson & Sztejnb. ex Denchev & T. Denchev 2021

Evolution

Exobasidiales is mostly parasites of dicots or monocots, but there are evolutionary lines of asexual species represented by yeasts or yeast-like fungi on various substrates. Host phylogeny plays an important role in the evolution of the Exobasidiales (Begerow et al. 2002a). Due to the long-term co-existence, the connection of Exobasidiales with their hosts is revealed. The trend towards specialization on the host is clearly visible: Graphiolaceae on Arecaceae, Brachybasidiaceae on monocots, Exobasidiaceae almost exclusively on Ericaceae, and Cryptobasidiaceae on Lauraceae, with a few exceptions (Begerow et al. 2002a).

The separation of Laurobasidiaceae may be controversial at present. On the one hand, it is confirmed by molecular phylogenetic data, on the other hand, the family does not have a precise morphological description like other families of the order. Representatives of Laurobasidiaceae have a number of intermediate features between Exobasidiaceae (morphological features) and Cryptobasidiaceae (basidial morphology and specialization on hosts in the Lauraceae) and the final decision on the status of this family is yet to be made.

Division of the order into these families has been confirmed by phylogenetic analyses that also reflect the existing phylogenetic system of the hosts. It is also noted that like the mono- and eudicots in molecular phylogenetic studies of angiosperms, the monocot-parasitizing Brachybasidiaceae and Graphiolaceae are separated from the eudicot-parasitizing Exobasidiaceae (Begerow et al. 2002a). It is considered that the separation of the four exobasidiaceous families and their respective host distribution can be best interpreted as a result of cospeciation or association by origin (Begerow et al. 2002a). Appearance of species *Arcticomyces* on Saxifragaceae, *Coniodictyum* on Rhamnaceae, *Muribasidiospora* on Anacardiaceae, and others may reflect jumps to new hosts or relictual co-evolution (Begerow et al. 2002a).

Justification of the order and problems

Despite the well-known peculiarity of the order Exobasidiales, phylogenetic and evolutionary aspects within this group are poorly studied. *Exobasidium* is in need of revision as well as many other species in the order. *Kordyana* has a number of taxonomic and nomenclatural problems (Piepenbring et al. 2020), the position of *Lelum* should be clarified (Piepenbring et al. 2020). Taxonomic position of *Austrobasidium* needs to be clarified by molecular data (Somrithipol et al. 2018). One important problem in the taxonomy of Exobasidiales is the small number of available sequences of type specimens, which creates problems with the identification accuracy and phylogeny construction within the order and leads to the description of already known species. It is also important to study different aspects of the species biology, the diversity of Exobasidiales worldwide and to expand the understanding of the geography of this group of fungi.

Economic importance

Species of Exobasidiales are of great economic importance as they are parasites of agriculturally important plants. So, *Exobasidium vexans* and *E. reticulatum* parasitize tea leaves, reducing their quality. In the northern regions of the world, representatives of *Exobasidium* infect wild berries (*Vaccinium oxycoccus*, *V. myrtillus*, *V. uliginosum*) traditionally gathered by the locals. Also, the *Exobasidium* species are parasites of the ornamental plants from *Rhododendron*.

Laurobasidium lauri is a parasite of *Laurus nobilis*, a widespread spice. *Graphiola phoenicis* is a parasite of *Phoenix* spp. including *P. dactylifera*, as well as palm species that are commonly used in urban landscaping.

Filobasidiales Jülich 1982

Contributed by: Virginia Ramírez-Cruz, Teun Boekhout, Andrey Yurkov, Nathan Schoutteten

Introduction

Filobasidiales is placed in Tremellomycetes (Hibbett et al. 2007) and comprises both dimorphic and yeast-like fungi. Basidiomes are usually absent, but some mycoparasites from *Syzygospora* produce minute, waxy to gelatinous galls on host basidiomes. Dimorphic species usually alternate between a haploid yeast morph and a dikaryotic hyphal morph in which holobasidia develop for sexual reproduction. (Weiss et al. 2014). Previously, yeast taxa in the order were classified in the anamorphic genus *Cryptococcus* (Boekhout et al. 2011). Currently, there are eight genera grouped in two monophyletic families: Filobasidiaceae and Piskurozymaceae (Liu et al. 2015a, b). Filobasidiaceae was proposed by Olive (1968), later emended by Liu et al. (2015b), and includes four genera. Piskurozymaceae was proposed by Liu et al. (2015b) and includes two genera.

History

History of Filobasidiales began when Olive (1968) described *Filobasidium floriforme*, found on dead florets of the large plume grass *Erianthus giganteus* (Kwon-Chung 2011). Olive (1968) classified Filobasidiaceae in Ustilaginales based on the basidia which are morphologically similar to those found in *Tilletia*. Later, Jülich (1981) proposed Filobasidiales to accommodate this genus. According to Kwon-Chung (1977) Filobasidiaceae included three genera: *Cystofilobasidium*, *Filobasidiella*, and *Filobasidium*. Presently, only the former genus remains in Filobasidiales, and the two others have been transferred to Tremellales and in Cystobasidiales, respectively. Based on early comparative phylogenetic studies using the ribosomal 5.8S locus, Mitchell et al. (1992) found that *Filobasidum* and *Filobasidiella* clearly represented distinct lineages, which currently belong to separate orders (Weiss et al. 2014; Liu et al 2015a, b). Filobasidiales was resolved as a distinct, monophyletic lineage in several subsequent phylogenies based on ribosomal and multi-locus datasets (Fell et al. 2000; Scortzetti et al. 2002; Hibbett et al. 2007; Liu et al. 2015a, b). Using a broad taxonon sampling and multi-locus phylogenetic reconstructions incorporating ribosomal and protein-coding loci, Liu et al. (2015b) redefined the order and families to accommodate the following genera: *Filobasidium, Goffeauzymia*, *Heterocephalacria*, *Naganishia*, *Piskurozyma*, *Solicczozym*a, and *Syzygospora* pro parte, recognizing two families: Filobasidiaceae and Piskurozymaceae.

Characters that define the taxa in the order

Dimorphic fungi with or without distinct basidiomes, mycoparasitic representatives produce cerebriform or pustulate gelatinous structures on host basidiomes. Sexual reproduction present in some species. Basidia have been observed in culture conditions of some species and in vivo in mycoparasites (e.g., *Heterocephalacria*, *Syzygospora*). In lichenicolous species, basidiomes are cream or white, waxy to gelatinous. Hyphae with clamp connection, haustorial branches may be present in teleomorphic states. Hyphal septa have dolipores. Teliospores are not formed. Holobasidia are tubular, producing four to six sterigmata and producing sessile basidiospores. Yeast morphs are characterized by budding cells and produce white to pinkish cultures. Pseudohyphae occasionally produced in culture. Fermentation usually absent, but present in *Piskurozyma capsuligena*, nitrate utilized by several species (Fonseca et al. 2011; Millanes et al. 2011; Liu et al. 2015a, b). Some morphological features indicate a close relationship with Tremellales, such as haustorial branches and hyphal septa with dolipores.

Plates

See figures 115.2, figures 115.3 in Kwon-Chung (2011).

Genera included

- Family Filobasidiaceae L.S. Olive 1968
  - *Filobasidium* L.S. Olive 1968
  - *Goffeauzyma* Xin Zhan Liu, F.Y. Bai, M. Groenew. & Boekhout 2015
  - *Heterocephalacria* Berthier 1980
  - *Naganishia* S. Goto 1963
  - *Syzygospora* G.W. Martin 1937 pro parte
  - = *Christiansenia* Hauerslev 1969
  - *Zyzygomyces* Diederich, Millanes & Wedin 2022
- Family Piskurozymaceae Xin Zhan Liu, F.Y. Bai, M. Groenew. & Boekhout 2015
  - *Piskurozyma* Xin Zhan Liu, F.Y. Bai, M. Groenew. & Boekhout 2015
  - *Solicoccozyma* Xin Zhan Liu, F.Y. Bai, M. Groenew. & Boekhout 2015

Evolution

Filobasidiales is the second-most basal lineage in Tremellomycetes (Fig. 1), but their phenotypic features are difficult to explain in an evolutionary framework due to their homoplastic nature. The limited available morphological characters can also be found in other lineages of Tremellomycetes (Figs. 19, 20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30, 31, 32, 33, 34, 35, 36, 37, 38, 39).

Justification of order and problems

Similar to previous phylogenetic studies, our phylogenomic reconstruction recovered this order as a monophyletic group (Hibbett et al. 2007; Weiss et al. 2014; Liu et al. 2015a, b). Due to lack of morphological characters of most yeast species, it is not easy to find morphological characters to distinguish these yeasts from yeasts in Tremellales and Cystofilobasidiales. Physiological assimilation tests incorporating aldaric acids and low-weight aromatic compounds may help to distinguish yeasts in Filobasidiales and Tremelalles (Fonseca 1992; Sampaio et al. 1999a, b).

Significance

Ecological and economical roles

Some species are psychrophilic and have been isolated from various polar and non-polar cold habitats (Cannon and Kirk 2007; Buzzini et al. 2017). *Filobasidium uniguttulatum* has been repeatedly reported in association with human sources, but does not appear to be a relevant pathogen because of its inability to grow at human body temperature. Other reports of *Naganishia* and *Filobasidium* species from human samples need to be taken critically as many of these yeasts are psychrophilic. These yeasts are geographically widespread, successfully growing even in deserts and tundra (Vishniac 2006). *Filobasidium* yeasts are common phylloplane species, and *Solicoccozyma* are prominent soil-borne yeasts (Kemler et al. 2017; Yurkov 2018). *Heterocephalacria bachmannii* is a lichenicolous fungus that takes as hosts numerous lichen species of the genus *Cladonia* (Pino-Bodas et al. 2017). Several species of the genus *Syzygospora* are haustorium-interacting mycoparasites of other Basidiomycota species Ginns (1986). Also, various *Filobasidium* species are reported to develop haustoria in the presence of ascomycetous hosts (Olive 1968; Bandoni et al. 1991; Kwon-Chung 1977). *Filobasidium magnum* was reported as the causative agent of stem and branch canker of stone fruit trees (Begerow et al. 2017). Some Filobasidiales occur in marine environments, including *Filobasidum capsuligenum*, *F. magnum*, *F. uniguttulatum*, *Naganishia albida*, *N. liquefaciens*, *N. qatarensis*, *Solicoccozyma keelungensi*, and *S. terrea* (Gareth Jones et al. 2019). *Goffeauzyma* have been recovered from highly acidic aquatic environments (Nutarat et al. 2022).

Chemical diversity

Fonseca and Inácio (2006) recorded enzymatic activities, e.g., proteases, lipases, pectinases, xylanases, among a set of representative strains from a survey of yeasts on the phylloplane of Mediterranean plants. One species in the Filobasidiales, *Filobasidium capsuligenum*, can also ferment glucose and maltose, while the other known *Filobasidium* species cannot ferment glucose (Liu et al. 2015b). Some species have been reported to produce photoprotective compounds mycosporines and auxins (Fernández et al. 2011). Utilization of complex carbon sources, including low-weight aromatic compounds, has been reported for members of *Solicoccozyma* (Stosiek et al. 2019).

Other relevant data and future recommendations

Li et al. (2022a) generated the first two mitochondrial genomes for the order Filobasidiales.

Franziozymales Q.M. Wang, Begerow & M. Groenew. 2022

Contributed by: Teun Boekhout

Introduction

A new lineage in the Exobasidiomycetes, Ustilaginomycotina, was proposed as Franziozymales (Li et al. 2022c).

History

In 2022, a multigene phylogenetic reconstruction identified Franziozymales as a separate lineage near Golubeviales (nom. invalid) and Robbauerales (Li et al. 2022c). These orders are placed in Exobasidiomycetes, although they appeare as sister groups to Malasseziomycetes and Ustilaginomycetes, rather than to other members of Exobasidiomycetes. The order is monotypic and, so far, contains only one species, one genus, one family, and is based on a single isolate only (Li et al. 2022c).

Characters that define the taxa in the order

Franziozymales is defined solely based on its phylogenetic position, close to Golubeviales and Robbauerales. Members of all these three orders produce hyphae and ballistoconidia. Only known as anamorph (Li et al. 2022c).

Plates

See Fig. 8N-P in Li et al. (2022c).

Genera included

Family Franziozymaceae Q.M. Wang, Begerow & M. Groenew. 2022

Franziozyma Q.M. Wang, Begerow & M. Groenew. 2022

Evolution

Franziozymales is closely related to other hyphae- and ballistoconidia-forming fungi classified in Golubeviales and Robbauerales (Li et al. 2022c). Apparently, fungi with a similar phenotype form distinct lineages. As Franziozymales is based only on a single isolate, further sampling is needed to identify the boundaries between these lineages appropriately.

Justification of order and problems

As indicated above, further sampling is needed to set the boundaries between Franziozymales, Golubeviales, and Robbauerales.

Significance

Ecological and economical roles

Only known from leaves of bamboo, Bomi County, Tibet, China.

Chemical diversity

Not known.

Geastrales K. Hosaka & Castellano 2007

Contributed by: Juan Carlos Zamora

Introduction

Geastrales is one of the five currently accepted orders in Phallomycetidae (the others being Gomphales, Hymenogastrales, Phallales, and Stereopsidales), and comprises ca. 160 species distributed in four families and a total of ca. seven genera. Geastrales was proposed by Hosaka et al. (2006) for a group of primarily saprotrophic gasteroid fungi with bi- to pluristratified peridium, often able to form conspicuous rhizomorphs that bear ampullaceous septa at generative hyphae. Clamp-connections are typically present in all primary septa of these generative hyphae. Basidia are frequently polysporic ([1–]4–8[–11]-spored) and basidiospores are thick-walled, symmetrically attached to the sterigmata, and passively released (statismospores). Hosaka & al.'s name was based on the *nomina nuda* "Geastrales Kreisel" (Kreisel 1969) and "Geastrales Locquin" (Locquin 1974), but these two authors based their order concepts on what is currently considered the family Geastraceae only. Krüger et al. (2001) provided molecular data that further justified the separation of Geastrales (again including species of Geastraceae only) from other groups of gasteroid fungi, particularly the Lycoperdales, where they were traditionally placed. Hosaka et al. (2006), in addition to validly publishing the name Geastrales, expanded its definition to also encompass the families Schenellaceae (as Pyrenogastraceae), Sphaerobolaceae, and Sclerogastraceae (indicated only as the genus Sclerogaster), the latter validly published in Kirk et al. (2008). Geastrales, as so defined, has been accepted as a distinct monophyletic group in all subsequent studies.

Regarding the current concepts of the families, Schenellaceae and Sphaerobolaceae are considered to contain a single genus each: *Schenella* and *Sphaerobolus*, respectively, with less than ten accepted species altogether (Estrada-Torres et al. 2005; Geml et al. 2005a). In turn, two genera are accepted in Sclerogastraceae, viz., *Sclerogaster* (taxonomy poorly known: Hosaka and Castellano 2008; Sulzbacher et al. 2016a, b, c, but possibly

12–15 species) and *Boninogaster* (one species, Kobayasi 1937a; Hosaka 2014), while there are possibly three in Geastraceae, viz., *Geastrum* (ca. 130 species, Zamora et al. 2014a; He et al. 2019a), *Myriostoma* (at least five species, Sousa et al. 2017, 2019), and *Terrostella* (one species, Long 1917, 1945). The latter was only tentatively assigned to this family by Sunhede (1989), and no molecular data are available yet from its single species, *T. texensis*. The morphology, however, strongly suggests that this is a member of Geastraceae.

Three fossils have been attributed to the order Geastrales. The first one described was *Geaster florissantensis* (Cockerell 1908), from the Oligocene, which Tiffney (1981) considered unlikely to be an earthstar or even a gasteroid fungus. Subsequently, Magallón-Puebla and Cevallos-Ferriz (1993) described *Geastrum tepexensis*, from the late Eocene, which seems to be the most unambiguous fossil of Geastrales discovered to date. Another earthstar-like fossil is *Geastroidea lobata*, described by Krassilov and Makulbekov (2003) and dating from the Cretaceous. This has also been considered as possibly representing a species of earthstars by Taylor et al. (2009) and, if that taxonomic position is accepted, it would represent the oldest known fossil in Geastraceae or, at least, Geastrales.

History

Species of Geastrales have been early noticed in botanical history, especially those of the genus *Geastrum*, which have been mentioned and illustrated in some pre-Linnaean treatments such as Boccone (1697), Plumier (1705), and Micheli (1729), among others. Micheli (1729) had already treated two genera of Geastrales, viz., *Geaster* (p. 220, tab. 100, currently *Geastrum*) and *Carpobolus* (p. 221, tab. 101, currently *Sphaerobolus*) in Nova Plantarum Genera. Being pre-Linnaean, both names are however not validly published (Art. 13 or the ICN, Turland et al. 2018). The two first validly published species names, precisely referring to Micheli's concepts, appeared in Linnaeus (1753): *Lycoperdon stellatum* for what is currently *Geastrum*, and *L. carpobolus* for the current *Sphaerobolus*. The corresponding generic names were validly published in Persoon (1794b) and Tode (1790), and both sanctioned in Persoon (1801). Later on, the remaining accepted genera were proposed in different studies: *Myriostoma* Desv. (Desvaux 1809), *Sclerogaster* R. Hesse (Hesse 1891), *Schenella* T. Macbr. (Macbride 1911), *Boninogaster* Kobayasi (Kobayasi 1937a), and *Terrostella* Long (Long 1945, as a replacement name for *Geasteroides* Long *non* Battarra, see below). For a list of generic names considered synonyms of *Geastrum*, see Zamora and al. (2014a).

Geastraceae was recognized and validly published as an independent family already in the nineteenth century (Corda 1842). It is, by far, the largest one of Geastrales in terms of number of species, with surely at least 135–140 species and three genera: *Geastrum*, *Myriostoma*, and *Terrostella* (a replacement name for the illegitimate *Geasteroides* Long, in Long 1917). Although only tentatively included in the family by Sunhede (1989), *Terrostella* shares many characteristics with *Geastrum*, such as the same exoperidial dehiscence, the same arrangement of capillitial hyphae radiating both from the columella and the endoperidium, and nearly identical basidiospores. The most striking difference is that *Terrostella* possesses a prominent sterile base in the endoperidial body that penetrates into the glebal mass to form a broad, dome-shape columella, this being absent in *Geastrum* and present, but much less conspicuously, in *Myriostoma* (the lower part of the endoperidium in *Myriostoma* is clearly thickened, but not as much as in *Terrostella*). Taking into account this information, *Terrostella* most likely belongs to Geastraceae and it seems wise to keep it as an independent genus for the time being.

Sphaerobolaceae was proposed by Schröter (1889) as "*Sphaerobolacei*", exclusively for the genus *Sphaerobolus*. *Nidulariopsis* (Greis 1935) has sometimes been treated as an independent genus, but the differences of the type, *N. melanocarpa*, with *S. iowensis* are minimal, as noted by Zeller (1948). Geml et al. (2005a) treated *Nidulariopsis* as a probable synonym of *Sphaerobolus*. The only characteristic that could, perhaps, justify their separation is the presence of a pigmented middle peridial layer of rounded thick-walled cells in *Nidulariopsis*, but Walker (1927) already showed that layer in the protologue of *S. iowensis*. As a result, *Nidulariopsis* and *Sphaerobolus* are treated as taxonomic synonyms here.

Schenellaceae was first described by Nannenga-Bremekamp (1967) as a family in *Myxomycetes* (*Amoebozoa*), for the single genus and species *Schenella simplex* (Macbride 1911). This was a puzzling, enigmatic taxon for myxomycetologists for decades, until Estrada-Torres et al. (2005) clarified its taxonomy and revealed that it corresponded to the gasteroid basidiomycete formerly known as *Pyrenogaster atrogleba*. As such, the genus *Pyrenogaster* (Malençon and Riousset 1977) and the family Pyrenogastraceae (Jülich 1981) became latter synonyms of *Schenella* and Schenellaceae, respectively.

Sclerogastraceae is the last recognized family, already distinguished by Locquin (1974) but not validly published there. Kirk et al. (2008) validated Locquin's name in the tenth edition of the Ainsworth & Bisby's Dictionary of the Fungi, for the lineage represented by *Sclerogaster* in Hosaka et al. (2006) and, later on, in Hosaka and Castellano (2008). Originally believed to encompass only *Sclerogaster*, Hosaka (2014) placed *Boninogaster* also in this same family, thanks to molecular and morphological studies of recently collected specimens attributable to *B. phalloides*, the single species in the genus (Kobayasi 1937a). As a result, *Boninogaster* was excluded from Hymenogastraceae, where it had been formerly placed.

Characters that define the taxa in the order

In Geastraceae, the exoperidium often splits at maturity in a star-like shape, hence the vernacular name "earthstars", although some species are truffle-like and indehiscent (e.g., many of the ones formerly named as *Radiigera*), with distinct mycelial, fibrous and fleshy (pseudoparenchymatous) layers from the external to the internal part. The endoperidium is prosoplectechymatous, sometimes inconspicuous (truffle-like taxa and *G. melanocephalum*), and the gleba is always powdery at maturity, ochraceous brown to black. Basidia are rather variable, from nearly subglobose to ellipsoid, cylindric, claviform, pyriform, lecythiform or lageniform, not rarely with a distinct epibasidial part (bearing the sterigmata) separated from the hypobasidial part by a constriction. Basidiospores are frequently globose or subglobose (exceptionally ovoid) and always ornamented with verruca, bacula or pila (Sunhede 1989; Zamora et al. 2014a).

Schenellaceae is characterized by truffle-like basidiomes, which are indehiscent or split irregularly at maturity, by the presence of radially arranged glebal peridioles, at least in immature fruitbodies (they may disintegrate to form a dark, powdery mass in mature basidiomes), exoperidium with an inconspicuous or absent fibrous layer, prosoplectenchymatous endoperidium, particularly elongated basidia, and smooth and very elastic capillitial threats (Sunhede 1989; Domínguez de Toledo and Castellano 1998, both as *Pyrenogaster*). Basidiospores are often more or less ellipsoid when immature, becoming more rounded and developing a baculate ornamentation at maturity.

Sclerogastraceae can be characterized by the truffle-like fruitbodies with a green to yellow or orange glebal mass, never powdery, and a more or less pseudoparenchymatous endoperidium. Basidiospores are usually ornamented when mature, but *Boninogaster* is characterized by having smooth basidiospores (Kobayasi 1937a) and some species in *Sclerogaster* may have smooth basidiospores as well (Hosaka 2014).

Sphaerobolaceae is characterized by the small fruitbodies (<4 mm in diam.) with an elastic inner peridial layer, formed by thick-walled anticlinal cells, that acts as a catapult throwing the whole glebal mass at maturity. The glebal mass is internally pale-colored and soft when fresh (never powdery), and the basidiospores are always smooth, hyaline, and more or less ellipsoid. Basidia bear much shorter sterigmata compared to other taxa in the other families of the order.

Species in the order have been described based on the teleomorphs (basidiomes), although chlamydospore formation has been reported in axenic cultures of several *Geastrum* species (Sunhede 1989; Stoytchev et al. 2001; Zamora et al. 2014b).

Plates

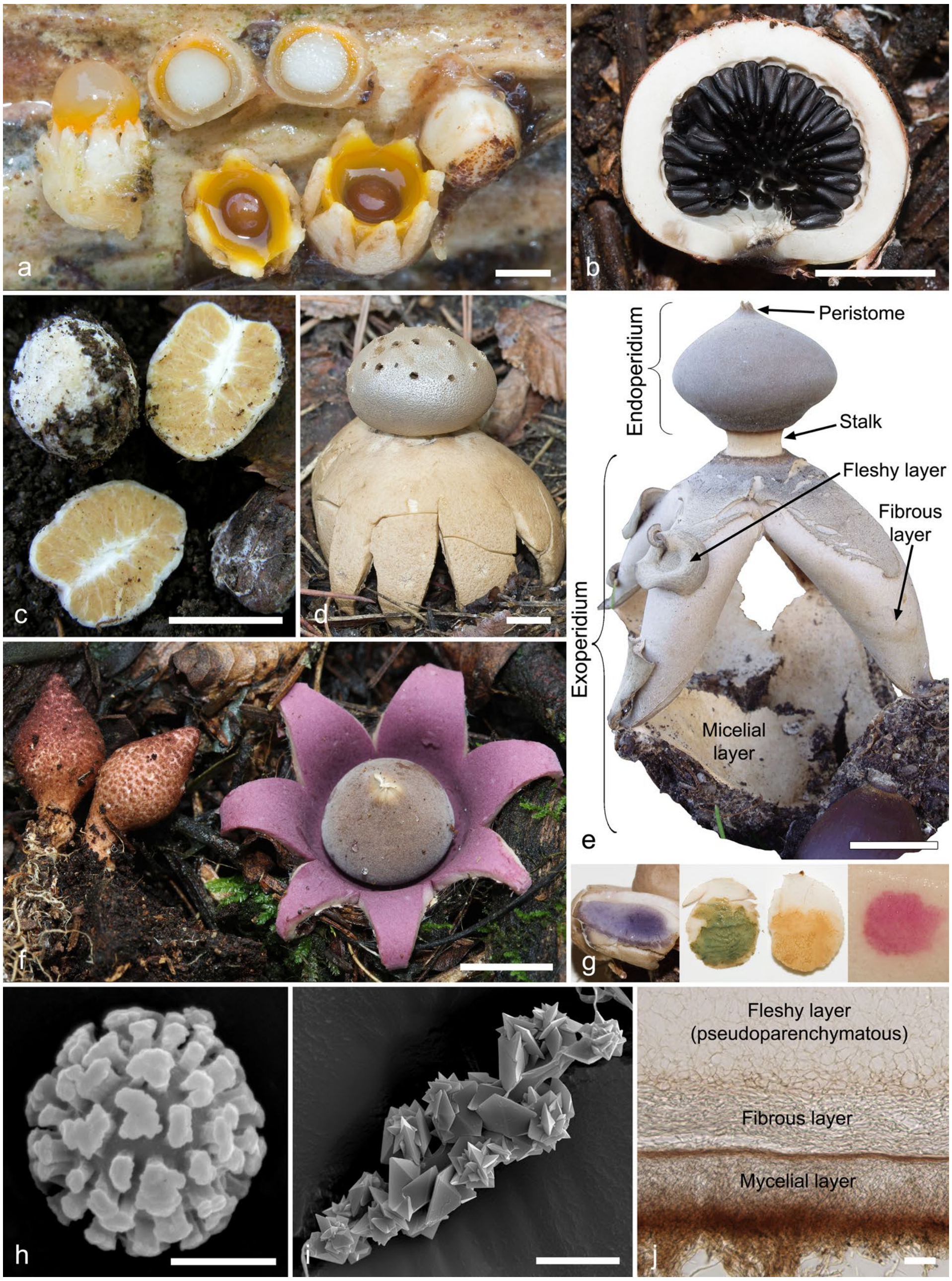


Fig. 25 Morphological characters of Geastrales. **a** *Sphaerobolus iowensis* (Zamora s.n., Spain). **b** *Schenella pityophila* (Zamora 531, Spain). **c** *Sclerogaster compactus* (Rodríguez AR090908, Hungary). **d** *Myriostoma coliforme* (Zamora 497, Spain). **e** macromorphologic elements of a basidiome of *Geastrum fornicatum* (Zamora 255, Spain). **f** *G. violaceum* (MA-Fungi 82489, Argentina). **g** macrochemical spot test to detect phenoloxydases (positive reaction with α-naphtol, positive and negative reactions with guaiac gum, and positive reaction with syringaldazine). **h** basidiospore of *G. michelianum* s.l. (Kers 8888, Sweden). **i** rhizomorph crystals of *G. parvistriatum* (Zamora 539, Spain). **j** section of the exoperidium of *G. argentinum* (MA-Fungi 82604, Argentina) showing the arrangement of the different layers at a microscopic level. Scale bars: a = 1 mm; b–c = 5 mm; d, f = 10 mm; h = 2 µm; i–j = 10 µm. Photos: a–b, d–j: J.C. Zamora, c: A. Rodríguez

Genera included

- **Family *Geastraceae*** Corda 1842
    - *Geastrum* Pers. 1794 ("*Geaster*" P. Micheli ex Fr. 1829)
        - ≡ *Plecostoma* Desv. 1809
        - = *Cycloderma* Klotzsch 1832
        - = *Coilomyces* Berk. & M.A. Curtis 1854
        - = *Geasteroides* Battarra 1755
        - = *Radiigera* Zeller 1944
        - = *Trichaster* Czern. 1845
    - *Myriostoma* Desv. 1809
        - = *Bovistoides* Lloyd 1919
        - = *Polystoma* Gray 1821
    - *Terrostella* Long 1945
        - ≡ *Geasteroides* Long 1917
    - *Phialastrum* Sunhede 1989
- **Family *Schenellaceae*** Nann.-Bremek. 1967
    - = *Pyrenogastraceae* Jülich 1982
    - *Schenella* T. Macbr. 1911
        - = *Pyrenogaster* Malençon & Riousset 1977
- **Family *Sphaerobolaceae*** J. Schröt. 1889
    - *Sphaerobolus* Tode 1790
        - = *Carpobolus* P. Micheli ex Willd. 1787
        - = *Nidulariopsis* Greis 1935

Family ***Sclerogastraceae*** Locq. ex P.M. Kirk 2008
Boninogaster Kobayasi 1937
Sclerogaster R. Hesse 1891

Evolution

Early evolution of basidiome morphology in Phallomycetidae is complex to ascertain due to the enormous morphological plasticity of the fruitbodies across genera and families. They are gasteroid in Geastrales (all species, including earthstars, cannon-ball fungi, and false truffles), Phallales (all species, including stinkhorns, lattice stinkhorns, and false truffles), Hysterangiales (all species, typically false truffles) and Gomphales p.p. (e.g., *Gautieria*), and aphyllophoroid in Stereopsidales (all species, corticioid fungi) and the majority of Gomphales (e.g., coral fungi, club fungi, cantharelloid fungi, and resupinate or pileate tooth fungi). Within Geastrales, it is unclear whether the ancestor was truffle-like or not (Hosaka et al. 2006), although Hosaka and Castellano (2008) suggested that a truffle-like morphology may be ancestral to the above-ground, earthstar morphology. On the other hand, within Geastraceae, Hosaka et al. (2006) commented that truffle-like morphologies of *Radiigera* were probably derived forms, while Zamora et al. (2014a), with a larger sampling, supported the same idea, i.e., that truffle-like morphology appeared several times throughout the evolution of *Geastrum*. Considering also the early-diverging position of Sphaerobolaceae, with epigeous star-like fruitbodies, it is possible that both morphologies, i.e., star-like and truffle-like, have been switched more than once.

Justification of order and problems

The different genera currently accepted to belong to Geastrales have been placed in a variety of families and orders in the past. *Sphaerobolus*, for example, was included in the order Sclerodermatales by, e.g., Fischer (1933) and Calonge (1998), in Nidulariales by, e.g., Zeller (1948) and Cejp (1958), and treated as Sphaerobolales by Ainsworth (1971). *Boninogaster* was often considered as a member of Hysterangiales (Kirk et al. 2008). The family Geastraceae had been treated in the majority of taxonomic studies within the order Lycoperdales, until the valid description and definitive acceptation of Geastrales as an independent order in Phallomycetidae by Hosaka et al. (2006). The historical taxonomic problems related to the placement of *Schenella* are perhaps the most remarkable ones, since it was included within the *Myxomycetes* (in Dianemataceae, which is part of the order Trichiales, or in Amaurochaetaceae-Stemonitidaceae, within the order Stemonitidales) for almost a century, until Estrada-Torres et al. (2005) clarified its identity.

While at generic level, the taxonomic problems are relatively of minor importance in Geastrales, the species-level taxonomy is far from being solved. The precise number of species in Sclerogastraceae is rather uncertain (Hosaka and Castellano 2008; Hosaka 2014). In Geastraceae, numerous new species have been described in the last decades, the immense majority including morphological, molecular and ecological data (e.g., Zamora et al. 2015; Sousa et al. 2017; Accioly et al. 2019). An important number of old names are poorly known. For more information about species delimitation in Geastrales, the reader is referred to Cao et al. (2021a, b).

Significance

Ecological and economical roles

All known species of Geastrales are presumably saprotrophic, and in many cases, they form dense masses of mycelium in the form of a subiculum, a net of rhizomorphs, or both. Many species are humicolous, but lignicolous species are also common, especially in the tropics, and *Sphaerobolus* can be coprophilous as well. However, there is a notorious difference of growth in axenic media, and while cultures of *Sphaerobolus* are easily obtained, preserved, and grow rapidly (Geml et al. 2005b), species of *Geastrum* are difficult to isolate and tend to grow very slowly (Sunhede 1989; Kuhar et al. 2016b). This fact, together with the findings of a possible mycorrhizal association between *G. fimbriatum* and the roots of *Fagus sylvatica* (Agerer and Beenken 1998), indicates that the trophic strategies in Geastrales may be more diverse.

Geastrales is distributed worldwide and is especially abundant in temperate and tropical areas (Ponce de León 1968). They have been found from deserts to rain forests, in calcareous or siliceous soils, and even in parks and gardens. Geastrales grows in the humus and wood of large number of spermatophytes, for example in the families Anacardiaceae, Arecaceae, Betulaceae, Bignoniaceae, Cactaceae, Cistaceae, Casuarinaceae, Cupressaceae, Euphorbiaceae, Fagaceae, Gramineae, Malvaceae, Myrtaceae, Oleaceae, Pandanaceae, Pinaceae, Rosaceae, Salicaceae, Sapindaceae, Scrophulariaceae, Tamaricaceae, and Ulmaceae (e.g., Sunhede 1989; Bates 2004; Douanla-Meli et al. 2005; Ochoa and Moreno 2006; Kuhar and Papinutti 2009; Hemmes and Desjardin 2011; Hernández Caffot et al. 2013; Kuhar et al. 2013; Hosaka 2014; Zamora et al. 2015).

Species in the group display a diverse set of dispersal strategies, including anemochory in taxa with powdery gleba (often rainfall driven as in *Geastrum* and *Myriostoma*, Sunhede 1989), zoochory in at least some hypogeous species (Domínguez de Toledo and Castellano 1998), and the well-studied active discharge of the whole glebal mass in *Sphaerobolus* (Aladoasura 1963; Ingold 1972).

No species of Geastrales are considered edible. They should not be confused with other earthstars in the genus *Astraeus* (Boletales), which are consumed and sold at local scales in Asia (Petcharat 2008; Pandey and Ghosh 2022). Species in the genus *Sphaerobolus* are sometimes considered a nuisance due to their ability to throw their glebal masses several centimeters to a few meters of distance, adhering to nearby plants, furniture, and cars, drying out as dark spots that are difficult to remove (Douglas 2010). *Sphaerobolus* has also been associated with the so-called "thatch collapse" disease on golf turfs (Baetsen-Young et al. 2015).

Chemical diversity

Besides the common production of calcium oxalate crystals of various morphologies (Sunhede 1989; Zamora et al. 2013, 2015), the chemistry in Geastrales is largely unknown. The analysis of the *Sphaerobolus stellatus* genome revealed numerous copies of lignocellulose-degrading oxidoreductases and carbohydrate-active enzymes (Kohler et al. 2015), and its enzymatic machinery implied in lignocellulosic metabolism includes laccase, cellulase, peroxidase, and xylanase activities (Baetsen-Young et al. 2017). Some species of *Geastrum* are also known to produce a variety of enzymes putatively implied in degradation of lignocellulosic substrates, with activities in laccase, cellulase, pectinase, amylase, manganese peroxidase, β-glycosidase, β-xylosidase, and lipase (Kuhar et al. 2016b). On the other hand, macroscopic spot tests to detect phenoloxidase activity with syringaldazine, guaiac gum, and α-naphtol have proven useful for taxonomic purposes (Zamora et al. 2013).

Geminibasidiales H.D.T. Nguyen, N.L. Nick. & Seifert 2013

Contributed by: Teun Boekhout, Andrey Yurkov

Introduction

Representatives of two basidiomycetous genera, *Basidioascus* and *Geminibasidium*, were isolated from soil after a heat treatment (Nguyen et al. 2013). Both genera are phylogenetically related and cluster with the genus *Wallemia* in Wallemiomycetes (Nguyen et al. 2013). *Geminibasidium*, with two species, is peculiar in how the basidia are formed (Nguyen et al. 2013).

History

Geminibasidiales was described in 2014 for isolates obtained from heat treated soil in Canada to accommodate the genera *Basidioascus* and *Geminibasidium* (Nguyen et al. 2013).

Characters that define the taxa in the order

According to the description provided by Nguyen et al. (2013), basidiomes are absent. Putative basidia form singly or in clusters, and arise from hyphae or from so-called primary cells, viz., swollen basidium bearing cells, and have a lateral projection. These basidia-like structures are deciduous or forcibly discharged before the development of basidiospores. One basidiospore that is not forcibly discharged is formed on, usually, one sterigma that forms on the apical two-thirds part of the basidium, initially hyaline but becoming dark brown at age. Basidia of *Basidioascus* are dikaryotic, but four nuclei occurred in non-discharged and discharged basidia from telophase II, and one nucleus migrates into the basidiospores and three remained in the collapsed basidium (Nguyen et al. 2015). Arthroconidia-like monokaryotic cells may be present. Septal pores somewhat thickened near the central pore, without a septal pore cap, but with electron dense zonate materials in and just outside the pore (Nguyen et al. 2015). Interestingly, the septal pore structure reminds those of *Itersonilia*, a genus that is classified in Cystofilobasidiales, the most basal lineage of Tremellomycetes (Boekhout 1991b).

Plates

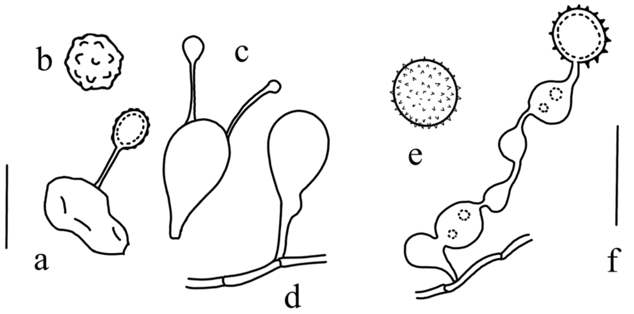


Fig. 26 Geminibasidiales. **a**–**d** *Basidioascus magus*. **a** basidium collapses to develop basidiospore; **b** basidiospore; **c** basidium; **d** basidia with basal lateral projection develop on hyphae; **e**, **f** *Geminibasidium donsium*; **e** basidiospore; **f** basidium produces a chain of swollen cells with sterigma-like connectors with the terminal swollen cell becoming a mature basidiospore. Redraw from Nguyen et al. (2014) by Mao-Qiang He

Genera included

Family Geminibasidiaceae H.D.T. Nguyen, N.L. Nick. & Seifert 2013

Basidioascus Matsush. 2003

Geminibasidium H.D.T. Nguyen, N.L. Nick. & Seifert 2013

Evolution

Initial phylogenetic analysis placed the order as a sister group to Wallemiales in Wallemiomycetes, but phylogenetic analysis and differences in septal pore morphology suggested a separate class, Geminibasidiomycetes (Nguyen et al. 2015). A genome analysis identified genes involved in meiosis (Nguyen et al. 2015). Using whole genome data, the split between *Basidioascus* and *Wallemia* was estimated 250 ± 29 million years ago (Nguyen et al. 2015).

Justification of order and problems

Geminibasidiales is justified based on molecular phylogenetic analyses, as well as the peculiar morphology and the, often xerotolerant nature of its members. As Geminibasidiales sits at the base of Agaricomycotina, phylogenomic analysis using high quality genomes of species in Geminibasidiales and Wallemiales may provide insight in the origin of Agaricomycotina.

The asexual genus *Chernovia* was described to accommodate an unusual yeast isolate from soil (Yurkov et al. 2016). Whether this monotypic genus is a member of Geminibasidiales or represents a separate lineage in Wallemiomycetes requires additional studies.

Significance

Ecological and economical roles

Species of Geminibasidiales are mainly known from soil, including heat-treated soil, often xerotolerant and able to grow at media with water activity (A_w) < 0.85, but they grow better at somewhat higher water activities (Nguyen et al. 2013; Nasr et al. 2014b). It has also been suggested that these fungi may be able to live or survive in seawater (Nguyen et al. 2013).

Chemical diversity

Unknown.

Georgefischeriales R. Bauer, Begerow & Oberw. 1997

Contributed by: Teodor T. Denchev, Cvetomir M. Denchev, Dominik Begerow, Martin Kemler

Introduction

In the Exobasidiomycetidae, Georgefischeriales was erected to accommodate species having local interaction zones without interaction apparatus in intercellular hyphae, and poreless septa at maturity (Bauer et al. 1997). They produce small local interaction sites with small electron-opaque deposits of variable shape and size at the host-parasite interface. Intracellular hyphae and haustoria are lacking. The basidia and basidiospore discharge are diverse but characteristic for each family (Bauer et al. 1997, 2005; Begerow and McTaggart 2018). Georgefischeriales contains four families and seven genera, with a total of 51 species, mostly plant parasites. Parasitic members produce teliospores in vegetative parts of the hosts, mostly in leaves. Additionally, this order includes some species, known from the anamorphic stage only. The species are united by ultrastructural characteristics and molecular data (Bauer et al. 1997, 2001a, b; Begerow and McTaggart 2018).

Characters that define the taxa in the order

Species of Georgefischeriales are predominantly plant parasites that sporulate in vegetative parts of the hosts. Host spectrum includes monocots (with exception of *Georgefischeria*). Georgefischeriales is divided into four families: Georgefischeriaceae, Tilletiariaceae, Eballistraceae, and Gjaerumiaceae.

Georgefischeriaceae species are characterized by the formation of holobasidia and ballistosporic propagules, and loss of septal pores at maturity. *Georgefischeria* are parasites on Convolvulaceae. Infection is systemic. Their sori are in leaves, causing yellowing of leaves and blackening of veins, or caulicolous, causing hypertrophy and witches' brooms on the axillary shoots. Spore mass is dark, agglutinated, not bursting. Spores are lightly pigmented (pale yellowish to olive-brown), with a thick and multilayered spore wall, and gelatinized outer layers. Spore germination results in a holobasidium bearing apically 2–4 basidiospores which germinate by hyphae and also by ballistospores (Bauer et al. 1997, 2001a, b; Vánky 2013; Begerow and McTaggart 2018). *Jamesdicksonia* are mostly parasites (on Poaceae and Cyperaceae). Their sori are in leaves, leaf sheaths or stems as black spots, pustules or crusts. Spores are solitary or in groups, not agglutinated in balls, darkly pigmented, embedded in the host tissue or erumpent, not powdery, or occurring on the surface of the plant and powdery. Spore germination results in a holobasidium with ballistic basidiospores or secondary ballistospores (Bauer et al. 1997, 2001a, b; Vánky 2013; Denchev and Denchev 2016; Begerow and McTaggart 2018). Based on molecular phylogenetic analyses, two asexual yeast species, isolated from plant surfaces, were also added to *Jamesdicksonia* (Richter et al. 2019; Li et al. 2022c).

Tilletiariaceae species are characterized by the formation of phragmobasidia with lateral ballistosporic basidiospores, and loss of septal pores at maturity. *Phragmotaenium* consists of one plant parasitic species, *P. indicum* (Vánky et al.) R. Bauer et al. (2001a), and five asexual yeast species, isolated from plant surfaces (Wang et al. 2015d; Li et al. 2022c). *Phragmotaenium indicum* is a parasite on Poaceae, that forms sori in leaves and stems as black spots. Spores are single or in groups but not aggregated in balls, embedded in the host tissue, not erumpent and not powdery; pigmented (olive-brown). Spore germination results in a phragmobasidium with ballistosporic basidiospores (Bauer et al. 2001a; Vánky 2013; Begerow and McTaggart 2018). *Tilletiaria* is a monotypic genus. *Tilletiaria anomala* Bandoni & B.N. Johri is isolated from dead wood. This species has tough, grayish brown colonies and monokaryotic, hyaline, branched, septate hyphae that bear both teliospores and ballistospores. Mature septa is poreless. Spore germination results in a four-celled phragmobasidium with ballistosporic basidiospores (Bandoni and Johri 1972; Vánky 2013; Begerow and McTaggart 2018). *Tolyposporella* are parasites on Poaceae and Eriocaulaceae. Sori are mostly in leaves or leaf sheaths, sometimes in axis of aborted inflorescence. Spores are with a thickened outer wall, firmly agglutinated into spore balls; lightly to darkly pigmented. The spore germination results in a phragmobasidium producing laterally ballisto-basidiospores (Vánky 2013; Begerow and McTaggart 2018).

Eballistraceae includes a single genus, *Eballistra*. It is characterized by having holobasidia and lacking ballistic basidiospores and ballistoconidia. Sori are in leaves and stems of Poaceae as lead coloured, non-erumpent spots. Spores are solitary or in groups but not aggregated in balls, embedded in the host tissue, not powdery; pigmented (olive-brown). Spore germination results in a holobasidium on which apically, passively released basidiospores are produced (Bauer et al. 2001a; Vánky 2011, 2013; Begerow and McTaggart 2018). *Eballistra* do not produce ballistoconidia but form budding yeasts, that are globose to ellipsoidal in form (Singh and Pavgi 1973). A septal pore is absent (Bauer et al. 2001a).

Gjaerumiaceae is a monotypic family. *Gjaerumia* is characterized by having holobasidia, ballistosporic propagules, and a dolipore in young parasitic hyphae. This genus consists of three plant parasitic species and five asexual yeast species. Parasitic species form sori in leaves, as dark-colored spots. Spores are single, embedded in the host tissue, pigmented. Spore germination results in a holobasidium with terminal basidiospores. Basidiospores are fusiform and are passively released. Occasionally, they conjugated on the basidium. Conjugated basidiospores germinate while still connected to the basidium, producing ballistoconidia. Unconjugated basidiospores, while still connected to the basidium, also may form ballistoconidia (Bauer et al. 2005; Vánky 2008, 2011, 2013). In young parasitic hyphae, septal pore is a dolipore (Bauer et al. 2005). Hosts are members of monocots families: Asparagaceae, Asphodelaceae, and Nartheciaceae (Vánky 2011, 2013). Five free-living yeast species with unknown sexual states were recently described in *Gjaerumia*, based on molecular phylogenetic analyses (Wang et al. 2015d; Tan et al. 2021; Li et al. 2022c).

Plates

Fig. 27 Georgefischeriales. **a**–**i** habit. **a** *Eballistra brachiariae* on *Urochloa trichopus,* Zimbabwe (Vánky Ustil. Exs. 1070); **b** *Eballistra lineata* on *Zizania palustris,* Canada (Vánky Ustil. Exs. 741); **c** *Eballistra oryzae* on *Oryza sativa,* India (Vánky Ustil. Exs. 910); **d** *Gjaerumia ossifragi* on *Narthecium ossifragum,* Norway (Vánky Ustil. Exs. 1187); **e** *Jamesdicksonia brunkii* on *Bothriochloa saccharoides,* Mexico (Vánky Ustil. Exs. 1206); **f** *Jamesdicksonia dactylidis* on *Dactylis glomerata,* Bulgaria (SOMF 401); **g** *Jamesdicksonia festucae* on *Festuca tolucensis,* Mexico (Vánky Ustil. Exs. 1207); **h** *Jamesdicksonia ischaemiana* on *Ischaemum semisagittatum,* India (Vánky Ustil. Exs. 1344); **i** *Phragmotaenium indicum* on *Polytrias indica,* India (Vánky Ustil. Exs. 1345). Arrows in **a**, **c**–**i** indicate sori. Scale bars: a–i = 1 cm

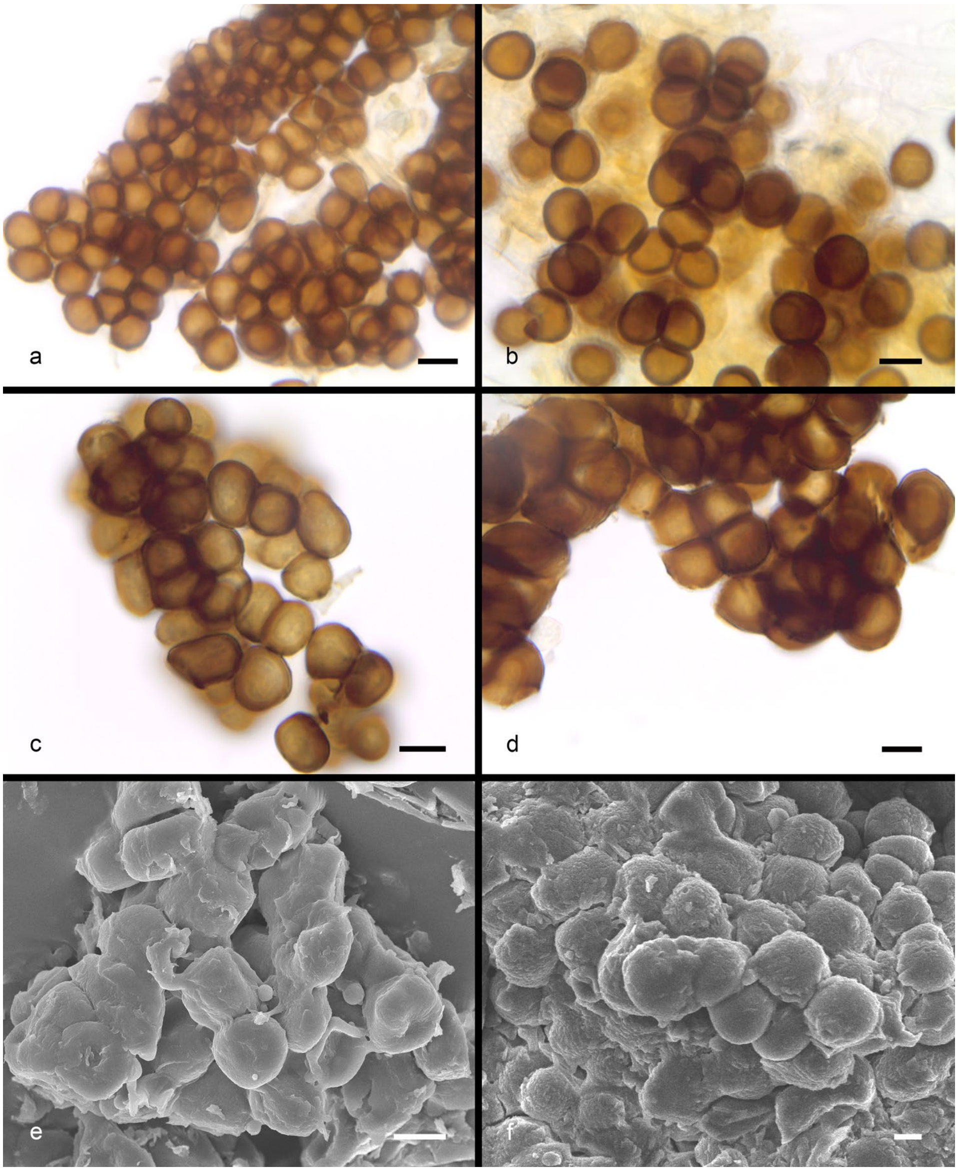


Fig. 28 Georgefischeriales. **a**–**d** spores in LM. **a** *Eballistra brachiariae* on *Urochloa distachya,* Reunion, Denchev 2647; **b** *Gjaerumia ossifragi* on *Narthecium ossifragum,* Norway (Vánky Ustil. Exs. 1187); **c** *Jamesdicksonia anadelphiae* on *Anadelphia pumila,* Guinea (HUV 13669, isotype); **d** *Jamesdicksonia anadelphiae-trichaetae* on *Anadelphia trichaeta,* Guinea (B 70 0015713, holotype). **e**, **f** Spores in SEM. **e** *Eballistra brachiariae* on *Urochloa distachya,* Reunion, Denchev 2647; **f** *Jamesdicksonia anadelphiae-trichaetae* on *Anadelphia trichaeta*, Guinea (B 70 0015713, holotype). Scale bars: a–d = 10 µm, e, f = 5 µm

Genera included

- Family Eballistraceae R. Bauer, Begerow, A. Nagler & Oberw. 2001
  - *Eballistra* R. Bauer, Begerow, A. Nagler & Oberw. 2001
- Family Georgefischeriaceae R. Bauer, Begerow & Oberw. 1997
  - *Georgefischeria* Thirum. & Naras. 1963
  - *Jamesdicksonia* Thirum., Pavgi & Payak 1961
- Family Gjaerumiaceae R. Bauer, M. Lutz & Oberw. 2005
  - *Gjaerumia* R. Bauer, M. Lutz & Oberw. 2005
- Family Tilletiariaceae R.T. Moore 1980
  - *Phragmotaenium* R. Bauer, Begerow, A. Nagler & Oberw. 2001
  - *Tilletiaria* Bandoni & B.N. Johri 1972
  - *Tolyposporella* G.F. Atk. 1897

Evolution

Families of Georgefischeriales are well defined, based on the basidial morphology and ultrastructural data, and the molecular phylogeny is highly congruent with these data. Basal dichotomy is between Eballistraceae and the branch uniting Georgefischeriaceae and Tilletiariaceae (Bauer et al. 2001a). *Eballistra* are characterized by having a holobasidium, but ballistic basidiospores and ballistoconidia are absent. Loss of the ballistospore mechanism represents an apomorphy for the Eballistraceae (Bauer et al. 2001a). Triradiate basidiospores of *Eballistra oryzae* (Syd. & P. Syd.) R. Bauer et al. on rice resemble radiate conidia of aquatic ascomycetes and is adaptation to water dispersal (Bauer et al. 2001a).

Georgefischeriaceae shares the formation of holobasidia with the *Eballistraceae* and the formation of ballistic propagules with the *Tilletiariaceae*. Basidia observed in *Jamesdicksonia* with basidiospores having a characteristic abaxial orientation of the hilar appendices are typical for Exobasidiaceae but occur also in species of the Tilletiales (e.g., *Ingoldiomyces*, *Oberwinkleria*, *Tilletia*) and Dossansiales (*Melaniella*) (Ingold 1995; Vánky and Bauer 1995, 1996; Bauer et al. 1997, 1999a, b). Bauer et al. (2001a) considered the exobasidaceous basidium as apomorphic for Exobasidiomycetes and plesiomorphic for Georgefischeriales; and accordingly, the presence of ballistic propagules in Ustilaginomycetes and Exobasidiomycetes as indicator that the ballistospore mechanism was already established before Georgefischeriales diverged from the other groups of Exobasidiomycetes. Presence of phragmpobasidia separates the *Tilletiariaceae* from the other members of this order.

Poreless septa are an apomorphic character for Georgefischeriales. They also occur in Ustilaginales, an order showing no further ultrastructural similarity to Georgefischeriales. Bauer et al. (2001a) considered the presence of poreless septa in these two orders as a result of convergent evolution.

As the other members of Georgefischeriales, the septa in the soral hyphae of *Gjaerumia* are poreless at maturity, however, in young parasitic hyphae, the septal pore is a dolipore (Bauer et al. 2005). It was concluded that in *Gjaerumia* the septa close later during maturation than in the other species of Georgefischeriales (Bauer et al. op.c.). Because in Exobasidiomycetes poreless septa occur only in Georgefischeriales, Bauer et al. (op.c.). considered the loss of septal pores as apomorphic for Georgefischeriales. Formation of dolipores in maturing soral hyphae of *Gjaerumia* reflects that Georgefischeriales arose from a doliporic ancestor (Bauer et al. op.c.).

Justification of order and problems

The members of *Tilletiopsis* (Entylomatales) are saprotrophic yeast-like fungi. Description of species in *Tilletiopsis* was originally based on morphological characteristics, but the phylogenetic analyses performed by Wang et al. (2015d) and Richter et al. (2019) show that this genus was polyphyletic and its taxonomic scheme was changed. *Tilletiopsis derxii* M. Takash. & Nakase (nom. inval.), *T. flava* (Tubaki) Boekhout, *T. fulvescens* Gokhale, and *T. oryzicola* M. Takash. & Nakase (nom. inval.) were transferred to *Phragmobasidium* (Begerow et al. 2000; Wang et al. 2015d), while *T. minor* Nyland and *T. penniseti* Takashima & Nakase (nom. inval.) were considered to be members of *Gjaerumia* (Bauer et al. 2005; Wang et al. 2015d). Currently, only five species are recognized in *Tilletiopsis* (He et al. 2022).

Economic importance

Eballistra oryzae is the causal agent of leaf smut on rice. It is a widely distributed species, where rice is cultivated, but it does not cause crop losses.

Gloeophyllales Thorn 2007

Contributed by: Ricardo García-Sandoval, Sergio P. Gorjón

Introduction

Gloeophyllales is a small order containing a morphologically diverse fungal group of polypores, agarics, and resupinate fungi, mostly producing a brown rot wood decay and being found mainly on coniferous substrata. Even when this order is consistently recovered as a monophyletic group (Binder et al. 2005; García-Sandoval et al. 2011; Chen et al. 2020), there is no evident synapomorphy, either morphological, ecological, or physiological, and this results on a quite diverse and interesting group. According to He et al. (2019a, b) it contains the single family Gloeophyllaceae, 13 genera and about 50 species. The order includes a single family, Gleophyllaceae, and even when two other families have tentatively been proposed for genera in the order, Boreostereaceae and Jaapiaceae, there is no consistent phylogenetic evidence supporting their existence inside the order (Chen et al. 2020).

Morphological and physiological diversity in the order, even considering its relatively small size, make this group a very interesting subject for further studies on the evolution of morphology and physiology. So far, only a preliminary attempt on ancestral character reconstruction analysis for wood decay pattern, with parsimony, has been made (García-Sandoval et al. 2011), but formal analysis on morphology and physiology are still missing.

History

Gloeophyllales was first considered as an order by Thorn (Hibbett et al. 2007), supported on the phylogenetic evidence available at the time (Thorn et al. 2000; Binder et al. 2005) and subsequently considered in multigene analyses as a separated order related to Corticiales, Thelephorales, and Polyporales (García-Sandoval et al. 2011) or even related to the Phallomycetidae in the gomphoid-phalloid clade (Gomphales, Geastrales, Phallales, and Hysterangiales) (He et al. 2019a). The initial delimitation included the polypore genus *Donkioporia*, but subsequent phylogenetic analysis (García-Sandoval et al. 2011) places the genus in its current position in the Polyporaceae.

Traditionally, species of *Gloeophyllum*, have been considered within the Polyporaceae and related to genera such as *Daedalea* for presenting the same type of brown rot and type of spores. In any case, some characteristics such as colored vegetative hyphae and other chemical characteristics have long been pointed out as characters that deviate from what is typical for the family (Ryvarden 2005). Species of the pileate-stipitate *Neolentinus* and *Heliocybe* were considered long time among the Agaricales.

García-Sandoval et al. (2011) considered seven genera in the order, all included in a single family, Gloeophyllaceae. Later, He et al. (2014) resurrected *Griseoporia*, describing a new species in the genus, *G. taiwanensis* Y.C. Dai & S.H. He, and propose a new genus in the family, *Hispidaedalea*, based in the phylogenetic placement of *Daedalea imponens* Ces., raising to nine the number of genera in the order.

Recently Chen et al. (2020) investigated the phylogenetic position of two previously described genera, *Paratrichaptum* and *Jaapia*, and recovered both taxa in the Gloeophyllaes. Both genera were recovered with very high support, even when the relationships inside the order were not so clear, a situation frequently observed in previous studies.

Paratrichaptum was originally described as a monotypic genus in the polypores sensu lato (Corner 1987), and very few specimens were available for their study. The finding of fresh material made possible to investigate their phylogenetic relationships, discovering its relationship with the Gloeophyllales (Chen et al. 2020).

More surprising what discovering *Jaapia* as part of the Gloeophyllales in a six-gene phylogeny. Binder et al. (2010) recovered *Jaapia argillacea* Bres. as a monotypic lineage between Atheliales and Russulales and decided to propose a new order and family. Worth to mention that the authors did not include any member of the Gloeophyllales in their taxonomic sampling. Further analysis with a larger sampling (Chen et al. 2020) recovered *Jaapia* nested inside the Gloeophyllales with high support.

Currently the most comprehensive analysis (Chen et al. 2020) recover eleven genera with high support as a sister clade with a larger group that includes Polyporales and Thelephorales. This relationship was also recovered previously (García-Sandoval et al. 2011), with the addition of Corticiales to the sister group. Most likely the Gloeophyllales is closely related to Polyporales and Thelephorales, with an uncertain affinity with Corticiales. Considering the wide morphological diversity in the order, these relationships are not surprising.

Several phylogenetic analyses were published for genera in the order since the Gloeophyllales was first proposed. Most of the studies were restricted to particular subclades of the Gloeophyllales since the main objective was to describe new species in *Heliocybe* (Zhang et al. 2018), *Veluticeps* (He and Li 2013; Yang and He 2016), *Gloeophyllum* (Mattoo et al. 2022), and even one species was described in *Neolentinus* without phylogenetic evidence (Wartchow 2019).

Characters that define the taxa in the order

Gloeophyllales is a variable and diverse group containing resupinate, effuse-reflexed to pileate polyporoid and stipitate and pileate agaricoid species. In the resupinate species, the hymenophore varies from smooth to more or less odontioid, sometimes with aculei formed by sterile hyphal elements. In the pileate polyporoid species, the basidiome is usually dimidiate and triquetros to applanate in section, and the hymenophore is very variable with round to angular pores, and labyrinthine to daedaleoid or laminar pores. In those agaricoid species, the hymenophore is laminar, protected by a typical cap as pileal surface and erected by a central to lateral stipe. Usually, the basidiome of Gloeophyllales presents some color change, darkening or turning green in the presence of potassium hydroxide.

Microscopically, the species of Gloeophyllales construct their basidiomes with a dimitic to trimitic hyphal system with brown vegetative hyphae. The resupinate species also posseses skeletal hyphae (if we except *Jaapia* and consider it within the Gloeophyllales), and the pileate species produce more complex basidiomes with skeletal and binding hyphae. The generative hyphae may or not have clamp-connections, and present thickened walls. Cystidial elements are usual among the Gloeophyllales, as thick-walled skeletocystidia, smooth or encrusted, pale to dark reddish brown. The basidia bear 4-sterigmate and basidiospores are smooth, cylindrical to fusiform, thin to thick-walled, with hyaline to yellowish walls, not reacting in Melzer's reagent (cyanophilous and dextrinoid in *Jaapia*).

Gloeophyllum, the generic type, encompasses species with pileated basidiomes of a polyporoid appearance, with the hymenophore very variable, from poroid to lamellar, or with irregular to labyrinthine pores. He et al. (2014) proposed a phylogeny supporting the separation of *Gloeophyllum* s.l. in smaller entities, establishing differences between *Gloeophyllum* s.str., *Griseoporia* (with typically poroid hymenophore and resupinate to effused-reflexed basidiomes), *Osmoporus* (poroid hymenophore and pileate basidiomes), and *Hispidaedalea* (daedaleoid to lamellate hymenophore, pileate basidiomes, and trimitic hyphal system).

Among the resupinate genera, *Boreostereum* presumably causes a white rot and is considered basal in the evolution of the group (García-Sandoval et al. 2011). Species of *Boreostereum* have a dimitic hyphal system and the hyphae bear encrustations that turn greenish when potassium hydroxide is applied. The other genera of Gloeophyllales with the greatest number of species and a resupinated habit are *Veluticeps* and *Chaetodermella*, but unlike *Boreostereum* they produce a brown decomposition of the wood.

Gloeophyllales comprises some agaricoid genera, with a typical stipe and pileus. *Neolentinus* (similar to the genus *Lentinus* but differing in the white rot and the phylogenetical placement in the Polyporales), and *Heliocybe*, a small agaricoid genus with a circular cap and cuticle radially furrowed with brown-ochraceous scales, which crack radially, giving the appearance of sun rays (hence the name). Sterile coralloid forms are reported in *Neolentinus* (Vlasenko et al. 2017).

Mating systems also are variable; *Neolentinus* and *Gloeophyllum* are bipolar, *Veluticeps* is reportedly tetrapolar, and *Boreostereum* has been suggested to be homothallic (Redhead and Ginns 1985; Gilbertson and Ryvarden 1986; Martin and Gilbertson 1973; Nakasone 1990).

All the genera are known for been wood decayers, and brown rot type is the most frequent condition reported (*Neolentinus, Gloeophyllum, Veluticeps,* and *Paratrichaptum*), but contradictory reports exist for white or brown rot condition for *Boreostereum* (Chamuris 1988) and *Jaapia* (Binder et al. 2010). It is worth to mention that a better understanding of the wood decay process needs the comparative analysis of genomic information (Riley et al. 2014), in order to properly understand the process, and been able to study this character in the context of phylogeny.

Plates

Fig. 29 Diversity of basidiome types in Gloeophyllales. **a** *Veluticeps berkeleyi* (SPG 2412, Spain); **b** *Osmoporus odoratus* (ERD 8755, Spain); **c** *Osmoporus protractus* (ERD 9047, Spain); **d** *Osmoporus protractus*, detail (ERD 9047, Spain); **e** *Gloeophyllum sepiarium* (ERD 23-XII-2022, Spain); **f** *Gloeophyllum sepiarium*, detail (ERD 23-XII-2022, Spain); **g** *Neolentinus adhaerens* (ERD 4222, Spain); **h** *Heliocybe sulcata* (MOA 3899, Spain); **i** *Neolentinus lepideus* (LS, Spain); **j** *Gloeophyllum trabeum* (LS, Spain). Credit: **a** Sergio P. Gorjón; **b**–**g** Enrique Rubio Domíguez; **h** Miguel Olivera Amaya; **i**, **j** Leandro Sánchez

Genera included

Family Gloeophyllaceae Jülich 1982
 = Boreostereaceae Jülich
  Boreostereum Parmasto 1968
  Chaetodermella Rauschert 1988
  = *Chaetoderma* Parmasto 1968
  Gloeophyllum P. Karst. 1882
  = *Anisomyces* Theiss. & Syd. 1914
  = *Ceratophora* Humb. 1793
  = *Lenzitina* P. Karst. 1889
  = *Phaeocoriolellus* Kotl. & Pouzar 1957
  = *Reisneria* Velen. 1922
  = *Serda* Adans. 1763
  = *Sesia* Adans. 1763
  Griseoporia Ginns 1984
  Heliocybe Redhead & Ginns 1985

Hispidaedalea Y.C. Dai & S.H. He 2014
Neolentinus Redhead & Ginns 1985
Osmoporus Singer 1944
Paratrichaptum Corner 1987
Veluticeps Cooke 1879
= *Chaetocarpus* P. Karst. 1889
= *Columnocystis* Pouzar 1959
genera *incertae sedis*
Campylomyces Nakasone 2004
Pileodon P. Roberts & Hjortstam 1998
Mycothele Jülich 1976
Stiptophyllum Ryvarden 1973

Evolution

The most comprehensive phylogenies (García-Sandoval et al. 2011; Chen et al. 2020) have recovered Gloeophyllales with high support, and as sister group with a clade including Thelephorales and Polyporales. In one of the studies (García-Sandoval et al. 2011) the sister clade also included Corticiales, and recently a phylogeny with a genomic data set (Li et al. 2021c) recovered Gloeophyllales (plus *Jaapia*) as sister group with Corticiales, as well as another multigene data set (Sulistyo et al. 2021) that recovers the four orders in a monophyletic group.

Inside the Gloeophyllales relationships are less clear. *Veluticeps* and *Chaetodemella* are consistently recovered as monophyletic, as well as *Osmoporus* and *Griseoporia*, and *Neolentinus* and *Heliocybe*. *Gloeophyllum* sensu stricto also is recovered as monophyletic, but relationships between the small clades retrieved are unclear. *Boreostereum* was recovered as the sister group with the rest of the order (García-Sandoval et al. 2011), and *Jaapia* was recovered in close association with it (Chen et al. 2020), maybe related with their contradicted status as white or brown decayers, but also *Paratrichaptum* is recovered as sister group with *Borostereum*.

Almost all genera in Gloeophyllales cause brown rot, except for *Boreostereum*. *Boreostereum* is possibly associated with a white rot (Martin and Gilbertson 1980) but also viewed as brown rot (Chamuris 1988). If we consider *Boreostereum* as the basal lineage in Gloeophyllales (García-Sandoval et al. 2011), then the plesiomorphic characters are the resupinate basidiomes and the white type of rot, if this type of rot is confirmed for *Boreostereum*. If *Paratrichaptum* represents the earliest diverging lineage in Gloeophyllales, as stated by Chen et al. (2020), pileate basidiomes and brown rot appear to be ancestral states of Gloeophyllales. If considering *Jaapia*, the type of rot is still not clear, but may belong to a new type of brown rot based on genomic analyses (Riley et al. 2014).

Justification of order and problems

The taxonomy and phylogenetic placement of Gloeophyllales among Agaricomyces is still controversial, and recently some new proposals have raised about the natural relationships with other orders. If we follow the phylogenetical proposal by Chen et al. (2020) based on the analyses of 5.8S, nuc 18S, nuc 28S, *rpb1*, *rpb2*, and *tef1* sequences, Jaapiales should be considered a synonym of Gloeophyllales, and *Jaapia* and *Paratrichaptum* be included in the order. Previous six-gene phylogeny placed *Jaapia* as the sister group to Agaricomycetidae, consisting of Agaricales, Amylocorticiales, Atheliales, and Boletales (Binder et al. 2010).

As advised by Chen et al. (2020), deviating taxon- or gene-sampling applied to different analyses may result in different positions of the taxa on trees. The six-gene phylogeny by García-Sandoval et al. (2011), placed *Boreostereum radiatum* (Peck) Parmasto as the sister group to the core group of Gloeophyllales, consisting of the genera *Chaetodermella*, *Gloeophyllum*, *Heliocybe*, *Neolentinus*, *Osmoporus*, and *Veluticeps*. In the analysis by Chen et al. (2020), *B. radiatum* is recovered as a sister taxon to *Paratrichaptum accuratum*, but the position is weakly supported.

Gloeophyllales is consistently recovered as a clade with high support. The order includes a single family, Gloeophyllaceae, and so far, there is no solid or consistent phylogenetic evidence for adding more families. The Boreostereaceae (*Boreostereum* and *Veluticeps*) is consistently recovered inside the order, but not at as a clade, and in consequence the family is included as a synonym of Gloeophyllaceae. The Jaapiales, and Jaapiaceae, are recovered nested in the Gloeophyllales (Chen et al. 2020) or as a sister group with it (Sulistyo et al. 2021; Zhao et al. 2017). It is worth to mention that the relationship between Jaapiales and Gloeophyllales was not suspected before because the phylogenetic evidence available was lacking a comprehensive taxonomic sampling, neither Binder et al. (2010) include Glophyllaes in their study of Jaapiales, or García-Sandoval et al. (2011) included *Jaapia* in their analysis of Gloeophyllales.

The present phylogenomic tree is more in accordance with the partial multigene analysis by Chen et al. (2020). Jaapiales and Gloeophyllales are two orders very closely related, but we have no included *Paratrichaptum* in the analyses. If including *Paratrichaptum,* the results are like those of Chen et al. (2020), there should not be problematic to consider Jaapiales and Gloeophyllales as a unique entity as order level. It should be of great interest to known better the type of rot of *Jaapia* to contemplate if the brown rot type is common to Jaapiales/Gloeophyllales, or some evolutionary process arised from an original brown type of rot. Considering that the phylogenies with the most comprehensive taxonomic sampling recovers the Jaapiales inside

Gloeophyllales, we can simply consider Jaapiales as a synonym of Gloeophyllales, mostly because of two reasons: (1) the taxonomic decisions should be supported on the most inclusive phylogenetic evidence, which in this case points to *Jaapia* to be inside Gloeophyllales; (2) even if Jaapiales were confirmed to be sister group to Gloeophyllales, an independent order and family containing only two species will be undesirable because it will introduce an artificial increase of family diversity, derived from a nomenclatural decision.

A more comprehensive data set, including more genes and more species, is needed to address relationships inside the Gloeophyllales, and to be able to perform formal ancestral character state analysis for the study of morphology and physiology. So far is not possible to conclude that resupinate basidiome or a particular decay pattern are the conditions in the most recent common ancestor, and even when we know that resupinate is the ancestral condition in Agaricales, and that resupinate basidiomes have a high transformation rate (Sánchez-García et al. 2020) phylogenetic evidence for the Gloeophyllales is not well supported yet.

Significance

Ecological and economical roles

Several studies of wood decay chemistry are conducted in species of the order (Goodell et al. 2020), and their ecological impact also is considered significant (Fukasawa 2021). Resolving the relationships of the Gloeophyllales is important to understanding the evolution of the brown-rot mode of wood decay in Agaricomycotina (García-Sandoval et al. 2011). Hibbett and Donoghue (2001) inferred six independent origins of brown rot, including one in the lineage leading to Gloeophyllales, and suggested that the evolution of a brown rot promoted shifts to specialization on coniferous substrates. Currently the most frequent, but not exclusive, substrates for brown rot Agaricomycetes are conifers (Hibbett and Donoghue 2001), so the species of Gloeophyllales are of major importance in coniferous forest as plant remains efficient decomposers.

Some species, as *Neolentinus lepideus* (Fr.) Redhead & Ginns, are edible and considered of gastronomic interest in Asia and Mexico (Moreno-Fuentes et al. 1996), and some tests have been done to cultivate it commercially (Kim et al. 1994, 2013).

Chemical diversity

Various vibralactones have been isolated and studied in *Boreostereum vibrans* (Berk. & M.A. Curtis) Davydkina & Bondartseva. These compounds were no cytotoxic against human cancer cell lines and showed no inhibitory activity on the pancreatic lipase (Wang et al. 2014a) or are only weak cytotoxicity to determinate human cancer cell lines (He et al. 2019b).

Some studies indicated that the extract of culture filtrate of *Neolentinus lepideus* effectively inhibited tyrosinase activity, that controls melanin formation in the human skin (Ishihara et al. 2018).

Golubeviales Q.M. Wang, F.Y. Bai, Begerow & Boekhout 2023

Contributed by: Martin Kemler, Cvetomir M. Denchev, Dominik Begerow, Teodor T. Denchev, Teun Boekhout

Introduction

Golubeviales was erected to accommodate the species *Golubevia pallescens* (Gokhale) Q.M. Wang et al. previously residing in the genus *Tilletiopsis* (Wang et al. 2015d). The order was erected purely on phylogenetic evidence, it is monotypic and only contains Golubeviaceae with *Golubevia*. Since the erection of the order a second species, *G. heteromorpha* Boekhout et al., was described (Richter et al. 2019). A further species is assumed (Köhl et al. 2019; Russ et al. 2021). Currently, one family, one genus, and three species are included in this order.

History

In 1972, Gokhale described a filamentous-growing basidiomycetous fungus in *Tilletiopsis* Derx ex Derx (Derx 1930) that only reproduced asexually with sausage-shaped ballistoconidia (Gokhale 1972) as *Tilletiopsis pallecens* Gokhale. Although the species in *Tilletiopsis* differed morphologically to some extent, it took molecular evolutionary studies to show that the genus was polyphyletic (Boekhout. 1991a, b; Boekhout et al. 1995; Begerow et al. 2000; Fell et al. 2000; Wang et al. 2015d; Richter et al. 2019; Guarnaccia et al. 2024). These studies also revealed that *T. pallescens* was only remotely related to other such fungi and hence it was proposed to place it in a separate genus for which the name *Golubevia* was proposed (Wang et al. 2015d). Unfortunately, the basionym was lacking in the original description, and, hence, the name was invalidly published. Richter et al. (2019) validated this genus name, but did not make a correct mycobank number, and, hence, this attempt, also failed. Guarnaccia et al. (2024) validated the genus *Golubevia* Q.M. Wang, F.Y. Bai, Begerow & Boekhout, MycoBank MB 847646 with *Golubevia pallescens* (Gokhale) Q.M. Wang, F.Y. Bai, Begerow & Boekhout as type species. A new combination was made, namely *Golubevia pallescens* (Gokhale) Q.M. Wang, F.Y. Bai, Begerow & Boekhout, MycoBank MB 847647, and two species were described, namely *Golubevia heteromorpha* Boekhout, C. Richt. & Yurkov, MycoBank, MB 847648, and *Golubevia mali* Guarnaccia, Spadaro & Boekhout, MB 847651. Furthermore, family Golubeviaceae Q.M. Wang, F.Y. Bai, Begerow & Boekhout, MycoBank MB847649, and order Golubeviales Q.M. Wang, F.Y. Bai, Begerow & Boekhout, MycoBank MB 847650 were described. The cited molecular phylogenetic studies placed this order in class Exobasidiomycetes, subphylum Ustilaginomycotina.

Characters that define the taxa in the order

The two published species are only known in their yeast stage and are characterized either by whitish (*G. pallescens*) or whitish to creamish brown yeast colonies (*G. heteromorpha*) that can have uneven margins (Boekhout 1991a; Richter et al. 2019). The yeast stage proliferates via budding. Sexual reproduction is unknown, but in *G. pallescens* ballistospores are produced on holobasidial-like structures. These germinate from conidia (Boekhout 1991a). Hyphal growth is known on artificial media for *G. pallescens*. The hyphae are septate and branch regularly. Chlamydospores are formed intercalary or terminal. Although both species grow on a wide range of carbon sources, they only do so in the presence of oxygen and fermentation is not known (Boekhout 1991a, 2011; Richter et al. 2019).

Plates

For illustrations, see Boekhout (1991a, b: Fig. 52), Boekhout (2011: Fig. 160.11 & Fig. 160.12), Richter et al. (2019: Fig. 3II), and Figs. 6 and 7 in Guarnaccia et al. (2024).

Genera included

Family Golubeviaceae Q.M. Wang, F.Y. Bai, Begerow & Boekhout 2023
  Golubevia Q.M. Wang, F.Y. Bai, Begerow & Boekhout 2023
  [*Golubevia* Q.M. Wang, F.Y. Bai, Begerow & Boekhout 2015] (nom. inval.)
  [*Golubevia* Q.M. Wang, F.Y. Bai, Begerow & Boekhout 2019] (nom. inval.)

Evolution

Not much is known about the evolutionary trends within this order as presently it contains only one family and one genus with only three species. Similar ballistoconidium-forming fungi belong to various orders in Exobasidiomycetes, such as Georgefischeriales, Robbauerales, and Entylomatales (Wang et al. 2015d). Figure 52E in Boekhout (1991a, b) does remind a germinating chlamydospore [or is it a teliospore?] with a basidium-like structure. However, the possibility of a sexual cycle needs further determination.

Justification of order and problems

Golubeviales is only phylogenetically characterized and used to be part of the anamorphous genus *Tilletiopsis*. Together with the Robbauerales, they form a sister group to the rest of the Exobasidiomycetes (Richter et al. 2019). In other phylogenetic studies the Golubeviales are sister group to the Microstromatales or the Tilletiales within the Exobasidiomycetes (McTaggart et al. 2020). The members of this clade are ecologically not well characterized, but are known to occur in the phyllosphere of plants (see Economic importance).

Although this is another example of a small monotypic order, the evolutionary distances do warrant recognition as a distinct lineage at a higher taxonomic level. Presently, recognition at the ordinal level seems justified, but further confirmation by increasing species sampling is suggested.

Economic importance

Species in the Golubeviales occur in plant phyllospheres where they can show antagonistic behaviour against other fungi, especially in their interaction with plant pathogenic mildews (Klecan et al. 1990; Boekhout 1991a, 2011; Urquhart et al. 1994; Köhl et al. 2019). *Golubevia* species might be relevant as biocontrol agents (Klecan et al. 1990; Urquhart et al 1994; Ng et al. 1997; Köhl et al. 2019; Russ et al. 2021). In the presence of the plant-pathogen, the tested *Golubevia* isolates upregulated the expression of an unspecific peroxygynase, potentially interfering with the H_2O_2 production during conidiogenesis of the pathogen (Russ et al. 2021). Additionally, *Golubevia* species might induce plant defenses, thereby indirectly increasing the resistance of the plant to specific plant pathogens (Russ et al. 2021).

Golubevia pallescens, *G. heteromorpha* and *G. mali* are also three of several yeast-like species adding to the post-harvest disorder "white haze" of apple fruits (Boekhout et al. 2006; Baric et al. 2009; Weber and Zabel 2011; Prencipe et al. 2016; Richter et al. 2019; Guarnaccia et al. 2024). A recently recognized species, *G. mali*, is also involved in causing white haze and was found in various orchards in the North of Italy (Guarnaccia et al. 2024). The value of apples can be lowered after long-term storage under low-oxygen conditions, as a white haze caused by increased yeast growth can occur. Since its description in 2006, white haze has been found to occur in various European countries, such as Croatia, Germany, Italy and The Netherlands (Boekhout et al.

2006; Baric et al. 2010; Weber and Zabel 2011; Prencipe et al. 2016; Guarnaccia et al. 2024).

Other relevant data and future recommendations

Species of Golubeviales may have applied potential as biocontrol agents. However, their involvement in causing white haze on apples may limit the use of isolates for this purpose, but enzyme cocktails produced by these fungi might be interesting to test for biocontrol capabilities against powdery mildews.

Gomphales Jülich 1982

Contributed by: Admir J. Giachini, André Felipe da Silva, Mao-Qiang He, Rui-Lin Zhao

Introduction

Gomphales (Agaricomycetes) is monophyletic and has three families that encompass approximately 410 species in 19 genera. These include *Beenakia*, *Clavariadelphus*, *Gautieria*, *Gloeocantharellus*, *Gomphus*, *Kavinia*, *Lentaria*, *Phaeoclavulina*, *Ramaria*, *Ramaricium* and *Turbinellus* (He et al. 2019a; Cao et al. 2021b). Species of Gomphales have different basidioma morphologies, ranging from coral-shaped (*Phaeoclavulina*, *Ramaria*, *Ramaricium*, Lentariaceae), club-shaped (Clavariadelphaceae), gilled (*Gloeocantharellus*), cantharelloid-gomphoid (*Gomphus*, *Phaeoclavulina*, *Turbinellus*), tooth-like (*Beenakia*), resupinated-odontoid (*Hydnocristella*, *Kavinia*) and sequestrate (Gautieriaceae*)* (Hosaka et al. 2006; Giachini et al. 2010; Hibbett et al. 2014; González-Ávila et al. 2020; Sandoval et al. 2022; Rincón et al. 2023). In sum, members of this order are cosmopolitan, especially in the Northern Hemisphere (He et al. 2019a). Recently, the species *Gloeocantharellus corneri* was cited as occurring in the Amazon region of Brazil (Wartchow et al. 2022), considering that the species had been described previously in the Atlantic Forest (Watling and de Meijer 1997).

History

Early classification studies of the Gomphales presented wide variation in terms of their taxonomic boundaries, e.g. in order, number of families and genera considered. In the 1960s, the family Gomphaceae was proposed by Donk (1961, 1964) to include the genera *Beenakia*, *Chloroneuron, Gloeocantharellus*, *Gomphus, Kavinia*, *Lentaria*, *Ramaria* and *Ramaricium*. In the 1970s, the family Ramariaceae was proposed by Corner (1970) to include *Delentaria*, *Kavinia*, *Lentaria* and *Ramaria*, excluding *Chloroneuron* and *Gomphus* due to the absence of intermediate species between gomphoid and ramarioid morphologies.

In 1981, Gomphales was described by W. Jülich and included genera of the families Gomphaceae (e.g. *Gloeocantarellus*, *Gomphus*, *Kavinia*, *Psathyrodon*) with smooth hymenia, which gave rise to intermediate cantharelloid species (e.g. *Cantharellus*, *Craterellus*), and from these derived the wrinkled or folded hymenial gomphoid species (e.g. *Gomphus*, *Turbinellus*), Lentariaceae (*Delenteria*, *Lentaria*) and Ramariaceae (*Ramaria*) (Jülich 1981). *Pseudogomphus* and *Terenodon* were included in Gomphaceae by Hawksworth and collaborators in 1995, while *Ramaricium* (Ramariaceae) was officially proposed by Villegas et al. in (1999).

Characters that define the taxa in the order

Comparative studies on the anatomy and biochemistry of taxa are necessary to fully unravel the morphological features (synapomorphies) that unite species of Gomphales, since these features vary by fungal genera (Giachini et al. 2010). For example, the speciation of *Ramaria* lineages can be determined by assessing the presence or absence of clamp connections (Corner 1950, 1966a, 1970), cyanophilic reaction of basidiospores to cotton blue (Kotlaba and Pouzar 1964) and spore ornamentation (Marr and Stuntz 1973). Basidiome characteristics (color, shape, size, habitat, general appearance), size and ornamentation of basidiospores and hyphae construction (clamp, non-clamped, branching pattern) are useful for the speciation of *Phaeoclavulina* and *Turbinellus*. Likewise, evaluation of basidiospore shape, ornamentation and size, and basidiome morphology favor *Beenakia*, *Hydnocrystella* and *Kavinia* speciation (Nuñez and Ryvarden 1994; Chen et al. 2015; Robledo and Urcelay 2017). Colorimetric reactions to KOH, $FeCl_3$ and NH_4OH also promote species delimitation of *Clavariadelphus* (Methven 1990; Huang et al. 2020).

However, molecular identification is a better alternative for speciation of lineages, since phenotypic plasticity may bring inconsistent data for morphological characterization (Giachini et al. 2010). In this context, the use of molecular markers such as ITS, SSU, LSU, mtSSU, *rpb*2, *tef*1 and *atp*6 have been used for this purpose (Humpert et al. 2001; Li et al. 2022b). For example, genome sequencing has allowed the segregation of the genera *Phaeoclavulina* and *Turbinellus* from others that were considered to be within the genera *Ramaria* and *Gomphus* (Giachini et al. 2010).

Plate

Fig. 30 Selected basidiome types of Gomphales. **a** *Clavariadelphus amplus* (ZRL20201286, Sichuan province of China); **b** *Ramariopsis pulchella* (ZRL20161642, Zhejiang province of China); **c** *Turbinellus szechwanensis* (ZRL20230234, Hubei province of China); **d** *Lentaria* sp. (ZRL202201444, Hubei province of China)

Genera included

- Family Clavariadelphaceae Corner 1970
    - *Beenakia* D.A. Reid 1956
    - = *Psathyrodon* Maas Geest. 1977
    - *Clavariadelphus* Donk 1933
- Family Gomphaceae Donk 1961
    - *Araeocoryne* Corner 1950
    - *Delentaria* Corner 1970
    - *Destuntzia* Fogel & Trappe 1985
    - *Gautieria* Vittad. 1831
    - = *Ciliciocarpus* Corda 1831
    - = *Uslaria* Nieuwl. 1916
    - *Gloeocantharellus* Singer 1945
    - = *Alectorolophoides* Battarra ex Earle 1909
    - = *Linderomyces* Singer 1947
    - *Gomphus* Pers. 1797
    - = *Gomphora* Fr. 1825
    - *Phaeoclavulina* Brinkmann 1897
    - = *Chloroneuron* Murrill 1911
    - *Protogautieria* A.H. Sm. 1965
    - *Pseudogomphus* R. Heim 1970
    - *Ramaria* Fr. ex Bonord. 1851
    - = *Capitoclavaria* Lloyd 1922
    - = *Cladaria* Ritgen 1828
    - = *Clavariella* P. Karst. 1881
    - = *Corallium* G. Hahn 1883
    - = *Coralloidea* Roussel 1806
    - = *Coralloides* Tourn. ex Battarra 1755
    - = *Dendrocladium* (Pat.) Lloyd 1919
    - *Ramaricium* J. Erikss. 1954
    - *Terenodon* Maas Geest. 1971
    - *Turbinellus* Earle 1909
- Family Lentariaceae Jülich 1982
    - *Hydnocristella* R.H. Petersen 1971
    - *Kavinia* Pilát 1938
    - *Lentaria* Corner 1950
    - *Gomphocantharellus* L. Fan, Y.Y. Xu, Zhu L.Yang & S.P. Jian 2022
- Genera *incertae sedis*
    - *Schildia* Franchi & M. Marchetti 2015

Evolution

In the 1970s, a gomphoid ancestral morphology was suggested by Petersen (1971), and the "Clavaria theory" proposed by Corner (1972) suggested that *Clavaria* with smooth hymenia gave rise to the species *Cantharellus* and *Craterellus*, which were precursors of the genera *Gomphus* and *Turbinellus*. Cantharelloid/gomphoid and clavarioid fungi are historically speculated as the origin of fleshy basidiomycetes (Petersen 1971; Corner 1972; Jülich 1981). It has been suggested that cantharelloid, ramarioid, and club-like fungi were derived from agaricoid ancestors (Petersen 1971; Singer 1986). Species of Gomphales have evolved to enhance their metabolism and affinity for different substrates (nutrition), which suggests the ability of species to colonize on lignocellulosic biomass or soils (e.g. *Phaeoclavulina*), as well as other species becoming mycorrhizal (*Gautieria*, *Gomphus*) (Giachini et al. 2010).

Significance

Ecological and economical roles

Species of Gomphales are generally ectomycorrhizal and/or wood decomposers, playing important ecological roles in different ecosystems (Giachini et al. 2010; He et al. 2019a). For example, it is speculated that the ectomycorrhizal species *Ramaria rubella* (subgenus *Lentoramaria*) probably degrades lignocellulosic biomass due to its genome containing genes related to excretion of hydrolytic and oxidative enzymes such as peroxidases and cellobiohydrolases (Miyauchi et al. 2020). In addition, species of Gomphales are economically important for human food (González-Ávila et al. 2016; Pérez-Moreno et al. 2021).

Chemical diversity

Chemical diversity of members belonging to Gomphales has been explored using cultivation-dependent and cultivation-independent techniques (Dong et al. 2020; Kalntremtziou et al. 2023). Among the metabolites produced by species of this order, enzymes, polysaccharides, sesquiterpenes, and glucans present potential for industrial and environmental applications due to their antioxidant, antigenotoxic, antitumor, antimicrobial or immunostimulant properties (Bhanja et al. 2013; Liu et al. 2013; Li 2017). For example, targeted functional metagenomic analysis of soils from Mediterranean forests revealed that Gomphales species are potential producers of manganese peroxidases (Kalntremtziou et al. 2023). In addition, genome screening of *Gautieria morchelliformis* also revealed the presence of genes related to peroxidase production (Miyauchi et al. 2020). Additionally, the fungus *Beenakia informis* produced metabolites such as γ-pyrone and isoprenylated cyclohexanoids in liquid medium, which showed antimicrobial activity towards the phytopathogen *Fusarium solani* (Rincón et al. 2023).

Heitmaniales Q.M. Wang & F.Y. Bai 2020

Contributed by: Teun Boekhout, Andrey Yurkov

Introduction

Biodiversity studies of the phylloplane in China revealed the presence of a new genus with three anamorphic yeast species, for which the name *Heitmania* was proposed (Liu et al. 2017b). This genus subsequently became the basis for the family Heitmaniaceae and order Heitmanniales (Li et al. 2020b).

History

Heitmaniales is another order that was recently created, based on molecular phylogenetic analyses, to accommodate the monotypic lineage comprising the family Heitmaniaceae and the genus *Heitmania* in Microbotryomycetes (Li et al. 2020b). The genus *Heitmania* was previously proposed by Liu et al. (2017a, b) to accommodate three species of anamorphic yeasts obtained from the phyllosphere in a subtropical, evergreen, broad-leaved forest in southern China. A fourth species was added by Li et al. (2020b).

Characters that define the taxa in the order

Heitmaniales is mainly defined by its phylogenetic position as a distinct branch in Microbotryomycetes, where it occurs as a basal lineage in a small clade with *Curvibasidium* and *Pseudoleucosporidium fasciculatum* (Liu et al. 2017b; Li et al. 2020b). Colonies smooth, cream-coloured, butyrous. Yeast cells present, pseudohyphae not observed. Ballistoconidia may be present or absent. Sexual reproduction not observed.

Plates

See Fig. 2 in Liu et al. (2017a, b).

Genera included

Family Heitmaniaceae Q.M. Wang & F.Y. Bai 2020

Heitmania Xin Zhan Liu, F.Y. Bai, M. Groenew. & Boekhout 2018

Evolution

Given the few known taxa that occur in Heitmaniales, nothing can currently be stated about their evolution.

Justification of order and problems

Heitmaniales seems to be the result of rank inflation. Additional sampling is needed to get an improved understanding of the extent of Heitmaniales.

Significance

Ecological and economical roles

Species of Heitmaniales are known from the phyllosphere (Liu et al. 2017b; Li et al. 2020b).

Chemical diversity

Not known.

Helicobasidiales R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw. 2006

Contributed by: Nathan Schoutteten, Merje Toome-Heller

Introduction

Helicobasidiales is an order within Pucciniomycetes, comprising fungi with complex life cycles, alternating between a dikaryotic and a haploid stage. In their dikaryotic stage (= *Helicobasidium* stage), members of Helicobasidiales are severe phytoparasites, with saprotrophic capabilities. In this stage, a corticioid basidiome with purplish tints and transversally septate basidia is produced, dwelling soil or plant parts. In their haploid stage (*Tuberculina* stage), Helicobasidiales acts as mycoparasite of the haploid stage (aecia) of phytoparasitic rust (Pucciniales), and produces pulvinate sporodochia-like structure for asexual reproduction. Because of the deviating morphology and ecology of these alternating stages, these two distinct morphs were long time interpreted as distinct organisms and were classified in different genera. It was only with the advent of molecular phylogenetics that these two stages could be linked, and the lifecycles of these organisms were elucidated.

History

Helicobasidium was already introduced early by Patouillard (1885), to accommodate a corticioid fungus producing violet basidiomes and transversally septate basidia. *Tuberculina* was instated by Saccardo (1880a, b) to accommodate anamorphic parasitic fungi. Lutz et al. (2004a, b) showed the link between these two genera and elucidated their complex life cycles. Several dozens of names are available for both genera, and this group is in serious need of a taxonomic and nomenclatorial revision (Lutz et al. 2004c). According to the priority principle, the name Tuberculina would have priority over *Helicobasidium*. Aime et al. (2018b) called for protection of the name *Helicobasidium* over *Tuberculina*, which is more widely used in literature and is more familiar in the mycological community.

Characters that define the taxa in the order

Helicobasidium-stages are characterized by the production of corticioid basidiomes and the presence of transversally three-septate basidia. *Tuberculina*-stages infect the aecia of phytoparasitic rusts, on which they develop subepidermal pulvinate sporodochia-like structures. These structures consist of palisade-arranged conidiophores, each producing a single conidium.

Host–parasite interaction of the mycoparasitic stage is characterized by a unique interaction mechanism, i.e., the µm-fusion pore interaction. At the contact interface of the fungal host and mycoparasite, a micropore is formed with a diameter of about 0.5–1 µm. Plasmamembrane of this pore fuses with the plasmamembranes of both host and mycoparasite, leading to a cytoplasmic bridge. Bauer et al. (2004) found evidence for the transfer of nuclei and mitochondria from mycoparasite to host fungus through the micropore.

Plates

Fig. 31 Basidiome of *Helicobasidium longisporum* (MG943, Netherlands, credit: Martin Gotink, Copyright Phragmoproject). Also see figures in Lutz et al. (2004a, b, c) and Miraline and Torta (2020)

Genera included

Family Helicobasidiaceae P.M. Kirk 2008
  Helicobasidium Pat. 1885
  = *Cordalia* Gobi 1885
  = *Helicobasis* Clem. & Shear 1931
  = *Stypinella* J. Schröt. 1887
  = *Thanatophytum* Nees 1816
  = *Tuberculina* Tode ex Sacc. 1880
  = *Uredinula* Speg. 1880

Evolution

Helicobasidiales is closely related to the Pucciniales, on which the haploid stages of its representatives are parasitic. The combination of mycoparasitic and phytoparasitic strategies in the lifecycle of these fungi is unique among Fungi. Helicobasidiales is evolutionarily a very interesting group of fungi. It has been hypothesized that the group first evolved as plant pathogens and made a later jump to also be able to infect rust fungi. To date, a few species are only known from their rust hosts, and it remains unknown whether they have lost their ability to cause root rot or their other hosts are yet to be identified (Lutz et al. 2004a).

Justification of order and problems

Helicobasidiales is supported by different types of data. Molecular phylogenetic studies have shown Helicobasidiales to be a monophyletic clade within Pucciniomycetes. Also, the unique lifecycle, morphology and ecology of its representatives justify their grouping in a separate order.

Significance

Ecological and economical roles

Helicobasidiales has a serious impact on plant and crop health, especially causing violet root-rot, for example, the species *Helicobasidium purpureum* and *H. mompa*. Since the fungi can infect a range of hosts, the disease is hard to control, and the pathogens are categorised as quarantine or regulated species in several countries that are free of them. The fact that these fungi are also capable of alternating between rust fungi and plants further complicates disease control and increases the impact on agricultural and horticultural systems. Violet root rot has been reported to cause significant impacts on numerous plant hosts, including apple, cranberry, and many root vegetables. As the fungus infects roots, the impact is the greatest in continuous monocultural fields.

A potential role as biocontrol agents may be suggested against phytoparasitic rusts during the asexual stage of the Helicobasidiales lifecycle, but this remains be investigated. Given the serious infection potential of the sexual stage of the lifecycle, these fungi may not be well suited for biocontrol applications.

Chemical diversity

Two *H. mompa* pigments, mompain and helicobasin (giving the fungus the deep violet colour), were isolated and described in 1960s in Japan (Natori et al. 1967). These were studied at the time for their toxic properties toward plants and microorganisms but very limited informiaton about the findings is available in English.

Other relevant data and future recommendations

Little research has been conducted on *Helicobasidium* species since the *Helicobasidium-Tuberculina* connection was revealed by Lutz et al. (2004a, b, c). Further studies are needed to better understand the biodiversity and distribution of fungi in Helicobasidiales and to resolve the taxonomy within the genus. Genomic studies would also be very interesting to better understand the evolution of pathogenic traits since *Helicobasidium* species are able to infect both plants and fungi.

Although the asexual stage of *Helicobasidium* (often still referred to as *Tuberculina*) is a parasite of rust fungi, it is not recommended to consider these fungi as potential biocontrol agents of rusts as *Helicobasidium* species can also be significant plant pathogens.

Heterogastridiales Oberw. & R. Bauer 1990

Contributed by: Nathan Schoutteten, Teun Boekhout

Introduction

The formation of pycnidioid basidiome structures is a rare trait among Basidiomycota. The widespread-occurring *Hyalopycnis blepharistoma* forms such structures and the species was initially considered to be an anamorphic ascomycete (Berkeley 1837). In two later studies, the basidiomycete affinity of this enigmatic fungus was discovered (Bandoni and Oberwinkler 1981), and the sexual stage was recognised with transversally septate basidia and tetraradiate basidiospores (Oberwinkler and Bauer 1990b). Due to the then-ruling dual nomenclature for sexual and asexual morphs, a new genus, *Heterogastridium* was proposed by Oberwinkler and Bauer (1990b).

History

Hyalopycnis blepharistoma was originally described as *Spaeronaema blepharistoma* by Berkeley (1837), as an asexual ascomycete producing pycnidia on blackening, decaying basidiomes of *Agaricus adustus*, interpreted to be a member of the *Russula* compactae group. Bandoni and Oberwinkler (1981) found that this species is a member of Basidiomycota based on the presence of infrequent clamp connections, dikaryotic hyphae and conidia, and a positive staining reaction with diazonium blue B. At the time, the authors believed that the species was asexually reproducing by means of conidia produced inside the pycnidia. Several years later they discovered that *Hyalopycnis blepharistoma* forms transversely septate basidia which produce tetraradiate basidiospores in minute pycnidioid basidiomes and proposed the genus *Heterogastridium* to accommodate the sexual form of the species, although basidia and conidiophores occur together in the same pycnidioid structures (Oberwinkler and Bauer 1990b). Due to the unique morphology, Heterogastridiaceaea and Heterogastridiales were proposed for this genus (Oberwinkler and Bauer 1990b). Several molecular phylogenetic reconstructions showed that Heterogastridiales is a member of Microbotryomycetes (Weiss et al. 2004a, b; Aime et al. 2006; Bauer et al. 2006; Wang et al. 2015a, b). A species with stilboid asexual structures was described by Toome and Aime (2014) as *Pycnopulvinus aurantiacus*, which was isolated from palm leave litter in Equador. A sexual stage for *P. aurantiacus* is not yet reported. Molecular phylogenetic analyses clearly cluster both species, but always on long branches with respect to other groups of Microbotryomycetes. Strictly following the guidelines established for the one fungus = one name principle, the name *Hyalopycnis* has priority over *Heterogastridium*. However, Aime et al. (2018b) called for the protection of the latter name. *H. blepharistoma* was found to be a colacosome-interacting mycoparasite by Bauer (2004). Because of the lack of DNA sequence data, several other genera and species of colacosome-interacting mycoparasites were initially assigned to this order (i.e., *Atractocolax*, *Colacogloea*, *Krieglsteinera*; Bauer et al. 2006, Aime et al. 2014, Oberwinkler 2017, Schoutteten et al. 2023). However, the phylogenetic relationships of colacosome-interacting mycoparasites were shown to be much more diverse in Microbotryomycetes, and these mycoparasites occur in various clades that are currently not assigned to existing orders (Schoutteten et al. 2023).

Characters that define the taxa in the order

Basidiomes are minute, pycnidioid or stilboid, whitish to orange. Basidia transversely septate, with tetraradiate or segmented spores. Teliospores absent. Asexual conidia ellipsoid formed on conidiophores inside pycnidioid structures. No yeast budding reported. Clamp connections infrequent. Colacosomes are present in hyphae. SPBs during metaphase inside the nucleus. Hyphal septal pore complexes have a ‘simple’ organisation (Bauer et al. 2006).

Plates

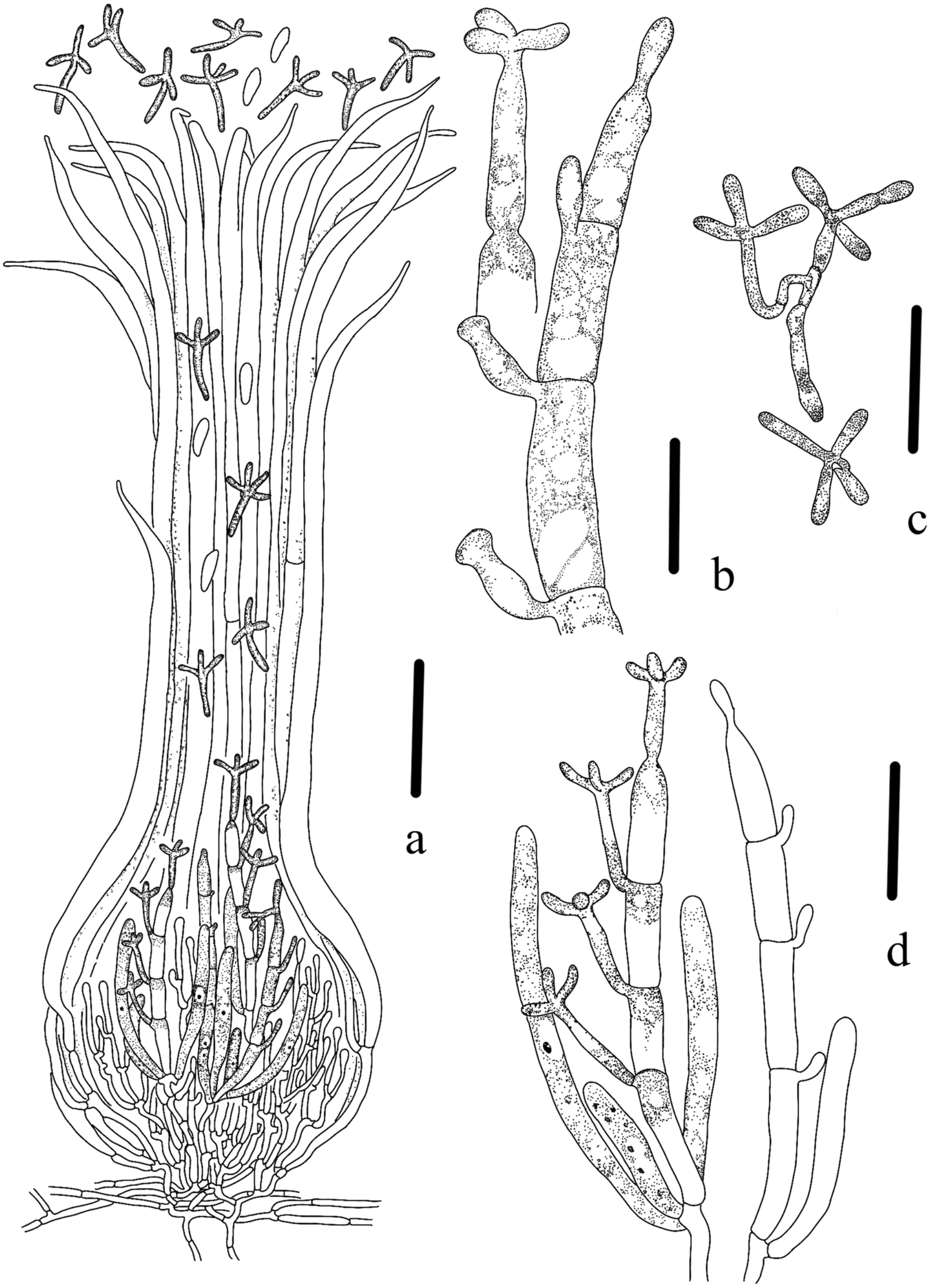


Fig. 32 *Hyalopycnis pycnidioideum*. **a** basidiome with basidia, basidiospores, conidiophores, and conidia; **b**, **d** basidia; **c** basidiospores. Scale bars: a = 40 µm; b = 10 µm; c, d = 20 µm. Redraw from Oberwinkler and Bauer (1990b) by Mao-Qiang He

Genera included

Family Heterogastridiaceae Oberw. & R. Bauer 1990
  Hyalopycnis Höhn. 1918
  = *Heterogastridium* Oberw. & R. Bauer 1990
  Krieglsteinera Pouzar 1987
  Pycnopulvinus Toome & Aime 2014

Evolution

Heterogastridium occurs as a distant lineage in Microbotryomycetes with a large genetic distance to other taxa (Weiss et al. 2004a, b; Aime et al. 2006; Bauer et al. 2006; Wang et al. 2015a, b; Zhao et al. 2017). Since the phylogenetic relationships of the currently accepted groups in Microbotryomycetes are unresolved, it is not yet possible to recognize evolutionary patterns within the class. Schoutteten et al. (2023) provided a seven-locus phylogenetic reconstruction of Microbotryomycetes, with a high sampling of colacosome-interacting mycoparasites. However, the relationships between the orders were unresolved, and many species, genera, and families remained unassigned to higher taxa. To further assess the relationships between the organisms and clades within Microbotryomycetes, whole genome-based phylogenomic reconstructions based on a dense taxon sampling are needed (Schoutteten et al 2023). The pycnidioid basidiome structures may be a synapomorphy for this lineage in Microbotryomycetes, since they are not found in any other groups currently known within this class.

Justification of order and problems

Heterogastridiales seems justified based on its peculiar morphology and its phylogenetic position.

Significance

Ecological and economical roles

Species of Heterogastridiales are mycoparasites acting via the formation of colacosomes (Bauer 2004). The host range is not explored, but the original description mentions a member of the *Russula* compactae group as substrate. As far as known, they have not been explored for commercial applications. *H. pycnidioideum* has also been isolated from rotten pumpkin, decaying tomatoes, and leaf litter of an oak tree (Oberwinkler and Bauer 1990b).

Chemical diversity

Unknown.

Holtermanniales Libkind, Wuczk., Turchetti & Boekhout 2011

Contributed by: Teun Boekhout, Nathan Schoutteten, Andrey Yurkov

Introduction

Holtermanniales is based on a molecular phylogenetic analysis using sequences of the D1-D2 regions of the LSU rDNA (Wuczkowski et al. 2011). The genus *Holtermannia* was described in 1910 to accommodate tremellaceous fungi with erect, clavarioid basidiomes (Saccardo and Traverso 1910). The genus is relatively unknown and poorly studied. A living culture is only available for one species, *Holtermannia corniformis*. Molecular studies identified several yeast-like species, previously classified in the genus *Cryptococcus*, to be phylogenetically related to *Holtermannia*.

History

Initially known as a small genus of tremellaceous fungi with small, erect, and clavarioid basidiomes, with seven species and two varieties (Kobayashi 1937b; Bandoni et al. 2011a), molecular studies showed that several yeast-like species are phylogenetically related. These anamorphic species have been described in the genus *Holtermanniella* with five species (Wuczkowski et al. 2011). Despite the phylogenetic proximity, the genera *Holtermannia* and *Holtermanniella* were maintained in the multigene phylogenetic reclassification of basidiomycetous yeasts and related fungi (Liu et al. 2015a, b).

Characters that define the taxa in the order

Given the morphological diversity of either the teleomorphic or anamorphic genus in the order, it is difficult to give a concise characterization of it. Based on Wuczkowski et al. (2011) we present the following description: Asexual or sexual species with free-living yeast phase with cream-colored colonies. Yeasts utilize myo-inositol and d-glucuronate, but not nitrate. Starch-like compounds produced. Hyphae, if present, with clamp connections and haustoria. Basidiomes of *Holtermannia* species are tough-gelatinous with simple to branching clavarioid lobes and have a layered substructure with a dimitic hyphal system (Bandoni et al. 2011a). Basidia two- to four celled and longitudinally septated. Hyphae in basidiomes clamped or not.

Plates

See figures 116.2 and 116.3 in The Yeasts, a Taxonomic Study (Bandoni et al. 2011a).

Genera included

Family Holtermanniaceae Redhead 2015
  Holtermannia Sacc. & Traverso 1910
  Holtermanniella Libkind, Wuczk., Turchetti & Boekhout 2011

Evolution

Molecular phylogenetic studies revealed Holtermanniales as a deeply rooted lineage within Tremellomycetes, with Cystofilobasidiales and Filobasidiales being more basal (Bandoni et al. 2011a; Liu et al. 2015a, b; Wuczkowski et al. 2011). It remains unknown whether all *Holtermannia* species produce a yeast-like morph like recently described *Holtermannia saccardoi* (Li et al. 2020b), and whether *Holtermanniella* species can form basidiomes. The mean time of origin of the order is estimated at 211 million years ago (Zhao et al. 2017).

Justification of order and problems

Molecular phylogenetic studies clearly showed the isolated position of the order within Tremellomycetes. It remains to be investigated whether the other *Holtermannia* species, which were not isolated in culture and for which no DNA sequence data is available, also belong to the same order.

Significance

Ecological and economical roles

Ecology of Holtermanniales species is poorly known. It has been suggested that *Holtermannia corniformis* grows on ascomycetous stromata or tree trunks that are also growing bracket fungi (Kobayasi 1937b; Bandoni et al. 2011a). The yeast-like species are from diverse habitats such as steppe plants, plant litter, grape berries, truffle, phylloplane, seawater, glacial meltwater, malting barley, soils, from geographically distributed areas, such as Antarctica, Argentina, and Chile (Patagonia), Austria, UK/Falkland Islands, Finland, Germany, Italy, Sweden, and China (Taiwan province). Likely, some species are psychrophilic.

Chemical diversity

Unknown.

Other relevant data and future recommendations

Species in the order for which molecular data is available can be successfully identified based on the combination of ribosomal ITS and LSU nucleotide sequences.

Hymenochaetales Oberw. 1977

Contributed by: Ricardo Valenzuela, Tania Raymundo, Tatiana B. Gibertoni, Viktor Papp.

Introduction

Hymenochaetales is a large order in Agaricomycetes with 14 families, 83 genera, and 1205 species, and include wood-inhabiting and ectomycorrhizal fungi with different kinds of basidiomes such as polyporoid, stereoid, corticioid, hydnoid, coralloid and agaricoid. Despite the diversity, the order forms a well supported clade, but its internal structure is largely unresolved (Hibbett et al. 2014). According to Larsson et al. (2006), and Wagner and Fisher (2002) there is some support for the clade that includes most of the typical Hymenochaetaceae species (*Inonotus* s.s., *Phylloporia*, *Fulvifomes*, *Inocutis*, *Fomitiporella*, *Aurificaria*, *Phellinus* s.s., *Pseudoinonotus*, *Fomitiporia*, *Porodaedalea*, *Onnia*, *Mensularia, Pseudochaete* and others new genera). This group agrees with the classical concept of the order Hymenochaetales by Oberwinkler (1977), however, its monophyletic origin is still uncertain. The remaining taxa of the typical Hymenochaetaceae (*Coltricia*, *Coltriciella*, *Pyrrhoderma*, *Fuscoporia*, *Phellinidium*, *Asterodon*, *Phellopilus*, and *Hymenochaete*) appear mixed with corticioid and polyporoid species of the genera *Basidioradulum*, *Bridgeoporus*, *Hyphodontia*, *Rigidoporus*, *Schizopora*, and *Trichaptum*, and most surprisingly, also with omphalinoid, agaricoid or stereoid fungi, such as *Cotylidia*, *Contumyces*, *Loreleia*, *Rickenella*, and *Sphagnomphalia*, as revealed by previous molecular studies (Hibbett and Donoghue 1995, 2001; Hibbett et al. 1997, 2000; Ko et al. 1997; Moncalvo et al. 2002; Redhead et al. 2002; Redberg et al. 2003; Larsson et al. 2006). Hibbett et al. (2014) points out that some of those clades were not corroborated by other studies using nrDNA, and the branching order of the groups varies from one analysis to another. Based on this remark, Wu et al. (2022b) have synonymized *Cotriciella* with *Cotricia* using ITS and LSU, while Valenzuela et al. (2012) showed the clades of *Coltriciella* and *Coltricia* as clearly separated. Therefore, it is important to use more nuclear markers or to have the genome of more speceis completely sequenced to better resolve the inner clades of Hymenochaetales.

History

Linnaeus established in the eighteenth century that nature could be divided into three kingdoms: mineral, vegetable and animal, and he placed fungi in the vegetable kingdom. In 1753, some polyporoid Hymenochaetales were placed in *Boletus*, a genus that Linnaeus used to include all fungi that had tubes or pores, so that the basidiomes could be fleshy or hard and/or woody and pileate-stipitate (Ryvarden and Gilbertson 1994). Persoon in 1801 in his work Synopsis Methodica Fungorum, placed the polyporoids within the group of the Aphyllophorales (Aphyllophoracés). His classification system was based on macroscopic characters, mainly of the hymenophore (Jülich 1981). Later, Fries, between 1821 and 1832, included in Aphyllophoracés, five families: Clavariaceae with erect basidiomes and amphigenous hymenium; Thelephoraceae with smooth hymenium; Hydnaceae, Polyporaceae and Agaricaceae with dentate, tubular and lamellate hymenophores, respectively. In Polyporaceae, he included all types of fungi with pores and harder consistency, placing in *Boletus*, the fungi with tubular hymenophore and fleshy consistency, in the family Agaricaceae.

The Friesian System must be discussed first as it provides the basis on which all subsequent classification systems were built or created. For this purpose we must analyze his first works: "Systema Mycologicum" (published in 1821) and "Epicrisis systematis mycologici" (in 1838). The classification of polyporoid fungi used by Fries is based exclusively on macroscopic characters. From these traits, the structure of the hymenophore, the characteristics of the mycelial tissue and the walls of the tubes and their interrelationships of these tissues are considered fundamental characters. On these principles, Fries established nine genera arranged in the following sequence: *Polyporus*, *Trametes*, *Daedalea*, *Cyclomyces*, *Hexagona*, *Favolus*, *Laschia*, *Merulius* and *Porothelium*. These genera are further divided into tribes and sections. In 1851, Fries divided the genus *Polyporus* into 3 subgenera: *Eupolyporus* characterized by fleshy and annual pileus; *Fomes* with woody and perennial pileus; and *Poria* which included all fungi with resupinate basidiomes. He also separated the genus *Polystictus* which was distinguished by the reciprocally perpendicular arrangement of the hyphae of the pileus tissue and the hyphal trame of the tubes. The above subgenera are recognized as independent genera by all mycologists who adopted the Friesian system. It is important to mention that the only genus considered in Hymenochaetaceae and described by Fries is *Cyclomyces*, while most of the current representatives of this group of fungi were found within *Polyporus* (in its three subgenera *Eupolyporus*, *Fomes* and *Poria*, the last two elevated to genus status later) and *Polystictus*.

The Friesian system had several drawbacks, as the artificial conception and inadequate number of genera, the absence of microscopic characters and the difficulty of differentiating the representatives of such close genera as *Polyporus* and *Polystictus* and so all the others. The deficiency of the classification system proposed by Fries regarding major categories, such as the inclusion in the same class of Ascomycetes and Basidiomycetes, was originated from his failure to take into account the evolutionary development of fungi, and because he ignored the taxonomic meaning of the asca and basidium. In addition, Fries occasionally ignored the meaning of polymorphism in fungi. This, coupled with the lack of microscopic examinations in the study of polyporoid fungi, led to the dispersal of many identical forms of polyporoid fungi into different genera.

On the other hand, a mycologist contemporary to Fries who described several genera of polyporoid fungi was S. F. Gray, who in 1821 proposed *Albatrellus* and *Coltricia* among others, the latter being a current member of the Hymenochaetales family. Later, a French mycologist made some superficial changes to the Friesian system was Lucien Quélet and was the first to introduce in his classification system the individual elements of evolution. The modifications made by Quélet in 1888 were mainly in the genus *Polyporus*. Using most of the data provided by Fries when he subdivided the genus *Polyporus* into tribes and series, and supplementing these with microscopic characters using mainly the spores, he recognized 9 new genera: *Leptoporus*, *Coriolus*, *Inodermus*, *Phellinus*, *Placodes*, *Pelloporus*, *Leucoporus*, *Caloporus* and *Cerioporus*. Of these, *Inodermus*, *Placodes* and *Pelloporus* include species placed in Hymenochaetales and *Phellinus* currently belongs to Hymenochaetaceae. In addition, he made several essential transpositions in the family Polyporaceae sensu lato by changing the limits and volume conferred by Fries. Quélet was the first to recognize *Irpex* (with some species currently considered representatives of Hymenochaetaceae) in this family by observing that in the juvenile stages this fungus presents an alveolar structure.

Petter Adolf Karsten, a Finnish mycologist and contemporary of Quélet, also helped in the classification of polyporoid fungi and added other characters for the classification of genera. Karsten, in 1879, considered the consistency of the hymenophore, the pigmentation of the basidioma, tissue and spores, the consistency of the basidioma, the texture of the pileus, the presence or absence of the stipe, in addition to those already mentioned for the Friesian system. He described more than 200 new genera including *Ganoderma*, *Inoderma*, *Inonotus*, *Onnia*, *Pycnoporus*, *Bjerkandera*, *Ischnoderma*, etc. (*Inoderma*, *Inonotus* and *Onnia* are accepted as members of Hymenochaetaceae). Furthermore, he was the first to propose that the genus *Lenzites* should be moved from the Agaricaceae, as Fries had proposed, to the family Polyporaceae, and this change was adopted by subsequent mycologists.

Another eminent Italian mycologist was Giacomo Bresadola, who described more than 1000 species and about 15 genera, working with Quélet, Patouillard, Boudort, among others. Among the new genera he described was *Hydnochaete*, proposed in 1896 and was a member of Hymenochaetaceae.

William Alphonso Murrill was another American mycologist who described, between 1905 and 1940, 343 species and 17 genera of polyporoid fungi, of which *Coltriciella* and *Phylloporia* belong to Hymenochaetaceae, and *Fulvifomes*, *Fomitiporia*, *Fuscoporia*, *Fomitiporella*, *Porodaedalea* and *Pyropolyporus* that were not accepted by contemporary mycologists of Murrill nor by current mycologists. However, they are so far being validated by molecular studies of certain regions of ribosomal DNA.

Narcisse Théophile Patouillard (1900) was the first to include all the fungi of Hymenochaetaceae in a group he called "Serie des Ignaires" and considered genera that had a very varied basidiomes morphology and hymenial configuration, but had in common the presence of mushrooms. However, some species and related genera lacked this type of sterile cells, but their golden to brown configuration and blackening of the basidioma in Potassium Hydroxide (KOH) are shared by all fungi in this group. The latter was recognized by Corner (1948) and mentioned Patouillard's "Ignaires" series in a broader sense, grouping them in the "Xanthocroic" series, while Donk (1948, fide Fiasson and Niemelä 1984) classified them within the family Hymenochaetaceae.

Reid (1963) described the genus *Aurificaria* within Hymenochaetaceae and included terrestrial or lignicolous fungi with centrally or laterally stipitate, lobed or sessile, dimidiate, imbricate and entire basidiomes, pileus with a black cuticle forming from the base to the margin, poroid hymenophore and zonate, corky to woody in consistency, hard and brittle context. The hyphal system is monomitic with simple septate generative hyphae, thin to thick-walled, hyaline to reddish brown in KOH, setae and setigerous elements are absent and basidiospores are hyaline to dark brown in water and olivaceous brown in KOH and inamyloid. However, recently this genus was synonymized with *Fulvifomes*.

Donk (1964) described the family Hymenochaetaceae with annual to perennial, resupinate to stipitate or clavarioid and coralloid basidiomycetous fungi, with the context generally dark-colored and of leathery to woody consistency, with xanthochroic reaction in KOH, the hymenophore may be smooth, dentate, rugose, irpiciform or poroid, very occasionally with concentric (never radial) lamellae. The hyphal system is monomitic or dimitic with skeletal hyphae, generative hyphae with simple septa. Setae and setal hyphae are present on the hymenium, context or surface of the pycelium or absent. Species of this family are generally lignicolous, causing a white rot in wood or are terricolous. He considered 19 genera in the family Hymenochaetaceae, 11 of these with poroid hymenophore.

Later, this group of fungi was elevated to the taxonomic category of order as Hymenochaetales by Oberwinkler (1977) with the same morphological characters of the family Hymenochaetaceae.

Fiasson and Niemelä (1984) carried out a phenetic and phylogenetic analysis of the European poroid species of the Hymenochaetales, recognizing and amending the order and dividing it into two new suborders: Phaeolinae and Hymenochaetinae. The inclusion of *Phaeolus schweinitzii* in the first suborder of the Hymenochaetales is based on the production of stilpyrones, the pigment that gives them the brown coloration typical of the species of this order (Fiasson 1982), the presence of generative hyphae with simple septa and the "imperfect" brown rot it produces in the wood. However, Parmasto and Parmasto (1979), Ryvarden and Johansen (1980), Gilbertson and Ryvarden (1987) considered *P. schweinitzii* within Polyporaceae because of the brown rot it causes and the presence of cystidia, recently it is confirmed by phylogenetic analysis that *Phaeolus* nested in Polyporales rather than Hymenochaetales (Yuan et al. 2022). On the other hand, the suborder Hymenochaetinae is subdivided into three families: Hymenochaetaceae (*Asterodon*, *Hydnochaete* and *Hymenochaete*), Inonotaceae (*Inocutis*, *Inonotus* and *Phylloporia*) and Phellinaceae (*Fomitiporia*, *Fulvifomes*, *Fuscoporia*, *Inonotopsis*, *Onnia*, *Phellinidium*, *Phellinus* and *Porodaedalea*). In the suborder Phaeolinae, they consider only the family Phaeolaceae with two genera *Phaeolus* and *Coltricia*, the latter sharing with the former the ultrastructure of the septum with perforated parentosome.

On the one hand, and according to Ryvarden (1991) the family Hymenochaetaceae is one of the most homogeneous groups among the Basidiomycetes and an example of the strong macroscopic morphological variation in relation to the microscopic evidence and proposes a monophyletic origin with the following arguments: presence of hyphae without fibulae, dolipore septum and non-perforated parentosome, xanthochroic reaction and white rot. Although it is now known that styrilpyrone compounds are not exclusive to the Hymenochaetales, these together with phenolic compounds are what give the positive xanthochroic reaction in the Hymenochaetaceae (Fiasson 1982).

Boidin et al. (1998), while analyzing the molecular taxonomy of 360 species of Aphyllophorales using ITS sequences, recognize that their results were similar to those of Hibbett and Donaghue (1995) with respect to the order Hymenochaetales and that these allowed them to delimit with certainty this order, to accept it as a monophyletic group with three families: Hymenochaetaceae (*Hymenochaete*), Coltriciaceae (*Coltricia*, *Inonotus* and *Phylloporia*) and Phellinaceae (*Phellinus*), and to consider the genus *Phaeolus* outside the order, not agreeing with Fiasson and Niemelä (1984).

Recent molecular phylogenetic studies by Hibbett and Thorn (2001) show eight major clades in the Homobasidiomycetes and one of them was the Hymenochaetoid clade, later corroborated by Binder and Hibbett (2002) and Moncalvo et al. (2002). This clade comprises all members of the family Hymenochaetaceae, as well as members of other groups of polyporoid, agaricoid, corticioid, and stereoid fungi (at least nine families of Homobasidiomycetes).

Contradictory to most Homobasidiomycetes, members of the clades hymenochaetoid, canthareloid and gomphoid-phalloid possess dolipore with unperforated parentosomes (Moore 1985; Langer and Oberwinkler 1993; Muller et al. 2000; Hibbett and Thorn 2001; Binder and Hibbett 2002). This character has been found in Auriculariales and Dacrymycetales, so it could be argued that it is a plesiomorphic condition in Homobasidiomycetes and this view would be in line with the basal position of the hymenochaetoid clade in the phylogeny of this group (Goes-Neto and Groposo 2005). However, Hibbett and Thorn (2001) pointed to the unperforated parentosome as a potentially homoplastic character because of its co-occurrence of perforated and unperforated parentosomes in the polyporoid, hymenochaetoid, canthareloid, and gomphoid-phalloid clades (van Driel et al. 2009), which would indicate that the basal position of this clade is not confirmed (Binder and Hibbett 2002; Goes-Neto and Groposo 2005). The exception in the hymenochaetoid clade is *Hyphoderma praetermissum* (P. Karst.) J. Erikss. & Å. Strid, *Irpex latemarginatus* (Durieu & Mont.) C.C. Chen & Sheng H. Wu and *Rickenella fibula* (Bull.) Raithelh., species not related to the Hymenochaetaceae s.s. because they have a perforated parentosome (van Driel et al. 2009).

On the other hand, the relationships among the hymenochaetoid subclades are not yet well resolved. According to Wagner and Fisher (2002) there is some support for the clade that includes most of the typical species of Hymenochaetaceae (*Inonotus* s.s., *Phylloporia*, *Fulvifomes*, *Inocutis*, *Fomitiporella*, *Aurificaria*, *Phellinus* s.s., *Pseudoinonotus*, *Fomitiporia*, *Porodaedalea*, *Onnia*, *Mensularia* and *Pseudochaete*). This group is in accordance with the classical concept of the order Hymenochaetales of Oberwinkler (1977), however, its monophyletic origin is still uncertain (Wagner and Fisher 2002; Larsson et al. 2006). The remaining taxa of the typical Hymenochaetaceae (*Coltricia*, *Coltriciella*, *Pyrrhoderma*, *Fuscoporia*, *Phellinidium*, *Asterodon*, *Phellopilus*, and *Hymenochaete*) occur mixed with corticioid and polyporoid species of the genera *Basidioradulum*, *Bridgeoporus*, *Hyphodontia*, *Rigidoporus*, *Schizopora*, and *Trichaptum*, and more surprisingly, also with omphalinoid, agaricoid or stereoid fungi, such as *Cotylidia*, *Rickenella*, *Loreleia*, *Contumyces* and *Sphagnomphalia*, as revealed by previous and recent molecular studies (Hibbett and Donoghue 1995, 2001; Hibbett et al. 1997, 2000; Ko et al. 1997; Moncalvo et al. 2002; Redhead et al. 2002; Redberg et al. 2003; Larsson et al. 2006).

In summary, the position of the hymenochaetoid clade and its internal relationships are still unresolved. This clade apparently has no morphological, physiological or ecological synapomorphies and can only be defined almost exclusively by its molecular characters (Goes-Neto and Groposo 2005; Larsson et al. 2006).

Recenttly, Wang et al. (2023a) made an analysis of classification of the order Hymenochaetales since Oberwinkler proposed the order in 1977 until to Wijayawardeneet al. (2022a) and then they proposed 14 families for Hymenochaetales, which are recognized in this work.

Characters that define the taxa in the order

According to Larsson et al. (2006), there are no morphological characters that delimit the order, as all characteristics are also found in the other Agaricomycetes. At lower taxonomic levels, morphological characters are better resolved and geographical distribution and host also seem to have relevant importance when defining genera and species. Currently, 14 families are accepted in Hymenochaetales (Wang et al. 2023a).

Chaetoporellaceae Jülich can be distinguished by the resupinate to effused, pale to brown basidiomes, smooth to hydnoid hymenophore, monomitic to pseudodimitic, hyphal system with clamp connections, presence of tubular cystidia in the trama, smooth, thin-walled or slightly thick-walled, cylindrical, ellipsoid or allantoid, hyaline, inamyloid, indextrinoid, acyanophilous basidiospores (Bernicchia and Gorjón 2010; Wang et al. 2021a, 2023a).

Hymenochaetaceae Donk is distinguished by annual to perennial, resupinate, effused-reflexed, pileate to stipitate, brownish basidiomes with a xanthochroic reaction in KOH, poroid or corticioid hymenophore, mono-, di- or trimitic hyphal, with and without clamp connections, presence or absence of setal elements, smooth, thin to thick-walled, globose to allantoid, hyaline ro brownish, indextrinoid or dextrinoid, acyanophilous or acyanophilous basidiospores (Wu et al 2022b). According to Wang et al. (2023a), the family includes Asterodontaceae Parmasto, Clavariachaetaceae

Jülich, Coltriciaceae Jülich, Inonotaceae Fiasson & Niemelä, Neoantrodiellaceae Y.C. Dai, B.K. Cui, Jia J. Chen & H.S. Yuan and Nigrofomitaceae Jülich.

Hyphodontiaceae Xue W. Wang & L.W. Zhou is characterized by the resupinate, pale to brownish basidiomes, smooth to poroid hymenophore, mono- to pseudodimitic, hyphal system with clamp connections, presence of either lagenocystidia strongly encrusted apically or capitate cystidia usually encrusted apically, usually dextrinoid basidia, smooth, thin-walled or slightly thick-walled, subglobose to cylindrical, hyaline, inamyloid, acyanophilous basidiospores (Wang et al. 2021a).

Odonticiaceae L.W. Zhou & Xue W. Wang has annual, resupinate to effused, cream to yellowish basidiomes, grandinioid to hydnoid hymenophore, mono- to pseudodimitic hyphal system, without clamp connections, presence or absence of s mooth or encrusted, cylindrical, thin to thick-walled, hyaline cystidia, smooth, thin-walled, ellipsoid to cylindrical, hyaline, inamyloid, acyanophilous basidiospores (Eriksson et al. 1981; Ginns 1998; Bernicchia & Gorjón 2010; Wang et al. 2023a).

Peniophorellaceae L.W. Zhou, Xue W. Wang & S.L. Liu has annual, resupinate to effused, white to yellowish basisiomata, smooth to tuberculate hymenophore, monomitic hyphal system with clamp connections, hyaline, thin-walled. Metuloids, gloeocystidia or leptocystidia, and echinulate cells usually present, smooth, thin-walled, ellipsoid, to allantoid, hyaline, with oily contents, inamyloid, acyanophilous basidiospores (Wang et al. 2023a).

Repetobasidiaceae Jülich has annual, resupinate to effused, white, yellowish to greyish basisiomata, smooth hymenophore, monomitic hyphal system with clamp connections, cylindrical or conical, with capitate or subulate apex, thin-walled cystidia, basidia subglobose to pyriform, produced by internal repetition from old basidia, with four sterigmata, smooth, thin-walled, ellipsoid or subfusiform, hyaline, inamyloid, acyanophilous basidiospores (Wang et al. 2023a).

Resiniciaceae L.W. Zhou & Xue W. Wang has annual, resupinate to effused, white to yellowish basidiomes, smooth to hydnoid hymenophore, monomitic hyphal system with clamp connections, presence of halocystidia, cylindrical with a capitate apex, and astrocystidia, at apex a stellate cluster of hyaline crystals, smooth, thin-walled, ellipsoid to cylindrical, hyaline, inamyloid, acyanophilous basidiospores (Wang et al. 2023a).

Rickenellaceae Vizzini has annual, omphalinoid, whitish, yellowish to brownish orange basidiomes, hymenophore lamellate, central stipe, monomitic hyphal system with clamp connections, presence of caulocystidia, cheilocystidia, pileocystidia and pleurocystidia, narrowly lageniform to obclavate often with subcapitate apex, smooth, thin-walled, ellipsoid to cylindrical, hyaline, inamyloid, acyanophilous basidiospores (Wang et al. 2023a).

Rigidoporaceae Jülich has annual to perennial, resupinate to pileate, reddish orange to pinkish, isabelline or ochraceous basidiomes, poroid hymenophore, monomitic to dimitic hyphal system without clamp connections, presence or absence of encrusted cystidia, smooth, thin-walled, hyaline, ovoid to globose, inamyloid, acyanophilous basidiospores (Wang et al. 2023a). According to Wang et al. (2023a), the family includes Oxyporaceae Zmitr. & Malysheva.

Schizocorticiaceae L.W. Zhou & Xue W. Wang has annual, widely effused, cream to pale yellow basidiomes, smooth or irregular, more or less cracked hymenophore, monomitic hyphal system with clamp connections, tubular leptocystidia, basidia cylindrical, often with a median constriction, smooth, thin-walled, hyaline, ellipsoid, inamyloid, acyanophilous basidiospores (Wang et al. 2023a).

Schizoporaceae Jülich is characterized by resupinate or pileate, withish to brownish, smooth to poroid hymenophore, monomitic, pseudodimitic, dimitic or trimitic hyphal system, with clamp connections, presence or absence of apitate to subcapitate, cylindrical to subcylindrical, fusiform, subulate, bladder-like, bottle-shaped, clavate, moniliform to submoniliform, pyriform, astro-, gloeo- or leptocystidia, lecythiform, rarely lagenocystidia and snake-like sinuous cystidia, smooth, globose to allantoid, hyaline, thin- or thick-walled, inamyloid, acyanophilous or slightly cyanophilous basidiospores (Wang et al 2021a, b).

Sideraceae L.W. Zhou & Xue W. Wang has annual to perennial, resupinate, white to yellowish basidiomes, hydnoid or poroid hymenophore, mono- or dimitic hyphal system with clamp connections, crystals usually abundant in subiculum, absence of cystidia absent, smooth, ellipsoid to cylindrical, hyaline, thin-walled, inamyloid, acyanophilous basidiospores (Wang et al. 2023a).

Skvortzoviaceae L.W. Zhou & Xue W. Wang has annual, resupinate to effused, cream to yellowish basidiomes, smooth to odontioid hymenophore, monomitic hyphal system usually with clamp connections, presence of tubular cystidia, smooth, cylindrical or allantoid, hyaline, thin-walled, inamyloid, acyanophilous basidiospores (Wang et al. 2023a).

Tubulicrinaceae Jülich has annual, resupinate to effused, white to pale ochraceous basidiomes, mooth, pruinose to porulose hymenophore, monomitic hyphal system with clamp connections, presence of cylindrical or conical cystidia, generally bi- or multi-radicate, smooth, thin-walled, subglobose to allantoid, hyaline, thin-walled, inamyloid, acyanophilous basidiospores (Wang et al. 2023a).

Plates

Fig. 33 Selected basidiome types of Hymenochaetales. **a** *Bridgeoporus sinensis* (VPapp-2009191, Changbai Mts, China); **b** *Coltricia dependens* (RV 14913, Oaxaca State, Mexico); **c** *Cotylidia aurantiaca* (RV 11870, San Luis Potosi State, Mexico); **d** *Echinoporia aculeifera* (TR & RV 1279, San Luis Potosí State, Mexico); **e** *Fuscoporia ferrea* (RV 18323, Hidalgo State, Mexico); f, *Hydnoporia olivacea* (RV 14458, Oaxaca State, Mexico); **g** *Hymenochaete damicornis* (RV 17029, Hidalgo State, Mexico); **h** *Hymenochaete resupinata* (RV 13750, Oaxaca State, Mexico); **i** *Inocutis texana* (RV 12710, Sonora State, Mexico); **j** *Leucophellinus irpicoides* (VPapp-1909191, Changbai Mts, China); **k** *Pseudoinonotus dryadeus* (RV 13085, Queretaro State, Mexico); **l** *Fulvoderma scaurum* (VPapp-1909192, Changbai Mts, China); **m** *Pallidohirschioporus biformis* (RV 17540, Tamaulipas State, Mexico); **n** *Trichaptum byssogenum* (RV 13163, Sonora State, Mexico); **o** *Tropicoporus linteus* (RV 13020, Sonora State, Mexico)

Genera included

Family Chaetoporellaceae Jülich 1982

Echinoporia Ryvarden 1980
= *Echinodia* Pat. 1918
Kneiffiella P. Karst. 1889
= *Alutaceodontia* (Parmasto) Hjortstam & Ryvarden 2002
= *Chaetoporellus* Bondartsev & Singer 1941
= *Deviodontia* (Parmasto) Hjortstam & Ryvarden 2009

Family Hymenochaetaceae Donk 1948
= Coltriciaceae Jülich 1982
= Neoantrodiellaceae Y.C. Dai, B.K. Cui, Jia J. Chen & H.S. Yuan 2015
= Nigrofomitaceae Jülich 1982
Asterodon Pat. 1894
= *Aciella* (P. Karst.) P. Karst. 1899
= *Hydnochaetella* Sacc. 1898
Basidioradulum Nobles 1967
Clavariachaete Corner 1950

= *Clavariachaeta* Lloyd 1922
= *Coltriciopsis* Teixeira 1991
= *Cycloporus* Murrill 1904
= *Pelloporus* Quél. 1886
= *Polystictus* Fr. 1851
= *Strilia* Gray 1821
= *Volvopolyporus* McGinty 1909
= *Xanthochrous* Pat. 1897
Coltricia Gray 1821
= *Coltriciella* Murrill 1904
Coniferiporia L.W. Zhou & Y.C. Dai 2016
Cyanotrama Ghobad-Nejhad & Y.C. Dai 2010
= *Neoantrodiella* Y.C. Dai, B.K. Cui, Jia J. Chen & H.S. Yuan 2015
Cylindrosporus L.W. Zhou 2015
Fibricium J. Erikss. 1958
Flaviporellus Murrill 1905
Fomitiporella Murrill 1907
= *Arambarria* Rajchenb. & Pildain 2015
= *Phellinotus* Drechsler-Santos, Robledo & Rajchenb. 2016
= *Rajchenbergia* Salvador-Montoya, Popoff & Drechsler-Santos 2020
Fomitiporia Murrill 1907
Fulvifomes Murrill 1914
= *Aurificaria* D.A. Reid 1963
Fulvoderma L.W. Zhou & Y.C. Dai 2018
Fuscoporia Murrill 1907
Hydnoporia Murrill 1907
= *Hymenochaetopsis* S.H. He & Jiao Yang 2016
= *Pseudochaete* T. Wagner & M. Fisch. 2002
Hymenochaete Lév. 1846
= *Cerrenella* Murrill 1905
= *Cyclomycetella* Murrill 1904
= *Cycloporellus* Murrill 1907
= *Dichochaete* Parmasto 2001
= *Hydnochaete* Bres. 1896
= *Hymenochaetella* P. Karst. 1889
= *Leptochaete* Lév. 1846
= *Stipitochaete* Ryvarden 1985
Inocutis Fiasson & Niemelä 1984
Inonotopsis Parmasto 1973
Inonotus P. Karst. 1879
= *Phaeoporus* J. Schröt. 1888
= *Polystictoides* Lázaro Ibiza 1916
= *Xanthoporia* Murrill 1916
Meganotus Y.C. Dai, F. Wu, L.W. Zhou, Vlasák & B.K. Cui 2022
Mensularia Lázaro Ibiza 1916
Neomensularia F. Wu, L.W. Zhou & Y.C. Dai 2016
Neophellinus Y.C. Dai, F. Wu, L.W. Zhou, Vlasák & B.K. Cui 2022
Nigrofomes Murrill 1904
= *Melanoporella* Murrill 1907
= *Melanoporia* Murrill 1907
Nothonotus Y.C. Dai, F. Wu, L.W. Zhou, Vlasák & B.K. Cui 2022
Nothophellinus Rajchenb. 2015
Ochrosporellus (Bondartseva & S. Herrera) Bondartseva & S. Herrera 1992
Onnia P. Karst. 1889
= *Mucronoporus* Ellis & Everh. 1889
Pachynotus Y.C. Dai, F. Wu, L.W. Zhou & B.K. Cui 2022
Perenninotus Y.C. Dai, F. Wu, L.W. Zhou, Vlasák & B.K. Cui 2022
Phellinidium (Kotl.) Fiasson & Niemelä 1984
Phellinopsis Y.C. Dai 2010
Phellinus Quél. 1886
= *Boletus* Dill. ex Gray 1821
= *Boudiera* Lázaro Ibiza 1916
= *Fuscoporella* Murrill 1907
= *Ochroporus* J. Schröt. 1888
= *Pseudofomes* Lázaro Ibiza 1916
= *Pyropolyporus* Murrill 1903
= *Scalaria* Lázaro Ibiza 1916
= *Scindalma* Hill ex Kuntze 1898
Phellopilus Niemelä, T. Wagner & M. Fisch. 2001
Phylloporia Murrill 1904
= *Cryptoderma* Imazeki 1943
= *Daedaloides* Lázaro Ibiza 1916
= *Phaeolopsis* Murrill 1905
Poriodontia Parmasto 1982
Porodaedalea Murrill 1905
Pseudoinonotus T. Wagner & M. Fisch. 2001
Pseudophylloporia Y.C. Dai, F. Wu, L.W. Zhou & B.K. Cui 2022
Pyrrhoderma Imazeki 1966
Rigidonotus Y.C. Dai, F. Wu, L.W. Zhou, Vlasák & B.K. Cui 2022
Sanghuangporus Sheng H. Wu, L.W. Zhou & Y.C. Dai 2015
Sclerotus Xavier de Lima 2022
Trichaptum Murrill 1904
= *Hirschioporus* Donk 1933
Tropicoporus L.W. Zhou, Y.C. Dai & Sheng H. Wu 2015

Family Hyphodontiaceae Xue W. Wang & L.W. Zhou 2021
Hyphodontia J. Erikss. 1958

Family Odonticiaceae L.W. Zhou & Xue W. Wang 2023
Leifia Ginns 1998
Odonticium Parmasto 1968

Family Peniophorellaceae L.W. Zhou, Xue W. Wang & S.L. Liu 2023
Peniophorella P. Karst. 1889

Family Repetobasidiaceae Jülich 1982
  Repetobasidium J. Erikss. 1958
Family Resiniciaceae L.W. Zhou & Xue W. Wang 2023
  Resinicium Parmasto 1968
Family Rickenellaceae Vizzini 2010
  Rickenella Raithelh. 1973
Family Rigidoporaceae Jülich 1982
= Oxyporaceae Zmitr. & V. Malysheva 2014
  Bridgeoporus T.J. Volk, Burds. & Ammirati 1996
  Leucophellinus Bondartsev & Singer 1944
  Rigidoporus Murrill 1905
  = *Botryodontia* (Hjortstam & Ryvarden) Hjortstam 1987
  = *Oxyporus* (Bourdot & Galzin) Donk 1933
Family Schizocorticiaceae L.W. Zhou & Xue W. Wang 2023
  Schizocorticium Sheng H. Wu 2021
  = *Skvortzoviella* Jia Yu, Xue W. Wang, S.L. Liu & L.W. Zhou 2021
Family Schizoporaceae Jülich 1982
  Fasciodontia Yurchenko & Riebesehl 2020
  Lyomyces P. Karst. 1881
  = *Rogersella* Liberta & A.J. Navas 1978
  Xylodon (Pers.) Gray 1821
  = *Lagarobasidium* Jülich 1974
  = *Odontiopsis* Hjortstam & Ryvarden 1980
  = *Palifer* Stalpers & P.K. Buchanan 1991
  = *Schizopora* Velen. 1922
Family Sideraceae L.W. Zhou & Xue W. Wang 2023
  Sidera Miettinen & K.H. Larss. 2011
Family Skvortzoviaceae L.W. Zhou & Xue W. Wang 2023
  Skvortzovia Bononi & Hjortstam 1987
Family Tubulicrinaceae Jülich 1982
  Tubulicrinis Donk 1956
Hymenochaetales genera *incertae sedis*
  Alloclavaria Dentinger & D.J. McLaughlin 2007
  Atheloderma Parmasto 1968
  Blasiphalia Redhead 2007
  Bryopistillaria Olariaga, Huhtinen, Læssøe, J.H. Petersen & K. Hansen 2020
  Cantharellopsis Kuyper 1986
  Contumyces Redhead, Moncalvo, Vilgalys & Lutzoni 2002
  = *Jacobia* Contu 1998
  Cotylidia P. Karst. 1881
  = *Bresadolina* Brinkmann 1909
  = *Craterella* Pers. 1794
  = *Stereophyllum* P. Karst. 1889
  Ginnsia Sheng H. Wu & Hallenb. 2010
  Globulicium Hjortstam 1973
  Gyroflexus Raithelh. 1981
  = *Sphagnomphalia* Redhead, Moncalvo, Vilgalys & Lutzoni 2002
  Hastodontia (Parmasto) Hjortstam & Ryvarden 2009
  Kurtia Karasiński 2014
  Lawrynomyces Karasiński 2013
  Litschauerella Oberw. 1965
  Loreleia Redhead, Moncalvo, Vilgalys & Lutzoni 2002
  Lyoathelia Hjortstam & Ryvarden 2004
  Muscinupta Redhead, Lücking & Lawrey 2009
  Sphaerobasidium Oberw. 1965
  Subulicium Hjortstam & Ryvarden 1979
  Tsugacorticium Nakasone & Burds. 2011

Caeruleomyces Stalpers 2000—its taxonomic placement at the order level is arbitrary due to the simple anamorphic morphological characters and lack of molecular evidence (see Wang et al. 2023a).

Erythromyces Hjortstam & Ryvarden 1990—fell within the clade being composed of genera in Polyporales (see Wang et al. 2023a).

Physodontia Ryvarden & H. Solheim 1977—the only available molecular sequence from this monotypic genus (KJ140741 in GenBank) indicates its position in Polyporales via BLAST search (see Wang et al. 2023a).

Evolution

Divergence time of Hymenochaetales has been estimated between 207.21 and 259 million years (Myr) (Feng et al. 2012; Zhu et al. 2019; He et al. 2019a; Wang et al. 2021a, 2023a). Wang et al. (2023a) found that the Hymenochaetales diverged into two evolutionary lineages, one 219.16 Myr that gave rise to the families Skvortzoviaceae, Sideraceae, Schizocorticiaceae, Resiniciaceae, Peniophorellaceae and Richnellaceae, and the other lineage diverged 206.95 Myr giving rise to Hymenochaetaceae, Tubulicrinaceae, Chaetoporellaceae, Schizoporaceae, Hyphodontiaceae, Rigidoporaceae, Odonticiaceae and Reptobasidiaceae. In the first lineage, the oldest families were Skvortzoviaceae and Sideraceae occurring in a mean crown age 148.68 Myr (between 114.97–182.96 Myr) and 124.92 (90.18–161.15 Myr) respectively; followed by Schizocorticiaceae, Resiniciaceae and Peniophorellaceae with a mean crown age 98.91 Myr (61.82–139.07 Myr), 82.43 Myr (54.41–113.23 Myr) and 71.36 Myr (39.39–108.21 Myr), respectively. The youngest family was Richnellaceae with a mean crown age 31.31 Myr (emerged between 15.4–49.12 Myr). In the second lineage the oldest families were Hymenochaetaceae and Rigidoporaceae occurring in a mean crown age 161.9 Myr (emerged between 139.64–183.13 Myr) and 153.43 Myr (emerged between 119.65–187.18 Myr) respectively, followed by Schizoporaceae, Chaetoporellaceae, and Tubulicrinaceae with a mean crown age 123.59 Myr (97.57–149.58 Myr), 112.14 Myr (72.4–151.87 Myr), and 108.26 Myr (69.79–145.89 Myr), respectively. After that, Odonticiaceae and Reptobasidiaceae occur in a mean crown age 96.11 Myr (44.85–149.57 Myr) and 70.65 Myr (37.95–106.77 Myr), respectively. While Hyphodontiaceae was the youngest family in this group, occurring in a mean crown age 27.5 Myr (emerged between 12.18 and 46.61 Myr), in contrast to what was indicated by Wang et al (2021a, b) who found that Hyphodontiaceae occurred in a mean crown age 92.78 Myr.

Basidiomes serve for the protection of developing reproductive organs (basidia) and the promotion of spore dispersal either by providing an enlarged supporting surface for the hymenium and/or by lifting it above ground level (Nagy et al. 2017). Several alternative solutions have evolved for these tasks during evolution, ranging from simple aggregations of basidia on a hyphal mat or subiculum to highly integrated complex types. The simplest such solutions in the Basidiomycota comprise crust-like, flat basidiomes that enclose basidia into a resupinate type. The evolution of basidiomes types has followed in the Basidiomycota a clear trend exists from crustlike, resupinate, to more complex morphologies (Hibbett and Binder 2002; Hibbett 2004; Binder et al. 2005). A great diversity of morphological types of basidiomes derived from the ancestral resupinate types, including coralloid, agaricoid (pileate-stipitate), polyporoid (bracket fungi), gasteroid (puffball-like), or reduced cup-shaped (cyphelloid), among others (Nagy et al. 2017). In Hymenochaetales, we found three basidiomes ancestral traits, the habit of basidiomes, hymenophoral configuration and hyphal system following to Wang et al. (2023a) and they are the resupinate habit, smooth hymenophore, and hyphal system monomitic. The ancestral resupinate habit remains in 13 families of Hymenochaetales, only Richnellaceae has an omphalinoid habit, and 10 families only have the resupinate habit, and envolved to more complex morphologies for Hymenochaetaceae, Schizoporaceae, and Rigidoporaceae. On the other hand, the ancestral smooth hymenophoral configuration is present in 10 families, except in Odonticiaceae, Richnellaceae, Rigidoporaceae and Sideraceae, and only Reptobasidiaceae preserves the smooth hymenophore. The major diversification of the hymenophoral configuation occurred in Chaetoporellaceae, Hymenochaetaceae, Hyphodontiaceae, Resiniciaceae and Schizoporaceae. Regarding the hyphal system, in Wang et al. (2023a) we can observe that the Hymenochaetales separated into two clades, as we mentioned before, the families Skvortzoviaceae, Schizocorticiaceae, Resiniciaceae, Peniophorellaceae and Richnellaceae remain the ancetral monomitic hyphal system and only Sideraceae diversified into a dimitic hyphal system. The first four families remain the ancestral resupinate habit and Richnellaceae with several genera insetae sedis of Hymenochaetales developed clavarioid and omphalinoid habit and diverged into more recent subclades. While the second clade with the eight families separated into four subclades, one that gave rise to the Tubulicrinaceae and Hymenochaetaceae. The first separated 108 Myr ago and retained the ancestral states resupinate and monomitic hyphal system. The second family diversifies from resupinate habit and monomitic hyphal system to effused-reflexed, pileate-sessile, pileate-stipitate and coralloid habit and to dimitic or trimitic hyphal system. The second subclade gave rise to the families Chaetoporellaceae, Hyphodontiaceae and Schizoporaceae. The first and second families remain its ancestral resupinat habit, but diversifies from monomitic to pseudodimitic hyphal system and the third family diversifies from resupinate to pileate habit and from monomitic to dimitic or trimitic hyphal system. The third subclade gave rise to the second oldest family, Rigidoporaceae that diversifies from resupinate to pileate habit and monomitic to dimitic hyphal system. The last subclade gave rise to Odonticiaceae and Reptobasidiaceae and they remain the ancestral resupinate habit, but the first diversifies to pseudodimitic hyphal system. It is important to mention that the only family that retained the three ancestral traits was Reptobasidiaceae in Hymenochaetales.

Justification of order and problems

Monophyly of Hymenochaetales is well supported, but the family-level classification of the order poses several unresolved taxonomic issues. The largest family within the Hymenochaetales is the Hymenochaetaceae, which comprises ca. 74% of the species has been accepted in the order by Dai et al. (2010), Wijayawardene et al. (2022a) and Wu et al. (2022b). While Hymenochaetaceae comprises a vast and varied assortment of taxa, current evidence does not provide sufficient justification for the subdivision of this group into smaller, monophyletic families. Despite numerous studies, a consensus on the appropriate classification of the Hymenochaetaceae family remains elusive. For example Korotkin et al. (2018) accepted the genera *Coltricia*, *Fibricium*, *Basidioradulum*, *Trichaptum*, and *Tubulicrinis* as part of the Hymenochaetaceae. In contrast, Wang et al. (2021a) excluded these taxa from Hymenochaetaceae and instead proposed *Coltricia* as the member of the monotypic family Coltriciaceae. According to the latter narrow systematic concept, the family-level classification of genera *Fibricium*, *Basidioradulum* and *Trichaptum* remain uncertain. In addition, phylogenetic analyses have revealed that the monotypic family Nigrofomitaceae (Zhou et al. 2018;

Wang et al. 2021a) and the genus *Neoantrodia*, which was initially classified in its own family (Neoantrodiellaceae) (Ariyawansa et al. 2015), are nested within the aforementioned taxa. Therefore, following the broad interpretation of the Hymenochaetaceae family proposed by Korotkin et al. (2018), the Coltriciaceae, Neoantrodiellaceae, and Nigrofomitaceae are considered synonymous. The placement of the Tubulicrinaceae, which is based on *Tubulicrinis*, has given rise to additional questions (Larsson et al. 2006; He et al. 2020). According to Wang et al. (2021a), the systematic classification of *Tubulicrinis* and Tubulicrinaceae is currently unresolved. Previous studies have suggested that the Hyphodontiod species (*Hyphodontia* s. lato) could be classified within the Tubulicrinaceae and Schizoporaceae families, as well as the *Kneiffiella* clade (i.e., *Chaetoporellaceae*) (Larsson 2007; Hibbett et al. 2014). More recently, Wang et al. (2021a, b) proposed that the six accepted genera of *Hyphodontia* s. lato belong to at least four clades, three of which have been elevated to the family level: Chaetoporellaceae, Hyphodontiaceae, and Schizoporaceae. However, the family-level classification of *Hastodontia* and several other corticioid taxa in Hymenochaetales remains unresolved (Luo et al. 2021; Wang et al. 2021a). The uncertainties surrounding the classification of certain taxa can be primarily attributed to the absence of type species in phylogenetic analyses. One such example is *Repetobasidium*, the genus on which the Repetobasidiaceae family was established (Wang et al. 2021a). Wang et al. (2021a) argue that the Rickenellaceae, which has been accepted by several studies (e.g., He et al. 2019a; Wijayawardene et al. 2022a; Liu et al. 2022c), is likely a nomenclaturally superfluous name for Repetobasidiaceae. This is because the original circumscription of the 'Rickenella family' by Larsson (2007) included *Repetobasidium* species. To address the taxonomic uncertainties mentioned above and achieve a more precise family-level classification of Hymenochaetales, a comprehensive multi-gene phylogenetic analysis using additional barcoding markers, such as tef, rpb1, rpb2, etc., is necessary. It is also important to include the type species of each genus and obtain more samples for analysis.

It is recommended to get sequences of material from or close to the type locality when sequencing the type material failed. Several sequences from type species (not from type material) are produced, but not from or close to the type locality, resulting in several taxonomical problems.

Significance

Hymenochaetales exhibits a wide variety of different ecological strategies, but most species are white rot fungi and often the dominant part of the wood-rot communities. There are some species that form ectomycorrhizae and a number of species are parasites or pathogens of woody plants. Several species of *Peniophorella* have specialized organs for catching invertebrates, apparently an adaptation to a nitrogen-deprived environment. A peculiar ecological group of mostly agarics are moss associated (Hibbett et al. 2014).

There are several species of Hymenochaetales as important pathogens of temperate and tropical trees. In temperate forest are pathogens of conifers and hardwoods trees such as *Fuscoporia coronadensis, Onnia circinata* and *Porodaedalea pini* (heartrot of *Pinus* spp.), *Fomitiporia hartigii* and *Coniferiporia qilianensis*, *C. sulphurascens*, *C. uzbekistanensis*, *C. weirii* (root or stem rot in conifers). Besides, *Fomitiporia calkinsii*, *F. robusta*, *Inocutis dryophilus, Inonotus hirsutus, I. quercustris, Phellinus everhartii*, *P. laevigatus* cause a heartrot in hardwood, mainly *Quercus* spp. and *Phellinus tremulae* cause a heartrot in *Populus tremuloides* and *Pseudoinonotus dryadeus* a root rot in *Quercus* spp. (Cibrian et al. 2007; Cui et al. 2015; Wang et al 2022a). In tropical forest are pathogenic species in natural forest and plantations such as *Rigidoporus microporus* in rubber and other tropical tree plantations, *Fulvifomes fastuosus* cause heartrot in Cedar (*Cedrela odorata*) and mahogany (*Swietenia macrophylla*), *Pyrrhoderma noxium* is a serious pathogen on many angiosperm trees in tropical Asia, *Tropicoporus linteus* cause a heartrot in *Cordia alliodora* and *C. elaeagnoides*, its wood is used for furniture construction in Mexico (Hibbett et al. 2014; Cibrian et al. 2007).

Many species of Hymenochaetales have medicinal properties. Hibbett et al. (2014) mentioned that the basidiomes of *Inonotus sanghuang* (= *Sanghuangporus sanghuang*), many *Phellinus* spp., and cankers of *I. obliquus* are used in herbal medicine and are reported to have anticancer activities in Asia (Sun et al. 2023). Rogers (2011), in his book of medicinal mushrooms of North America, cited several species of Hymenochaetales such as *Inonotus obliquus* with antibacterial, anti-inflammatory, antioxidant, antiviral, against diabetes, immune tonic, kidney tonic and antitumor properties; *Phellinus igniarius* and *P. tremulae* with antifungal, antitumor and antiviral properties; and *Trichaptum biforme* with antitumor property. *Sanghuangporus* spp. are traditional Chinese medicines that have been demonstrated to have antitumor, antioxidant, anti-inflammatory, antidiabetic, hepatoprotective, neuroprotective and immunomodulatory properties (Zhu and Cui 2016; Gafforov et al. 2023; Lv et al. 2023; Song et al. 2023; Wang et al. 2023b). A study result indicates that *Sanghuangporus sanghuang* and its phenolic compounds have latent capacity for preventing SARS-CoV-2 infection in the future (Chien et al. 2022).

Other relevant data and future recommendations

Hymenochaetales recently was included in subclass Agaricomycetidae by Index Fungorum page. However, the Hymenochaetales belongs to a very separate clade of the core of this subclass, with the Polyporales, Gloeophyllales, Thelephorales, Russulales, Corticiales, among others; and only Hymenochaetales has been placed within the Agaricomycetidae (He et al. 2019a; Wang et al. 2023a). On the other hand, we would like to mention that in *Hymenochaetaceae* there are two separate subclades, one that presents setae, styrilpyrones pigments and generative hyphae without clamp-conections and the other clade does not have the first two characters and there are clamp-conections in *Basidioradulum*, *Fibricium* and *Trichaptum*, so must be important to review the position of these genera of this family. Wang et al. (2023a) stated that clamp connections would be absent in the family.

Hysterangiales K. Hosaka & Castellano 2007

Contributed by: Naveed Davoodian

Introduction

Hosaka and Castellano circumscribed Hysterangiales to comprise Hysterangiaceae and related families based on phylogenetic evidence (Hosaka et al. 2006). Taxa in the order are sequestrate, nearly all are hypogeous to more or less so, and almost all are ectomycorrhizal, with the notable exception of the basal family Phallogastraceae which contains non-mycorrhizal species, some of which are epigeous. The order is fairly diverse and most of the species are undescribed (Davoodian et al. 2021).

History

Hysterangiales was first properly described and phylogenetically delineated by Hosaka and Castellano (Hosaka et al. 2006). Prior to that, multiple authors recognized Hysterangiales as a distinct order (segregated from Phallales) though it had never been validly described, and they included in it some taxa currently excluded (e.g., Zeller 1939; Jülich 1981). The separate but close relationship of Hysterangiales and Phallales that was previously posited (e.g., Jülich 1981) but not unanimously accepted (e.g., Hawksworth et al. 1995) was later confirmed by Hosaka et al. (2006). In the past, Phallales/Hysterangiales and many representative and allied taxa were classified under Gasteromycetes, a class no longer in use which accommodated numerous gasteroid fungi now known to have various affinities. Hysterangiaceae was established by Fischer (1899) to accommodate some gasteroid taxa, of which only the genus *Hysterangium* Vittad. remains. At that time Fischer included *Phallogaster* Morgan, which is now known to be outside of Hysterangiaceae though within Hysterangiales; the family Phallogastraceae was only recently validly described (Davoodian et al. 2021). Hysterangiales currently includes Phallogastraceae Castellano, T. Lebel, Davoodian & K. Hosaka, Gallaceaceae Locq. ex P.M. Kirk, Mesophelliaceae (G. Cunn.) Jülich, and Hysterangiaceae E. Fisch.

Characters that define the taxa in the order

The following is collated and adapted from Hosaka (2005) and Hosaka et al. (2006): All members of Hysterangiales are sequestrate, though some crack open and expose the gleba (Hosaka 2005). Almost all produce globose to irregular, hypogeous (or more or less so i.e. emerging/erumpent) sporocarps; some are epigeous. Many species form rhizomorphs. Peridia range from fragile/brittle to very hard; sometimes they are elastic/gummy. Root matter, soil, and other debris is often found sticking to or incorporated into the peridium. Peridia colors range from white to yellow to more richly colored (e.g., brown, violet) and at times stain (e.g., red, pink, yellow, other colors) when bruised. Peridia occur in one to four layers. The gleba is cartilaginous to gelatinous or powdery at maturity, with grey to green to olive to brown coloration, "with a dendroid, cartilaginous to gelatinous columella, or a soft to rubbery central core or lacking such structures" (Hosaka et al. 2006). Basidia are two to eight spored. The spores are statismosporic, generally "ellipsoid, oblong to fusoid, smooth to minutely verrucose, or sometimes ornamented with spines, often with wrinkled to inflated or ephemeral utricle" (Hosaka 2005). Spores range in color from hyaline to pale green to brown in KOH (Hosaka 2005; Hosaka et al. 2006).

Plates

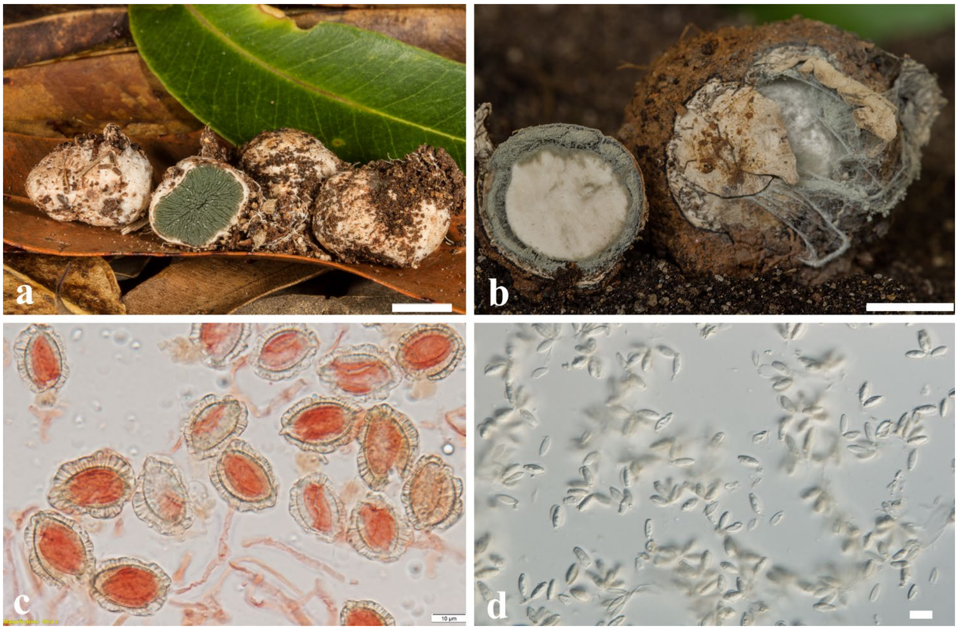


Fig. 34 Morphological characters of Hysterangiales. **a** basidiomes of *Mesophellia* sp., smaller basidiome on left in cross section showing whitish sterile core surrounded by mass of powdery spores encased in a peridium with debris on the outside (credit: Michael A. Castellano, scale bar = 1 cm); **b** basidiomes of *Hysterangium* sp., second on left in cross section exposing gleba (credit: Michael A. Castellano, scale bar = 1 cm); **c** basidiospores of *Hysterangium* sp. in KOH, with basidia faintly visible in some areas (credit: Naveed Davoodian, scale bar = 10 µm); **d** basidiospores of an undescribed Mesophelliaceae species in KOH and Congo red solution, spores with prominent utricle, cellular contents within cell walls stained red in background (credit: Naveed Davoodian, scale bar = 10 µm)

Genera included

- Family Gallaceaceae Locq. ex P.M. Kirk 2008
  - *Austrogautieria* E.L. Stewart & Trappe 1985
  - *Gallacea* Lloyd 1905
  - *Hallingea* Castellano 1996
- Family Hysterangiaceae E. Fisch. 1898
  - *Aroramyces* Castellano & Verbeken 2000
  - *Hysterangium* Vittad. 1831
  - *Statesia* Castellano, T. Lebel, Davoodian & K. Hosaka 2022
- Family Mesophelliaceae Jülich 1982
  - *Andebbia* Trappe, Castellano & Amar. 1996
  - *Castoreum* Cooke & Massee 1887
  - *Chondrogaster* Maire 1926
  - *Gummiglobus* Trappe, Castellano & Amar. 1996
  - *Gummivena* Trappe & Bougher 2002
  - *Malajczukia* Trappe & Castellano 1992
  - = *Potoromyces* Müll. bis ex Hollós 1902
  - *Mesophellia* Berk. 1857
  - *Nothocastoreum* G.W. Beaton 1984
- Family Phallogastraceae Castellano, T. Lebel, Davoodian & K. Hosaka 2021
  - = Phallogastraceae Locq. 1974
  - *Phallogaster* Morgan 1893
- Hysterangiales genera *incertae sedis*
  - *Circulocolumella* S. Ito & S. Imai 1957
  - = *Stalactocolumella* S. Imai 1950
  - *Clathrogaster* Petri 1900

Evolution

The present study infers Hysterangiales to have diverged about 113 Myr from a common ancestor shared with the Phallales/Geastrales clade (Fig. 1). The suborder Phallogastrineae contains the basal family Phallogastraceae, which comprises saprotrophic species; the suborder Hysterangineae contains the families Hysterangiaceae, Mesophelliaceae and Gallaceaceae, which are presumed to be completely mycorrhizal (Davoodian et al. 2021). Hysterangiaceae and Mesophelliaceae have a sister relationship to each other (Hosaka et al. 2006; Davoodian et al. 2021). Gallaceaceae and Mesophelliaceae are endemic to Australasia, with nearly all native occurrences of the latter recorded in Australia. Hosaka et al. (2008) investigated biogeographic hypotheses regarding Hysterangiales, with multiple potential scenarios emerging from their analyses including an eastern Gondwanan origin of the order and an important role for long-distance dispersal in explaining the diversification and distribution of the group.

Justification of order and problems

A recent major phylogenetic study of Hysterangiales revealed extensive, hitherto unknown generic and specific level diversity in the order and included formal description of two new suborders and a new family (Phallogastraceae, previously invalidly described); two new combinations were made to *Phallogaster* (Davoodian et al. 2021). It also confirmed a number of existing genera within Hysterangiales, and corroborated that true *Protubera* lies outside of Hysterangiales within Phallales (family Protophallaceae) and that true Trappeaceae lies outside of Hysterangiales in Phallales as well (Trierveiler-Pereira et al. 2014a; Sulzbacher et al. 2016b). The recent study by Davoodian et al. (2021) and previous ones have supported the monophyly of Hysterangiales (e.g., Hosaka 2005; Hosaka et al. 2006, 2008). From the study by Davoodian et al. (2021), it is clear that most taxa in Hysterangiales still need to be described.

Significance

Ecological and economical roles

Hysterangiales is a fungal order of major ecological importance. Most Hysterangiales form ectomycorrhizal symbioses in forests and woodlands, and many serve as critical food sources for wildlife, including endangered mammals such as *Potorous longipes* (Hayes et al. 1986; Nuske et al. 2017). Species of Mesophelliaceae are thought to play key roles in the recovery of Myrtaceae-dominated ecosystems after wildfires, providing food for animals after fires and maintaining mycorrhizal relationships and nutrient exchange (Claridge 1992). Hysterangiales is important to the forestry industry since they occur as ectomycorrhizal symbionts in many places where conifers and eucalypts are commercially harvested (Giachini et al. 2000; Carey 2003).

Chemical diversity

The chemistry of some *Mesophellia* species have been studied and speculated upon from the perspective of fungal volatile compounds attracting mammals to consume and disperse the fungi (Millington et al. 1998; Claridge and Trappe 2004). Mycelial mats of a *Hysterangium* species are known to exude oxalic acid which precipitates with calcium as calcium oxalate (Cromack et al. 1979). Taş et al. (2021) studied chemical constituents of *Hysterangium inflatum* and their anticancer, antioxidant, and enzyme inhibitory properties.

Other relevant data and future recommendations

Since the critically important study by Hosaka et al. (2006), new Hysterangiales taxa have continued to be described (Guevara-Guerrero et al. 2008; Davoodian et al. 2021). The study by Davoodian et al. (2021) revealed that the majority of Hysterangiales taxa are still undescribed. Given the diversity of this group and its ecological and potential economic importance, more research on the taxonomy, phylogeny, ecology, and genomics of this group is warranted.

Jaapiales Manfr. Binder, K.H. Larss. & Hibbett 2010

Contributed by: Arun Kumar Dutta

Introduction

Jaapiales is the smallest order in the Agaricomycetes class, which includes the monotypic family Jaapiaceae. It was first introduced in 2010 and contains the genus *Jaapia* with two known taxa, viz. *J. argillacea* and *J. ochroleuca*. The occurrence of *J. argillacea* has been reported from various regions of Europe, Canada, and the USA (Bresadola 1911; Nannfeldt and Eriksson 1953; Eriksson and Ryvarden 1976; Ginns and Lefebvre 1993; Legon et al. 2005). Compared to *J. argillacea*, the other known taxon of the family, *J. ochroleuca*, is widely distributed and has been reported from Europe, America, Canada, Argentina, Africa, and Asia (Rogers 1943; Nannfeldt and Eriksson 1953; Hjortstam 1987; Ginns and Lefebvre 1993; Dai 2011; Gorjón et al. 2012).

For 20 years, several authors recognized the monotypic genus *Jaapia* described by Bresadola (1911) as containing *J. argillacea* Bres. (von Höhnel 1912; Bourdot and Galzin 1928; Rogers 1935). Later, *Coniophora ochroleuca* Bres. was recognized as the second species of *Jaapia* by Nannfeldt and Eriksson (1953). *Jaapia* was previously believed to have a close relationship with *Pellicularia* Cooke (Rogers 1935) and *Coniophora* DC. (von Höhnel 1912), or even *Coniobotrys* Pouzar (Pouzar 1958) due to the peculiar morphology of its basidiospores which are relatively large, fusiform in shape, and possess a prominent apiculus that resembles a peg. *Jaapia* was classified as a member of the Coniophoraceae by Nannfeldt and Eriksson (1953) and Donk (1964), but Eriksson and Ryvarden (1976) included *Jaapia* in their broader definition of the Cortiaceae family.

Characteristically, members of Jaapiales show fully resupinate basidiomes and appear saprotrophic in nature. Binder et al. (2005) used nuclear and mitochondrial large and small subunit rRNA gene analysis to determine that *Jaapia* is the closest relative of the other members of the Agaricomycetidae. Larsson (2007) classified it as "*incertae sedis*" under the *Jaapia* family of corticioid fungi in his phylogenetic classification. According to Binder et al. (2010), Jaapiales contains the family Jaapiaceae, which is named after the solitary genus *Jaapia*. Jaapiales is also confirmed as the sister group to the remaining Agaricomycetidae (Binder et al. 2010). Chen et al. (2020) considered Jaapiales a synonym of Gloeophyllales based on multigene phylogeny. Regarding the pasasitic nature, the members of Jaapiales differ from causing typical brown rot, as do the members of the genera in Gloeophyllales (Riley et al. 2014).

History

Jaapiales was first named in 2010 with the family Jaapiaceae comprising *Jaapia* with two known species, *J. argillacea* and *J. ochroleuca* (Binder et al. 2010). Morphologically, members of the order possess a fully resupinate and effused basidiomes, a thin and smooth porous hymenophore, fusiform basidiospores with thick walls that are strongly cyanophilous, a 4-spored basidia-shaped cavate, long protruding cystidia, and a monomitic hyphal system, and habitat as saprophytes on decaying wood. Hibbett and Binder (2002) did a thorough study of the resupinate homobasidiomycetes and found that the only Jaapiales taxon, *J. argillacea*, was the sister to the Bolete clade based on mitochondrial and nuclear ribosomal DNA regions. However, the position was not supported. Larsson (2007) reclassified *Jaapia* as a Gloeophyllales, Corticiales, and Thelephorales-related species using the nuc-lsu rRNA sequence. Binder et al. (2010) used multiple gene datasets to show that *Jaapia argillacea* was on its own, below Boletales and Atheliales and next to Agaricomycetidae, with moderate to strong support (70% BS, 1.00 PP). Recently, Chen et al. (2020) used a multigene phylogeny, which included both nuclear rDNA regions and protein-coding genes, and concluded that the order Jaapiales should be considered a synonym of the Gloeophyllales. In terms of their parasitic nature, the members of the order Jaapiales are distinct from the members of the genera in the order Gloeophyllales in that they do not cause the typical brown rot (Riley et al. 2014).

Characters that define the taxa in the order

Basidiomes effused. Hymenophore porous, very thin, smooth. Basidiospores fusiform, smooth, strongly cyanophilous, thick-walled at maturity. Basidia clavate, 4-spored. Cystidia present, long, projecting. Hyphal system monomitic, hyphae nodose-septate. Habitat on decaying wood.

Plates

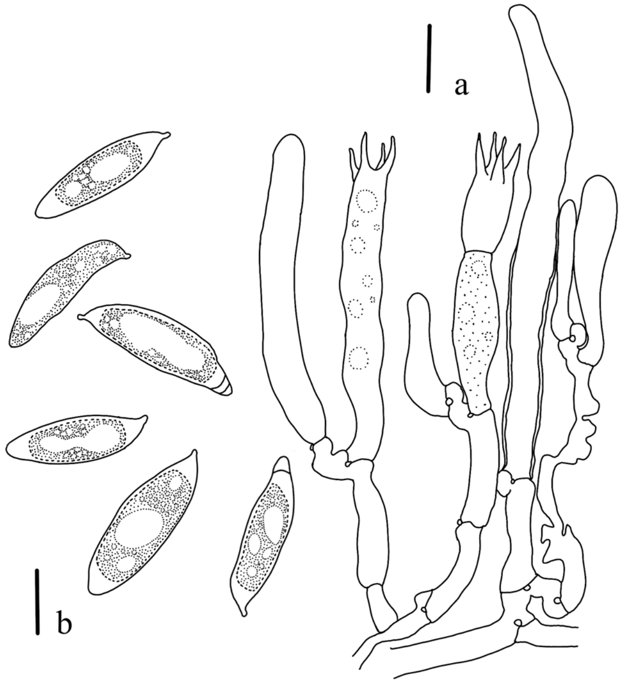


Fig. 35 Microscopic characters of *Jaapia argillacea*. **a** basal hyphae, basidia, and cystidia; **b** basidiospores. Scale bars: a, b = 10 μm. Redraw from Teresa Telleria et al. (2015) by Mao-Qiang He

Genera included

Family Jaapiaceae Manfr. Binder, K.H. Larss. & Hibbett 2010

Jaapia Bres. 1911

= *Coniobotrys* Pouzar 1958

Evolution

Hibbett and Binder (2002) performed a detailed phylogenetic study with 144 resupinate species of homobasidiomycetes. They showed that the only Jaapiales taxon, *Jaapia argillacea*, was sister to the Bolete clade based on mitochondrial and nuclear ribosomal DNA (rDNA) regions, but this position was not supported. Later, Larsson (2007) employed the nuc-lsu rRNA sequence to reclassify *Jaapia* as a near relative of the Gloeophyllales, Corticiales, and Thelephorales. Binder et al. (2010) used multiple gene datasets to show that *Jaapia argillacea* was on its own, below the clade of Boletales and Atheliales and next to the clade of Agaricomycetidae, with moderate to strong support (70% BS, 1.00 PP). This suggests that most pileate-stipitate mushrooms came from resupinate ancestors. In this analysis, the single included taxon, *Jaapia argillacea*, of the order Jaapiales falls within the clade Agaricomycetes and is resolved to be the sister group to the members of the order Gloeophyllales with full support value. This shows that the two orders split 135 million years ago in the lower Cretaceous. Basal to the orders Gloeophyllales and Jaapiales reside the members of Corticiales, and the divergence took place at 183 Myr in the Jurassic period.

Justification of order and problems

Jaapiales is known to contain a monotypic family with two known species, viz., *J. argillacea* and *J. ochroleuca*. Position of Jaapiales within the Agaricomycetidae or outside of the Agaricomycetidae has been a matter of debate for a long time. Binder et al. (2005) established *Jaapia*, the known taxa of the order Jaapiales, as the sister group of the rest of the Agaricomycetidae. However, some of the studies considered the genus *Jaapia* a member of the order Boletales. Larsson (2007) reclassified *Jaapia* as a Gloeophyllales, Corticiales, and Thelephorales-related species. Binder et al. (2010) used multiple gene datasets and showed that *J. argillacea* was on its own, below Boletales and Atheliales and next to Agaricomycetidae. More recently, Chen et al. (2020) considered the order Jaapiales a synonym of Gloeophyllales based on a multigene phylogeny. Hence, data from whole-genome studies is necessary to solve the problem of whether to consider Jaapiales as a separate order or synonymized with Gloeophyllales.

Significance

Ecological and economical roles

Jaapia argillacea, the type species of the order Jaapiales, is a wood-rotting fungus that causes white rot by decomposing the wood by digesting the cellulose, hemicellulose, and lignin. The mycelium of *J. argillacea* completely replaces the cell wall of wood. In the year 2014, the genome of *J. argillacea* was sequenced, which revealed that the taxon lacks ligninolytic class-II peroxidases but has several enzymes that act on crystalline cellulose (Riley et al. 2014). Evidence shows that the members of the genus cluster closely with *Phanerochaete chrysosporium*, which is the model white rot species. *Jaapia argillacea* destroys all wood components using carbohydrate- and lignin-active enzymes but does so without ligninolytic class II peroxidases. In laboratory testing, *J. argillacea* destroys all polymeric components of woody plant cell walls and similarly increases the number of genes for decreasing polyketide synthase. The genomes of *J. argillacea* also reveal unique CAZymes from the white-rot fungus (Riley et al. 2014). There is only one cellobiose dehydrogenase gene and 15 lytic polysaccharide monooxygenases (LPMOs) genes in white-rot fungi like *J. argillacea* (Riley et al. 2014). Laccase activity is absent in *J. argillacea* (Niku-Paavola et al. 1988).

Chemical diversity

Much work has not been carried out to explore the chemical diversity of the order Jaapiales. Riley et al. (2014), however, sequenced the genome of *Jaapia argillacea* of the order Jaapiales and found that the taxon does not have ligninolytic class II peroxidases, but it does have enzymes that break down cellulose, hemicellulose, and lignin. Besides, Niku-Paavola et al. (1988) also reported the absence of the laccase enzyme in *J. argillacea*. An in-depth look at the genome of *Jaapia argillacea* (Riley et al. 2014) showed that it has one cellobiose dehydrogenase gene, 15 lytic polysaccharide monooxygenase genes, and a gene that makes CAZymes.

Other relevant data and future recommendations

Jaapiales consists of the monotypic family Jaapiaceae and the well-known genus *Jaapia*. To date, there are only two known species of the genus *Jaapia* (*J. argillacea* and *J. ochroleuca*). The order was earlier referred to as the sister order of Boletales. The greatest radiation of mushroom-forming fungus, the Agaricomycetidae, is sister to Jaapiales, according to recent research. The basidiomes of *Jaapia argillacea* are made of loosely connected hyphae, and the fungus grows abundantly in old-growth woods across the northern hemisphere. *Jaapia argillacea* feeds on the rotting wood of conifers and is thought to produce a type of brown rot by breaking down cellulose, hemicellulose, and lignin. The fungus lacks ligninolytic class II peroxidases and laccase activity. Because of its position on the phylogenetic tree, *J. argillacea* is a good reference point for figuring out how the enzymatic decay machinery has grown and shrunk over time in the Agaricomycetidae group.

Kriegeriales Toome & Aime 2013

Contributed by: Teun Boekhout, Andrey Yurkov

Introduction

Molecular phylogenetic studies have largely contributed to our understanding of the phylogenetic and taxonomic relationships of teleomorphic and anamorphic, filamentous, and yeast-like taxa of Basidiomycota. Kriegeriales is a good example of a classification that bridges the gap traditionally held by mycologists and zymologists.

History

Kriegeria was described as a plant pathogenic fungus on *Eriophorum* leaves. *Camptobasidium* is a filamentous basidiomycete with transversely septate basidia, and that also forms chlamydospore-like structures (Marvanová and Suberkropp 1990). Various molecular phylogenetic studies found that free living yeasts belonged to both lineages that were corroborated in more recent multigene-based phylogenetic studies (Turchetti et al. 2011; Toome et al. 2013; de Garcia et al. 2020; Pontes et al. 2020; Perini et al. 2021). Wang et al. (2015a, b) observed that *Camptobasidium*, *Glaciozyma*, and *Kriegeria* might belong to separate lineages. Species of *Glaciozyma* may form teliospore- or chlamydospore-like structures, with a yet unknown function (Turchetti et al. 2011).

Characters that define the taxa in the order

It is almost impossible to provide a list of characters that occur in all representatives and that are also unique for the order. Kriegeriales is mainly defined by molecular phylogenetic data that show the order as a sister group to Leucosporidiales (Toome et al. 2013). Members of Microbotryomycetes are plant pathogenetic or saprotrophic. Hyphae, if present, may have clamp connections, with a 'simple' septal pore organisation, and multiple pores may be present in a septum. The sexual state of the plant pathogens develops at the underside of the host leaves (i.e., *Eriophorum* or *Scirpus* spp.), and both *Kriegeria* and *Camptobasidium* form transversely septate basidia that form basidiospores that may or may not be forcibly discharged. Basidiospores may be septate and germinate by repetition or budding. Aquatic species form tetraradiate conidia, and other species are known with a yeast morph. During budding several cells may remain attached forming a candelabra-like structure. Ballistoconidia may be present. Colacosomes not present (Marvanová and Suberkropp 1990; Sampaio and Oberwinkler 2011b; Turchetti et al. 2011; Toome et al. 2013; Kachalkin 2014). As indicated above, many, but not all molecular studies confirmed the monophyly of Kriegeriales.

Plates

See Fig. 118.2 in Sampaio and Oberwinkler (2011b), Figs. 1 and 2 in Marvanová and Suberkropp (1990), Figs. 3 and 4 in Turchetti et al. (2011).

Genera included

- Family Camptobasidiaceae R.T. Moore 1996
    - *Camptobasidium* Marvanová & Suberkr. 1990
    - = *Crucella* Marvanová & Suberkr. 1990
    - *Cryolevonia* A. Pontes, Ruethi, B. Frey & J.P. Samp. 2020
    - *Glaciozyma* Turchetti, Connell, Thomas-Hall & Boekhout ex M. Groenew. & Q.M. Wang 2020
    - = *Glaciozyma* Turchetti, Connell, Thomas-Hall & Boekhout 2011
    - *Psychromyces* Perini & Zalar 2021
- Family Kriegeriaceae Toome & Aime 2013
    - *Kriegeria* Bres. 1891
    - = *Xenogloea* Syd. & P. Syd. 1919
    - = *Zymoxenogloea* D.J. McLaughlin & Doublés 1992
    - *Kriegeriopsis* Etayo, Diederich, Millanes & Wedin 2022
    - *Meredithblackwellia* Toome & Aime 2013

Phenoliferia Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout 2015

Yamadamyces Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout 2020

= *Yamadamyces* Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout 2015

Evolution

At present it is difficult to understand any evolutionary trend within Kriegeriales given the broad diversity in lifestyles.

Justification of order and problems

Given the somewhat contradicting phylogenetic signals observed (see above), it may well be that with improved taxon- and marker sampling, further insights will emerge into the monophyly of the group and its evolutionary relationships. Hence it may also become an interesting model to understand the underlying evolutionary forces that resulted in the various lifestyles, e.g., saprotrophic versus plant pathogenic, hyphal versus yeasts, temperature adaptations and so on.

Significance

Ecological and economical roles

Kriegeria is phytoparasitic on *Eriophorum* and *Scirpus* leaves (Sampaio and Oberwinkler 2011b; Toome et al. 2013). *Camptobasidium* is an aquatic filamentous fungus from subtropical freshwater streams (Marvanová and Suberkropp 1990), and many species are from cold habitats, e.g. ice, permafrost, melting sea ice, glaciers (Turchetti et al. 2011; Kachalkin 2014; de Garcia et al. 2020; Pontes et al. 2020). *Meredithblackwellia* is known from the tropical rain forest in Guyana (Toome et al. 2013). The psychrophilic species may be a source for cold-adapted enzymes that will be useful in biotechnology. Members of the genus *Phenoliferia* have a remarkable ability to assimilate phenolic compounds at low temperature.

Chemical diversity

Not known.

Lepidostromatales B.P. Hodk. & Lücking 2013

Contributed by: Ibai Olariaga**,** Rodrigo Márquez**,** Isabel Salcedo**,** Sergio P. Gorjón

Introduction

Lepidostromatales is a small order in Agaricomycetidae, containing only lichenized species and currently comprising about 13 species (Liu et al. 2019b). It was proposed for a single family, Lepidostromataceae, characterized by clavarioid basidiomes combined with a lichenized basal thallus with a chlorococcoid photobiont, apparently of pantropical distribution (Hodkinson et al. 2014). Lepidostromales is the only order of Basidiomycota conformed entirely by lichens with no close, non-lichenized relative and further seems to be the most ancient lineage of basidiolichens (Hodkinson et al. 2014).

History

Lepidostroma, the generic type, closely resembles *Multiclavula* in the clavarioid basidiomes and its species were for long included in *Multiclavula* (Petersen 1967; Oberwinkler 1970), before it was recognized as a separate genus on account of its squamulose thallus and not crustose-granulose like in *Multiclavula*. Molecular phylogenetic analyses eventually confirmed *Lepidostroma* as a distinct lineage, Lepidostromataceae, unrelated to *Multiclavula* (Cantharellales) and instead close to Atheliales in subclass Agaricomycetidae (Ertz et al. 2008; Hodkinson et al. 2014).

Characters that define the taxa in the order

Lepidostromatales is the only entirely lichenized lineage at the family and order level in Basidiomycota. The photobiont taxa appear to be lineage specific in the three main lineages of Lepidostromales. Thus, *Lepidostroma* is associated with photobions of an undetermined genus of Prasiolales (Trebouxiophyceae) and *Sulzbacheromyces* with the freshwater algal genus *Bracteacoccus* (Chlorophyceae), whereas the algal partner of *Ertzia* is not known yet, and underlining the uniqueness of the Lepidostromatales and its independent lichenization (Hodkinson et al. 2014). *Sulzbacheromyces caatingae*, the generic type of *Sulzbacheromyces*, is the only example of a *Multiclavula*-like thallus. The photobiont of *Lepidostroma* is chlorococcoid instead of coccomyxoid, as in *Multiclavula* with which it has long been confused

(Oberwinkler 1984, 2012; Sulzbacher et al. 2012). Moreover, *Lepidostroma* and *Multiclavula* can be distinguished by shape of basidia and number of sterigmata; basidia of *Lepidostroma* are subclavate to clavate-cylindrical bearing 2–4 sterigmata, whereas *Multiclavula* produces suburniform basidia with 4–6(–8) sterigmata (Oberwinkler 2012; Ertz et al. 2008). Although there is no evidence of it, Lepidostroma is very likely to possess chiastobasidia —largely predominant type among the Agaricomycetidae— opposed to the stichic basidia of *Multiclavula* (reference).

Sexual stages in Lepidostromatales are characterized by the formation of reduced clavarioid to caloceroid basidiomes, that are filiform to club-shaped with an obtuse to subulate apical part of yellow, orange to red orange colour, turning ochraceous upon drying in the few known species. The hyphae are clampless or nodose-septate and the subhymenium sometimes contains a mass of algal cells. The hymenium sometimes presents discrete sterile hymenial elements resembling sterile basidia. Basidia are usually oblong, subclavate to clavate, bearing 2–4 sterigmata and producing pip-shaped, elliptical, slightly reniform or obpyriform to suballantoid, thin-walled, hyaline, smooth, with hilar appendix, usually guttulate, and non-amyloid basidiospores (Hodkinson et al. 2014; Sulzbacher et al. 2012, 2016c; Liu et al. 2017a, 2019b).

Most species of Lepidostromatales have been recorded from tropical areas, mainly in Africa and South America, but lately some species have been described from Asia and various asian *Multiclavula* have been assigned to *Sulzbacheromyces*, making it the most diverse genus of Lepidostromales at present.

Plates

Fig. 36 Basidiomes of *Sulzbacheromyces yunnanensis* in situ (ZRL20210258, Yunnan province of China)

Genera included

Lepidostromataceae Ertz, Eb. Fisch., Killmann, Sérus. & Lawrey 2008
- *Ertzia* B.P. Hodk. & Lücking 2014
- *Lepidostroma* Mägd. & S. Winkl. 1967
- *Sulzbacheromyces* B.P. Hodk. & Lücking 2014

Evolution

Several phylogenetic analyses suggest that the Lepidostromatales represent a different lineage than accepted orders in subclass Agaricomycetidae (Agaricales, Amylocorticiales, Atheliales and Boletales), even though relationships among the mentioned orders in Agaricomycetidae are still controversial (Hodkinson et al. 2014; Varga et al. 2019). Lepidostromatales seems however to be more closely related to Atheliales than other groups in the Agaricomycetidae (Varga et al. 2019; Sulistyo et al. 2021).

Justification of order and problems

According to Hodkinson et al. (2014), BLAST results confirm doubts on the algorithm's utility in making taxonomic assignments for conserved rRNA sequences suggesting that taxonomic identifications based on BLAST can be quite unreliable also in the case of Lepidostromatales.

Due to the lack of genomic information, the relationships between the different genera and species belonging to the Lepidostromatales are based on the analysis of few genes (Hodkinson et al. 2014; Yanaga et al. 2015; Liu et al. 2017a, 2019b). It would be desirable to incorporate more genomes into the phylogenies or to perform phylogenomic analyses. Also, it is important to highlight the poor field sampling of the group, particularly, in tropical and subtropical areas, can have led to underestimate the diversity of Lepidostromatales.

Significance

Ecological and economical roles

Species of Lepidostromatales may be of paramount important in the establishment of algal symbioses and colonization of in particular environments, such as roadsides, bare ground, soil banks and termite nests (Sulzbacher et al. 2016c), and contribute to the stabilization of bare soil and the creation of biocrusts.

Leucosporidiales J.P. Samp., M. Weiss & R. Bauer 2003

Contributed by: Teun Boekhout

Introduction

Leucosporidiales comprises basidiomycetous yeasts belonging to Microbotryomycetes (Pucciniomycotina) that have white colonies, that form teliospores in their sexual state producing transversally septate basidia, and that, likely, are colacosome-interacting mycoparasites.

History

In early phylogenetic studies, Fell et al. (2000) identified the genera *Leucosporidium* and *Mastigobasidium* as members of the Microbotryum-clade. In 2003, Leucosporidiales was proposed to accommodate the members of this clade (Sampaio et al. 2003).

Characters that define the taxa in the order

Non-plant pathogenic members of Microbotryomycetidae, which may reproduce asexually by yeast budding or sexually by the formation of globose teliospores that germinate with transversely septate basidia. Basidia germinate by basidiospores that are not actively released. Basidiospores germinate with an ontogenetic yeast stage. Clamp connections are present in the hyphal state. Hyphae with 'simple' septa organisation, and colacosomes. Yeasts reproduce by usually polar budding and ballistoconida may be present (Sampaio et al. 2003). Coenzymes CoQ-9 and CoQ-10 are present. Xylose is absent from cell hydrolysates (Sampaio 2011d). The limits of the order are mainly circumscribed in the various molecular phylogenetic analyses (Fell et al. 2000; Scorzetti et al. 2002; Sampaio et al. 2003; Aime et al. 2006; Bauer et al. 2006; Wang et al. 2015a, b).

Plates

See Figs. 14, 15, 16, 17, 18 in Sampaio et al. (2003).

Genera included

Family Leucosporidiaceae Jülich 1982
    Leucosporidium Fell, Statzell, I.L. Hunter & Phaff 1970
    = *Mastigobasidium* Golubev 1999
    = *Leucosporidiella* Samp. 2003

Evolution

Leucosporidiales appears as a sister group to Microbotryales in most analyses (Sampaio et al. 2003; Wang et al. 2015a, b). However, Zhao et al. (2017) included the order in Microbotryales due to a short time of divergence of 74 million years ago versus 118 million years ago for Microbotryales. Phylogenomics studies using high quality genomes and a sufficient taxon sampling are needed to settle the issue of internal systematics of Microbotryomycetes.

Justification of order and problems

As indicated above, a recent multigene-based phylogenetic study indicated that Leucosporidiales might be part of Microbotryales (Zhao et al. 2017). Thus, it remains to be seen whether the non-plant pathogenic versus the highly specialised plant pathogenic lifestyles of both will hold as a distinguishing character.

Significance

Ecological and economical roles

Members of Leucosporidiales likely have a mycoparasitic lifestyle. Its members have a widespread occurrence on diverse substrates, such as sea—and freshwater, forest—and tundra soils, litter, mushrooms, etc. Some species are only known from Antarctica. Several species have been isolated from polluted waters, and other species are known to utilize monoaromatic compounds. It has been suggested that the latter might be interesting for bioremediation in colder climate zones (Golubev 2011; Sampaio 2011d).

Chemical diversity

Coenzyme Q9 and CoQ10, once used as taxonomic marker molecules, are found in Leucosporidiales (Sampaio et al. 2003).

Malasseziales R.T. Moore 1980

Contributed by: Bart Theelen, Teun Boekhout

Introduction

Traditionally known as skin inhabitants of warm-blooded mammals, members of Malasseziales have recently received increased attention for their suspected involvement in human gut diseases and certain cancers (Spatz and Richard 2020; Gamal et al. 2022). In addition, direct sequencing approaches have found indications that these yeasts are ecologically very diverse (Amend 2014). Taxonomic placement among most plant pathogens, the gene content in relation to nutritional requirements (Wu et al. 2015d), their omnipresence in both health and disease states (Ianiri et al. 2022), and the occurrence of various hybridization events (Theelen et al. 2022), make this an order of interest from both functional and evolutionary perspectives.

History

The origin of the genus *Malassezia* dates back to 1846 when Eichstedt identified yeasts and filaments in skin lesions of the disease pityriasis versicolor (PV). Originally named *Microsporon furfur* by Robin in 1853, it was renamed to *Malassezia furfur* by Baillon in 1889 (Hay and Midgley 2010). Especially resulting from the arrival of DNA sequencing technology, the number of species increased to 18 formally described species to date (Lorch et al. 2018). Presently only one genus is known for the order. Biochemical tests, such as urease activity, and a positive staining with Diazoneum Blue B salt, already early on indicated a basidiomycetous affinity. However, its phylogenetic affiliation remained enigmatic for a long time, until molecular phylogenetic studies were introduced. Wang and coworkers assigned the genus to Ustilaginomycotina, and because of the deep node, they proposed the class Malasseziomycetes, order Malasseziales and family Malasseziaceae to accommodate these fungi (Wang et al. 2014b). Many more species than currently described may exist. Although sequence-only based species descriptions are not possible yet under current nomenclature rules, a recent study applying metagenomics approaches to the skin microbiome identified at least two likely new species (Saheb Kashaf et al. 2022). As members of the Malassezales are difficult to culture, especially from complex sources such as the human gut, exploring sequence diversity directly from these samples may provide additional insight into the diversity within this order. Sequence diversity from environmental DNA of samples such as coral, marine sediments, algae, and soil suggests that many more taxa may be present in the Malasseziales (Amend 2014) and further research in this area may also provide additional insight in the evolution of this group of yeasts.

Characters that define the taxa in the order

Cells are globose, ovoid or cylindrical. Budding is generally monopolar, with percurrent or sympodial proliferation leaving pronounced bud scars (Wang et al. 2014b). A sexual morph is unknown but the presence of mating type genes suggests the ability to reproduce sexually. Species with pseudobipolar or tetrapolar configuration occur and it was hypothesized that the pseudobipolar organization was ancestral in this group (Coelho et al. 2023). One of the most distinctive features is the lipid dependence of all described Malasseziales members, with the note that *Malassezia pachydermatis* is able to grow on sabouraud dextrose agar by utilizing the peptides that are present in the medium. The cell wall is thick and multi-lamellate, with a high lipid percentage and β-(1,6)-D-glucan was found to be the major carbohydrate component for *Malassezia restricta* (Stalhberger et al. 2014) and *Malassezia sympodialis* (Kruppa et al. 2009).

Plates

See figures on pages 29, 31, 33, 35, 37, 38, 40, 41, 43, 45, 46, 48, 50 (Guého-Kellermann et al. 2010) and Figs. 148.2–148.51 (Guého-Kellermann et al. 2011).

Genera included

Family Malasseziaceae Denchev & R.T. Moore
Malassezia Baill. 1889
= *Pityrosporum* Sabour. 1904

Evolution

Based on a phylogenetic analysis of six genes class Malasseziomycetes and order Malasseziales represented a deeply rooted lineage within the Ustilaginomycotina with a sister relationship to both Ustilaginomycetes and Exobasidiomycetes (Wang et al. 2014b). A whole genome based phylogenetic analysis confirmed the isolated position within the subphylum Ustilaginomycotina, but as a basal group, suggesting early divergence from its plant-pathogenic relatives (Wu et al. 2015d). Using a six-gene-based phylogeny, it was estimated that the order originated ca. 245 million years ago, only preceded by the Ustilaginomycetes within the subphylum Ustilaginomycotina. A phyloproteomic tree based on 396 protein alignments species of the order Malasseziales however indicated a basal position for this order within the Ustilaginomycotina (Zhao et al. 2017). Comparative genomics revealed the expansion of lipases, phospholipases, and aspartyl proteases; and a reduction of genes encoding enzymes required for lipid and carbohydrate metabolism, further underlining divergence from plant-pathogenic relatives and adaptation to human and animal skin (Wu et al. 2015d). The presence of mating type genes is suggestive that sexual reproduction may play a role in the evolutionary trajectory of the order. Furthermore, multiple hybridization events have contributed to the complex evolution of the M. furfur species complex (Theelen et al. 2022) and it would be interesting to explore whether similar events have also taken place elsewhere in the order Malasseziales.

Justification of order and problems

Most analyses illustrate a distinct position of the Malasseziales within Ustilaginomycotina, although the exact position differs based on the type of datasets that are used. Two studies applying whole genome based phylogenetic approaches both point to a basal position of the order within Ustilaginomycotina (Wu et al. 2015d; Zhao et al. 2017). In this study, Malasseziales (Malasseziomycetes) is shown to be a sister clade with Ustilaginomycetes.

Significance

Ecological and economical roles

Malassezia is the most abundant fungal genus on healthy human skin (Findley et al. 2013) but also plays a role in multiple skin diseases, such as as dandruff/seborrheic dermatitis, pityriasis versicolor, psoriasis, Malassezia folliculitis, and atopic dermatitis in humans; and otitis and dermatitis in cats, dogs and other animals (Theelen et al. 2018; Guillot and Bond 2020; Saunte et al. 2020). While these skin diseases are not life-threatening, they can be uncomfortable and it is important to also consider the negative social and psychological effects of these diseases. The number of people affected varies per disease, demographic, and prior conditions. In the case of dandruff, up to 50% of adults worldwide are affected to some extent, with an estimated economic burden estimated at $300 million annually for over-the-counter products in the USA alone (Borda and Wikramanayake 2015). The downside with many Malassezia-associated skin diseases is that treatment only results in temporary improvement, resulting in recurring discomfort and repeat-treatment and costs (Saunte et al. 2020). *Malassezia* can also cause bloodstream infections in certain patient groups, such as immunocompromised individuals and neonates, a phenomenon that is likely underdiagnosed due to the lack of lipid-supplementation in standard culture media in most clinics (Rhimi et al. 2020). Furthermore, a role for *Malassezia* in Crohn's disease and colitis has been suggested (Limon et al. 2019) as well as a role in the progression of certain cancers (Aykut et al. 2019; Das et al. 2021). Finally, studies applying direct sequencing approaches to various environmental samples have identified the presence of *Malassezia* in diverse ecologies such as soil and marine environments. Future research is needed to explore function and may add to our knowledge of the evolution and adaptation of members of Malasseziales (Amend et al. 2019).

Chemical diversity

As far as investigated, all Malasseziales species are lipid dependent as they lack a fatty acid synthase gene in their genomes (Xu et al. 2007). They have a co-enzyme Q system with 9 isoprenologues and xylose is absent in cell wall hydrolysates (Guého-Kellermann et al. 2011). Species can phenotypically be identified to some extent with physiological profiling, using various tweens and cremophor-EL as substrates, but also using growth at various temperatures, as well as β-glucosidase activity (Guého-Kellermann et al. 2011).

Other relevant data and future recommendations

Based on our current knowledge, it seems clear that *Malassezia* may take on different roles on human skin (and possibly elsewhere), namely that of a commensal, a mutualist, or a pathogen but much of what determines the shifts between these roles is still unknown (Vijaya Chandra et al. 2020; Ianiri et al. 2022). The omnipresence of *Malassezia* in health and disease states further complicates these matters but at the same time make members of this order interesting model organisms to study disease mechanisms.

Microbotryales R. Bauer & Oberw. 1997

Contributed by: Teodor T. Denchev, Martin Kemler, Dominik Begerow, Cvetomir M. Denchev

Introduction

Microbotryales was erected by Bauer et al. (1997) to accommodate the species of Microbotryaceae. They have a type A 5S rRNA secondary structure, mannose as the major cell wall carbohydrate, and cellular interactions without primary interactive vesicles (Bauer et al. 2001b). The microbotryaceous species have lifestyle of smut fungi similar to that of the phragmobasidiate species in the Ustilaginomycetes but are morphologically distinguishable from them by the lack of intracellular hyphae or haustoria (Bauer et al. 1997, 2001b). Members of the Microbotryales are characterized by the presence of transversely septate basidia with multiple production of sessile basidiospores, and only intercellular hyphae (Bauer et al. 1997).

Microbotryales is divided into two families: Microbotryaceae and Ustilentylomataceae.

Characters that define the taxa in the order

Microbotryaceae are characterized by the absence of pores in the mature septa. The family consists of plant parasitic fungi.

Microbotryum is the largest genus of the family. The hosts are members of the rosids (Onagraceae), superasterids (Polygonaceae, Caryophyllaceae, and Montiaceae), and asterids (? Primulaceae, Gentianaceae, Lentibulariaceae, Lamiaceae, Asteraceae, and Caprifoliaceae). Sori are formed in various organs of the infected plants (flowers, anthers, ovules, filaments of stamens, pedicels, inflorescence branches, capitula, stems, and leaves), containing powdery, pale yellowish brown to dark reddish brown or dark purple spore mass, without sterile cells. Spores are single, subhyaline to dark reddish brown or dark purple, variously ornamented (reticulate, verruculose, verruculose-reticulate, echinate or striate) (Vánky 2011, 2013; Denchev et al. 2020b). Spore germination results in a phragmobasidium, on which sessile basidiospores are produced. Members of *Sphacelotheca* form sori in ovaries of plants in the Polygonaceae. Infection is systemic. Sori are covered by a peridium, formed of host tissues and hyaline, non-sporogenous fungal cells. Columella is present, formed of non-sporogenous fungal cells. Spores are darkly pigmented, at first catenate, joined by disjunctors, later solitary. Spores germinate with transversely septate basidia (Vánky 2013). *Zundeliomyces* is a monotypic genus. *Zundeliomyces polygoni* Vánky forms sori on *Polygonum alpinum* All. Sori are in some flowers of the infected plant, as locular galls with central cavities; covered by a thick peridium; columella is lacking. Spore mass is in the cavities with two kinds: central, thin-walled and single, and peripheral, thick-walled and agglutinated. Spore germination is unknown (Vánky 2013). Species of *Kalmanago* produce sori that destroy seeds of plants in the Commelinaceae, filling the capsules with a powdery, dark reddish-brown spore mass; peridium, columellae, and sterile cells are absent. Spores are solitary, reticulate (Denchev et al. 2020a). Infection is systemic. Spore germination results in a two-celled phragmobasidium. Species of *Bauerago* form sori in seeds of hosts in the Cyperaceae and Juncaceae. Infection is systemic. Spores are single. Peridium, columellae, and sterile cells are absent (Vánky 2013; Denchev and Denchev 2018b). Spores germinate with transversely septate basidia.

Ustilentylomataceae are characterized by the presence of simple pores in the mature septa, without membrane caps (Bauer et al. 1997). The family consists of plant parasitic fungi and anamorphic yeast species.

Ustilentyloma are plant parasites in leaves of grasses, forming spots on the leaf surface. Spores are single, in loose or compact groups, embedded in host tissue; subhyaline to pale colored (Vánky 2013; Denchev et al. 2020b). Spores germinate with transversely septate basidia. An anamorphic yeast species, *U. graminis* (Rodr. Mir. & H.G. Diem) Q.M. Wang et al., was isolated from a grass phylloplane (Wang 2015b). *Fulvisporium* is a monotypic genus. *Fulvisporium restifaciens* (D.E. Shaw) Vánky forms sori in distal internodes of stems of *Austrostipa* (Poaceae). Spores are in permanent spore balls, composed of spores only, without sterile cells between the spores. Spore germination is phragmobasidiate (Vánky 2013). Species of *Aurantiosporium* form sori in hypertrophied spikelets of hosts in the Cyperaceae. Sori are filled with yellowish, orange or reddish brown, granular mass of loose or permanent spore balls (Piepenbring et al. 1999; Vánky 2013; Piepenbring et al. 1996). Spore germination is phragmobasidiate. *Microbotryozyma* includes two anamorphic yeast species. *Microbotryozyma collariae* S.O. Suh et al. was isolated from a culture with trypanosomatids obtained from the intestine of *Collaria oleosa* (Heteroptera) (Suh et al. 2012), while *M. swertiae* Q.M. Wang et al. was isolated from plant material (Li et al. 2020b).

Plates

Fig. 37 Microbotryales. **a**–**i** habit. **a** *Kalmanago commelinae* on *Commelina communis,* Japan (SOMF 30251); **b** *Microbotryum coronariae* on *Silene flos-cuculi,* Bulgaria, Denchev 1925; **c** *Microbotryum koenigiae* on *Koenigia islandica,* Greenland (C-F-102468, holotype); **d** *Microbotryum pustulatum* on *Bistorta vivipara,* Greenland (O s.n.); **e** *Microbotryum reticulatum* on *Persicaria lapathifolia,* Bulgaria, Denchev 1429; **f** *Microbotryum saponariae* on *Saponaria officinalis,* Bulgaria, Denchev 1652; **g** *Microbotryum stellariae* on *Stellaria aquatica,* Bulgaria, Denchev 1816; **h** *Microbotryum superbum* on *Dianthus superbus*, Bulgaria, Denchev 1657; **i** *Microbotryum tragopogonis-pratensis* on *Tragopogon pratensis,* Bulgaria, Denchev 1636. Arrows in **a**, **c** indicate sori. Scale bars: a–i = 1 cm

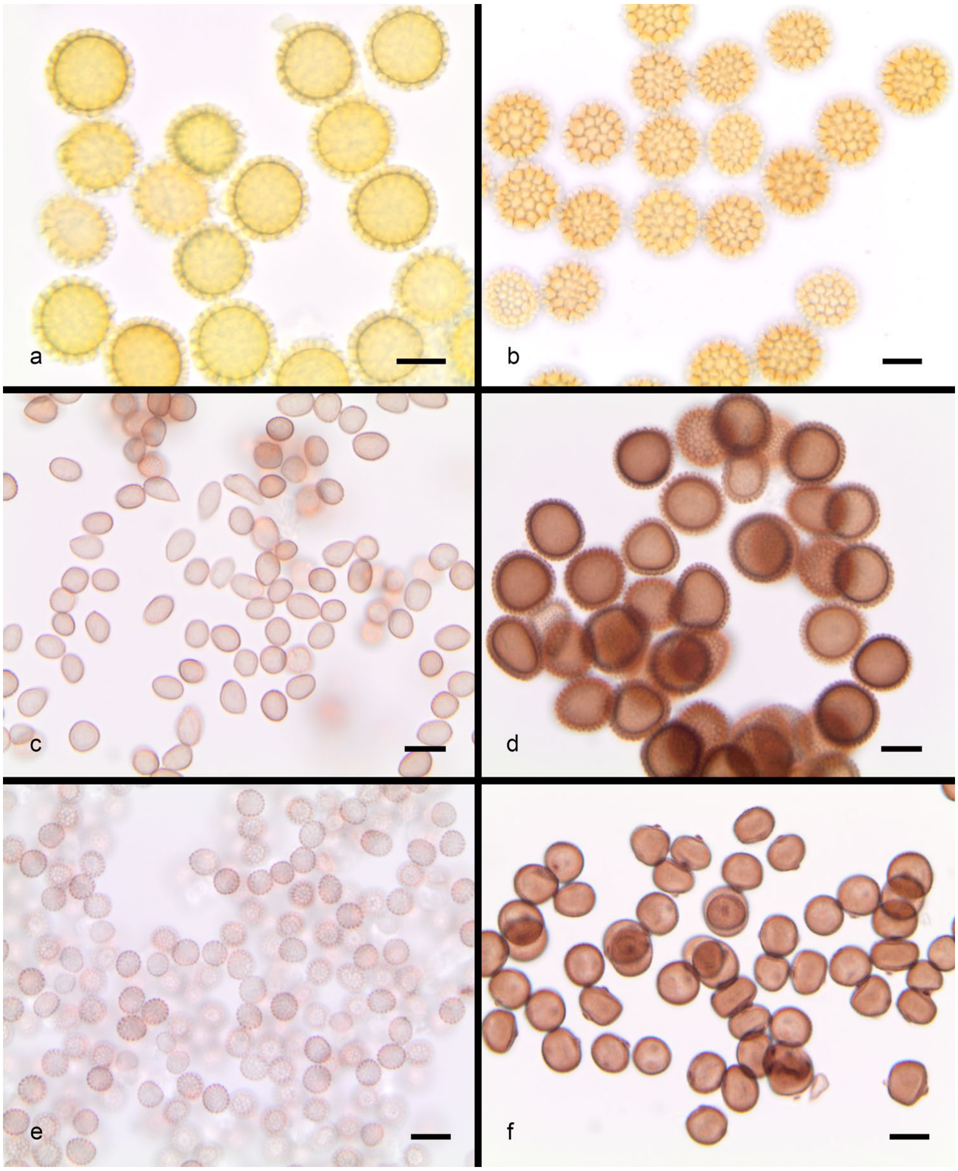


Fig. 38 Microbotryales. **a**–**f** spores in LM. **a** *Bauerago vuyckii* on *Luzula campestris*, Austria (MA 693431); **b** *Kalmanago commelinae* on *Commelina communis,* Japan (SOMF 30251); **c** *Microbotryum koenigiae* on *Koenigia islandica,* Greenland (C-F-102468, holotype); **d** *Microbotryum polycnemoides* on *Polygonum polycnemoides*, Turkey (SOMF 30200, holotype); **e** *Microbotryum silenes-dioicae* on *Silene dioica*, Bulgaria (SOMF s.n.); **f** *Sphacelotheca polygoni-senticosi* on *Persicaria senticosa*, Korea (KUS-F 10409). Scale bars: a–f = 10 µm

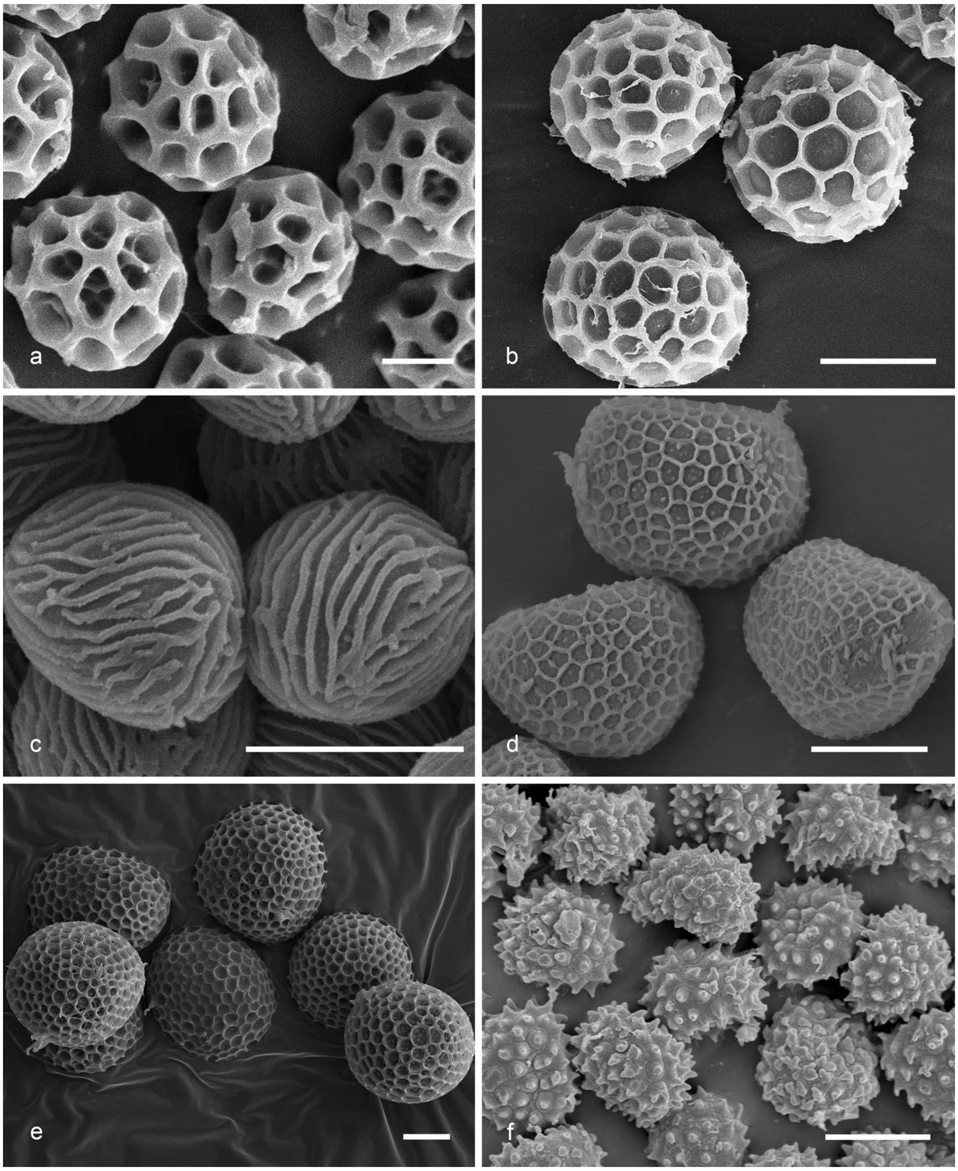


Fig. 39 Microbotryales. **a–c** spores in SEM. **a** *Bauerago capensis* on *Juncus capensis,* South Africa (W 1906-0005707, holotype); **b** *Microbotryum anomalum* on *Fallopia aubertii,* Bulgaria (SOMF 22363); **c** *Microbotryum koenigiae* on *Koenigia islandica*, Greenland (C-F-102468, holotype); **d** *Microbotryum nepalense* on *Polygonum nepalense,* Ethiopia (C s.n.); **e** *Microbotryum polycnemoides* on *Polygonum polycnemoides,* Turkey (SOMF 30200, holotype); **f** *Microbotryum violaceoverrucosum* on *Silene italica,* Greece, Denchev 3709. Scale bars: a–f = 5 µm

Genera included

- Family Microbotryaceae R.T. Moore 1996
  - *Bauerago* Vánky 1999
  - *Kalmanago* T. Denchev, Denchev, Kemler & Begerow 2020
  - *Microbotryum* Lév. 1847
  - = *Liroa* Cif. 1933
  - = *Bauhinus* R.T. Moore 1992
  - = *Haradaea* Denchev 2006
  - *Sphacelotheca* de Bary 1884
  - *Zundeliomyces* Vánky 1987
- Family Ustilentylomataceae R. Bauer & Oberw. 1997
  - *Aurantiosporium* M. Piepenbr., Vánky & Oberw. 1996
  - *Fulvisporium* Vánky 1997
  - *Microbotryozyma* S.O. Suh, D.A. Maslov, Molestina & J.J. Zhou 2012
  - *Ustilentyloma* Savile 1964

Evolution and justification of order

Grouping Microbotryales within Pucciniomycotina rather than Ustilaginomycotina was supported by sequence analyses. There are significant convergences between the microbotryaceous and ustilaginomycetous phragmobasidiate smut fungi with respect to life cycle, soral morphology, sporogenesis, and basidial morphology (Bauer et al. 1997, 2006; Begerow et al. 2014). Microbotryales are ultrastructurally well characterized and the molecular phylogeny is highly congruent with these data. Many species of Microbotryaceae were originally treated in *Ustilago* because of similar morphological characters that are a classical example of convergent evolution (Begerow et al. 2014).

Weiss et al. (2004a, b) suggested that phytoparasitic lineages in Microbotryomycetes, i.e., Microbotryales and *Kriegeria*, most likely evolved from colacosome-interacting mycoparasitic ancestors.

Kemler et al. (2020) demonstrated that the host preference and sorus location correlate with parasite phylogeny in *Microbotryum*. They found that monophyletic parasite clades correspond well with monophyletic host clades and also that monophyletic parasite groups in general produce their spores in the same plant organ.

Economic importance

A few species parasitize ornamental plants (*Dianthus, Gypsophila, Silene*) but little economic damage is caused.

Microstromatales R. Bauer & Oberw. 1997

Contributed by: Martin Kemler, Cvetomir M. Denchev, Dominik Begerow, Teodor T. Denchev

Introduction

Microstromatales was erected to accommodate fungi within Exobasidiomycetes that lack teliospores and a specific interaction apparatus, and have hyphae with a simple septal pore enclosed by a membrane cap (Bauer et al. 1997; Begerow et al. 2014). Since its erection species with dolipores have been included into the order. Several of the taxa in Microstromatales are known to be plant parasitic. Based on phylogenetic information anamorphic yeast taxa with unknown teleomorph have been described or included into the order in recent years (Li et al. 2022c; Nasr et al. 2017; Wang et al. 2015d). Recently, the genus and family concepts within Microstromatales were questioned based on phylogenetic evidence (Kijpornyongpan and Aime 2017). The type genus, *Microstroma*, was introduced by von Niessl (1861).

Currently, three families and eight genera are included in this order.

Characters that define the taxa in the order

Many species in the Microstromatales are plant parasites. However, they do not form teliospores, but instead directly produce holobasidia and basidiospores from the hyphae that emerge from the inside of leaves of the hosts. Host spectrum is diverse and includes many woody eudicots. Microstromatales contains three families, viz. Microstromataceae, Quambalariaceae, and Volvocisporiaceae. These are monotypic and contain the genera *Microstroma*, *Quambalaria*, and *Volvocisporium*, respectively. The taxonomic position of the genera *Baueromyces, Jaminea*, *Parajaminaea*, *Pseudomicrostroma*, and *Sympodiomycopsis* is not settled so far.

Traditionally, species of *Volvocisporium* and *Microstroma* were characterized by having simple pores with rounded pore lips, whereas *Quambalaria* species have a doliporus (de Beer et al. 2006). *Microstroma* species were characterized by aseptate basidiospores, while *Volvocisporium* species have septate basidiospores. No sexual stage is known for *Quambalaria* species. A recent taxonomic reorganization of the order (Kijpornyongpan and Aime 2017) has made the interpretation of morphological and ultrastructural characteristics with respect to phylogenetic evidence difficult. Phylogenetic evidence has resulted in the split of *Microstroma* and the erection of the new genera *Pseudomicrostroma* and *Parajaminea* that contain former *Microstroma* species (Kijpornyongpan and Aime 2017). Unfortunately, ultrastructural studies were mostly performed on *Pseudomicrostroma juglandis* (Bérenger) Kijporn. & Aime (=*Microstroma juglandis* Bérenger) and the pore structure in *Microstroma* s. str. is therefore unknown. Detailed morphological and ultrastructural studies on the genera *Baueromyces*, *Jaminea*, *Microstroma*, *Parajaminea*, *Pseudomicrostroma*, and *Sympodiomycopsis* are urgently needed to get more diagnostic characteristics that separate the genera from each other.

Plates

For illustrations, see Bauer et al. (1997, pore: Fig. 117, interaction zone: Fig. 111), de Beer et al. (2006, Fig. 3–8), Begerow et al. (2001), Begerow and McTaggart (2018, Fig. 4–19.4, Fig. 4–19.6), Kijpornyongpan and Aime (2017).

Genera included

Family Microstromataceae Jülich 1982
 Microstroma Niessl 1861
 =*Helostroma* Pat. 1902
 =*Leptophyma* Sacc. 1889
Family Quambalariaceae Z.W. de Beer, Begerow & R. Bauer 2006
 Quambalaria J.A. Simpson 2000
 =*Fugomyces* Sigler 2003
Family Volvocisporiaceae Begerow, R. Bauer & Oberw. 2001
 Volvocisporium Begerow, R. Bauer & Oberw. 2001
Microstromatales genera *incertae sedis*
 Baueromyces Q.M. Wang, Begerow & M. Groenew. 2022
 Jaminaea Sipiczki & Kajdacsi ex Kijporn. & Aime 2017

= *Jaminaea* Sipiczki & Kajdacsi 2009 (nom. inval.)
Parajaminaea Kijporn. & Aime 2017
Pseudomicrostroma Kijporn. & Aime 2017
Sympodiomycopsis Sugiy., Tokuoka & Komag. 1991

Evolution and justification of order

Microstromatales is systematically not well understood and recently the type genus *Microstroma* was split up due to polyphyly (Kijpornyongpan and Aime 2017).

Many species of this order have an association with leaves of woody plants in different plant orders making the evolutionary history of this group potentially very complex. However, the vast majority of Microstromatales species have not been studied using phylogenetic methods and their relationships to each other are unknown.

Although not well characterized as a monophyletic group based on morphological and ultrastructural traits, Microstromatales forms a well-supported clade in molecular phylogenetic studies (Wang et al. 2015d). Intraorder relationships are still unresolved, partially due to known species being understudied, as well as the discovery of new (mainly yeast) species (Nasr et al. 2017; Wang et al. 2015d).

Economic importance

Quambalaria species are known plant-pathogens of Myrtaceae and pose a substantial problem for industrial forestry by causing shoot blight and severe damage can lead to the death of trees (see de Beer et al. 2006; Pegg et al. 2009).

Mixiales R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw. 2006

Contributed by: Junta Sugiyama, Tsuyoshi Hosoya

Introduction

Mixiales is a fascinating taxon with an extensive research background in the kingdom *Fungi*. The single order *Mixiales* was assigned to the monotypic class *Mixiomycetes* (Bauer et al. 2006). *Mixiale*s consists of a single family *Mixiaceae* C.L. Kramer 1987 comprising a monotypic genus *Mixia* C.L. Kramer 1959 [‘1958’] (hereinafter referred to as 1959, except for the “Genera included” section). *Mixia* was proposed by Kramer (1959) in honor of A. J. Mix, an American mycologist at the University of Kansas, comprising only one species to date, namely *Mixia osmundae* (Nishida) C.L. Kramer 1959, which was initially proposed as *Taphrina osmundae* by Nishida in 1911. Kramer (1987) remarked, “*Taphrina* is a dimorphic organism that exists as a mycelium in the parasitic phase and as yeast in the saprophytic phase. The mycelium is dikaryotic, which is a unique feature in *Ascomycetes*. The mycelium gives rise to asci directly, without forming an ascocarp.” *Mixia* is similar to *Taphrina* in lifestyle and is a dimorphic fungus (Nishida et al. 1995; Toome et al. 2014). In the parasitic phase, *M. osmundae* is an intracellular parasite living on the *Osmunda* fern fronds/leaves (Nishida 1911; Mix 1947; Kramer 1959; Nishida et al. 1995; Sugiyama and Katumoto 2008a) and is phenotypically (morphologically) characterized by a unique spore-producing structure in the life cycle, namely, putative asexual spores (Toome et al. 2014; Sugiyama et al. 2018) that are produced exogenously, enteroblastically, and simultaneously from whole sporogenous cells on the surface of living *Osmunda* or *Osmundastrum* fern fronds (Nishida et al. 1995; Sugiyma and Katumoto 2008a; Sugiyama et al. 2018; for the host ferns, Kato 2007; Grimm et al. 2015; Bomfleur et al. 2017). The unique sporogenous and spores (or yeast cells) have been characterized by morphological and ultrastructural characteristics by light, scanning electron (SEM), and transmission electron (TEM) microscopes (Nishida et al. 1995; Bauer et al. 2006; for abbreviations, see Seifert et al. 2011).

In the saprophytic phase, *M. osmundae* grows slowly, forming creamy yeast-like colonies on artificial culture media and reproduces enteroblastic budding cells (Nishida et al. 1995, 2011b). The specific characteristics of yeasts and cells of *M. osmundae* in culture are similar to those of basidiomycetous yeasts, such as *Rhodotorula*, *Cryptococcus*, and *Sporobolomyces* (Nishida et al. 1995, 2011b). *Mixia*, one of the basidiomycetes yeasts, was adopted and described by Nishida et al. (2011b) in the book “The Yeasts, A Taxonomic Study, 5th Edition” (Kurtzman et al. 2011). In addition to the phenotypic characterization, Nishida et al. (1995), based on nuclear small-subunit rRNA (SSU; for other gene abbreviations, see Hibbett et al. 2007) gene sequence divergence of authentic *Taphrina osmundae/Mixia osmundae* isolates, indicated that *T. osmundae/M. osmundae* is not a member of *Taphrinales* or *Protomycetales* in *Ascomycota*. However, it is placed among simple-septate *Urediomycetes* (currently *Pucciniomycotina*) in *Basidiomycota* with two rust fungi *Cronartium ribicola* J. C. Fisch and *Peridermium harknessii* J. P. Moore, and a basidiomycetous yeast, *Erythrobasidium hasegawianum* Hamam., Sugiy. & Komag. Subsequently, their findings were reinforced by molecular phylogenetic analyses (e.g., Aime et al. 2006; Bauer et al. 2006; Hibbett et al. 2007). From the 2010s, genome sequencing of an authentic *M. osumdae* culture (IAM 14324 or JCM 22182 = IAM 14324) has been performed independently by two research groups, namely Nishida et al. (2011a) and Toome et al. (2014). Biogeographically, *M. osmundae* has been recorded in Japan (Honshu, Kyushu), China (Yunnan Province, Taichung), and the USA (Georgia, Michigan) to date (Sugiyama et al. 2018).

Historically, there is a very worrisome problem regarding the sporulating structure/spore-forming system and fertile spores of the fungus known as *M. osmundae* (≡*Taphrina osmundae*). A variety of designations, e.g., "ascus and ascospore" (Nishida 1911), "ascus and conidium/spore (blastospore)" (Mix 1947, 1949) or "spore sac and spore" (Kramer 1959, 1987), has been used over the past 100 years (for further notes on terms, see Sugiyama et al. 2018). In Toome et al. (2014), the terms "sporogenous cell and spore" (Ulloa and Hanlin 2012) were adopted. Hereafter, the terms "sporogenous cell and spore" describe the spore-producing structures on fern fronds of this fungus until cytologically proven, including nuclear and chromosome behavior.

The identity, systematic, and related evolutionary implications regarding the enigmatic fungus *Mixia* typified by *M. osmundae* (≡ *Taphrina osmundae*), are illuminated below.

History

The monotypic taxa Mixiomycetes, Mixiales, and Mixiaceae are circumscribed by the monotypic genus *Mixia*, containing only one species *M. osmundae* (Nishida) C.L. Kramer, as the type species. The root (basionym) of *M. osmundae* is *Taphrina osmundae* Nishida. In a monograph of the parasitic Exoascaceae (currently Taphrinaceae) of Japan, in 1911, Toji Nishida (1874–1927; cf. Udagawa et al. 2006), Japanese mycologist and plant pathologist, first described a new species, *Taphrina osmundae* that was parasitic to the living fronds (leaves) of *Osmunda regalis* L. var. *japonica* Wilde [as "Willd."] (sic), the Japanese royal fern, *Osmunda japonica* Thunb. (Osmundaceae), based on two collections from Province Higo (Kumamoto Prefecture) and Province Echigo (Niigata Prefecture) in Japan. In the 1940s, Mix (1947, 1949) redescribed *T. osmundae* based on three collections from Tottori, Iwate, and Mount Kirishima (Kyushu) in Japan, whereas Sawada (1952) listed the fungus from Iwate and Aomori in Tohoku district. In 1959, Kramer indicated that *T. osmundae* exhibited multiple similarities to *Taphrinaceae* and *Protomycetaceae*; both families are accommodated in the order *Taphrinales*. Consequently, Kramer (1959) proposed a new genus *Mixia*, represented by *Mixia osmundae* (≡*Taphrina osmundae* Nishida) and characterized by "the presence of a columella-like wall, a septum cutting the stalk cell from the spore sac, and a mycelium in the walls of the host cells" and is tentatively placed in *Protomycetaceae* (*Taphrinales*). Subsequently, Kramer (1973) placed *Mixia* in the family *Protomycetaceae* of the order *Protomycetales*. Ito (1964) accepted and recorded Nishida (1911) description with his comments for Mix (1949) and Kramer (1959). On the other hand, Kramer (1987) proposed a new family *Mixiaceae* to accommodate a unique, monotypic genus *Mixia* in *Protomycetales*. In the respective phylogenetic schemes, Savile (1955, 1968) and Kramer (1959, 1987) revealed a reliable estimate regarding early radiation, comprising *Taprhina*, *Protomyces*, and *Mixia*, of *Ascomycota*, and demonstrated the phylogenetic and evolutionary relationships of *Taphrinales* accommodating *Taphrina* and *Protomyces*. Therefore, until the 1980s, it was presumed in the mycological community that *Mixia*/*M. osmundae* is a taphrinalean fungus in *Ascomycota*.

Similar to the studies on molecular phylogeny among *Taphrina*, *Saitoella*, and other fungi (Nishida and Sugiyama 1993), Nishida et al. (1995) sequenced the SSU (18S) gene and determined 1,780 nucleotides of a living strain labeled as *Taphrina osmundae* IFO 32408 (currently NBRC 32408, initially isolated by Y. Ando as A-10-1 in May 1991 from the voucher specimen kept as NIAES 126-2-88 = 10,557 in Tsukiboshi et al. 2007) collected and identified by A. Ezuka; for the specimen and strain data, see Nishida et al. 1995 and Sugiyama et al. 2018). Unexpectedly, the *T. osmundae* isolate indicated as "strain X" (Fig. 1 in Nishida and Sugiyama 1994) or "IFO 32408" (Fig. 7 in Sugiyama and Nishida 1995, Fig. 3 in Sugiyama et al. 1996) formed a cluster with the basidiomycetous yeast genera *Sporobolomyces* and *Leucosporidium*, with 100% bootstrap confidence, within *Basidiomycota*. They suspected that the strain X/IFO 32408 was misidentified or erronenouly isolated. To verify the strain in question, in May 1993J. Sugiyama, H. Nishida, and Y. Ando successfully collected fresh samples (Fig. 1a) of *Osmunda japonica* ferns (Iwatsuki 1992; cf. Ebihara 2016) infected by *T. osmundae* (Nishida 1911; Mix 1949), namely *M. osmundae* (Kramer 1959), from a few stands (Mitsuma and Sesawa; Fig. 1a) on the roadside along the Ohwi River in Shizuoka Prefecture, Japan (voucher specimens TNS-F-13368 = IAM-F 0148 and TNS-F-30045 = IAM-F 0149; cf. Nishida et al. 1995; Sugiyama et al. 2018), in the same locality as *T. osmundae* IFO 32408. From an integrated analysis of the genotypic (SSU gene sequences) and phenotypic (morphological/ultrastructural observations of sporogenous cells using a light microscope, SEM, and TEM) characteristics based on fresh specimens and new isolates (derived from a single spore), Nishida et al. (1995) elucidated that *M. osmundae* is not a member of *Taphrinales* or *Protomycetales* in *Ascomycota*, but a member of the simple-septate basidiomycete lineage (Swann and Taylor 1993; Suh and Sugiyama 1994; cf. Swann et al. 2001) in *Basidiomycota*.

To summarize the new findings, numerous spores were blown out exogenously, blastically, and over the sporogenous cells (Fig. 40d–h), leaving numerous denticles of 0.5 µm diameter when mature spores secede (Fig. 40 i, j). On the other hand, their molecular phylogeny (Fig. 2 in Nishida et al. 1995) showed that *T. osmundae*, namely *M. osmundae*, was clustered with two rust fungi *Cronartium ribicola* and *Peridermium harknessii*, and the basidiomycetous yeast *Erythrobasidium hasegawianum*, among simple-septate *Urediniomycetes* (currently *Pucciniomycotina*; cf.

Bauer et al. 2006; Hibbett et al. 2007) of *Basidiomycota* (cf. Sugiyama 1998). In addition, the ultrastructure of the cell wall and sporogenesis of yeast cells in culture showed the presence of successive enteroblastic budding with bud scars showing percurrent extension (Fig. 40e; cf. Seifert et al. 2011) and a multi-layered cell wall (Fig. 40e), similar to that of "*Taphrina*" *maculans* CBS 427.69 and "*T.*" *californica* CBS 374.39 in Sjamsuridzal et al. (1997). Nishida et al. (1995) also found Q-10 as the primary ubiquinone system. This cumulative evidence completely denied the ascus/asci characterizing *M. osmundae* (≡*Taphrina osmundae*) in the descriptions of Nishida (1911), Mix (1947, 1949), Ito (1964), and Kramer (1959, 1987) and phylogenetic speculation for *Mixia* as early radiation with *Taphrina* and *Protomyces* by Saivle (1968), Reddy and Kramer (1975), and Kramer (1987). However, Nishida et al. (1995) could not determine whether the individual sporogenous cells were involved in producing meiospores or mitospores. Subsequently, the yeast *Mixia* and *M. osmundae*, one of the basidiomycetous yeast genera and species, have been characterized by their phenotypic and genotypic traits (Nishida et al. 2011b).

Based on Katumoto's search of Kaneyoshi Sawada's specimens, which were transferred from the Herbarium of National Taiwan University to the mycological Herbarium of the National Museum of Nature and Science in 1995 (Sawada 1959), Sugiyama and Katumoto (2008a) revealed that *M. osmundae* is morphologically conspecific to *Phytoceratiomyxa osmundae* Sawada gen. et sp. nov. based on a single collection indicated "Type" (=TNS-F-192985); *P. osmundae* represented a myxomycete similar to *Ceratiomyxa* parasitizes on fronds of the fern *Osmunda japonica* var. *sublancea* (sic) collected from about 2600 m altitude in Meishang, Taichung Prefecture, Taiwan province, China (Sawada 1929, 1931). In addition to the lectotypification of *T. osmundae*, Sugiyama and Katumoto (2008b) proposed to conserve the name *Mixia* C.L. Kramer (1959) (*Basidiomycota*) against the name *Phytoceratiomyxa* Sawada (1929) (*Myxomycetes*). As a result, the name *Mixia* was conserved officially by formal procedures at the 18th International Botanical Congress in 2011 (Norvell 2011; Wiersema et al. 2015). Subsequently, Sugiyama et al. (2018) determined a parasite (Fig. 40 b) on *O. japonica* fronds collected by M. Kakishima in Yunnan Province, China (voucher specimens TNS-F-54015, 54016, 54017) to be conspecific to *M. osmundae*; they also confirmed *Taphrina higginsii* Mix 1947, a parasite (Fig. 40c) on *Osmundastrum cinnamomeum* (≡*Osmunda cinnamomeum*) from Georgia, USA, a possible taxonomic synonym of *M. osmundae* treated by Kramer (1959), to be phenotypically identical to *M. osmundae*, with the lectotypification of *T. higginsii* (Fig. 1c; the lectotype specimen NY barcode 02226172 = A. J. Mix *Taphrina* T-487).

Back to molecular systematics, the phylogenetic placement of *Mixia* by Nishida et al. (1995) was reinforced by sequence analyses of single-locus data, namely SSU gene (Sjamsuridzal et al. 1997, 1999) or LSU D1/D2 gene (Sjamsuridzal et al. 2002), and two-locus data set (SSU and LSU genes) (Bauer et al. 2006; Aime et al. 2006). Bauer et al. (2006) proposed three high rank new taxa, namely *Mixiomycetes*, *Mixiales*, and *Mixiaceae*, typified by the genus *Mixia* (for further comments, see "Phylogeny and Evolution" section in this note). Their nomenclatural proposals were accepted in the higher-level classification of *Fungi* by Hibbett et al. (2007) under "Assembling the Fungal Tree of Life" and the Deep Hypha Research Coordination Network (Blackwell et al. 2007). In the 2010s, multigene sequence-based phylogenetic analyses were performed in fungal molecular systematics. A three-locus data set (SSU, LSU, and *tef* genes)-based phylogeny (Schell et al. 2011; Aime et al. 2014) showed that *Mixiomycetes* as a sister clade to *Agaricostilbomycetes* within *Pucciniomycotina* but with weak bootstrapped confidence level (75% of Maximum Likelihood). On the other hand, Wang et al. (2015a) expanded a comprehensive phylogenetic analysis of yeasts and yeast-like fungi, including *Mixia*, within *Pucciniomycotina* using a multigene data set, namely SSU, LSU D1/D2, internal transcribed spacer (ITS), *rpb1*, *rpb2*, *tef*, and *cytb*). The seven-gene phylogeny demonstrated by Wang et al. (2015a) indicated that the phylogenetic placement of *Mixiomycetes* as a sister of *Spiculogloeales*, an *Agaricostilbomycetes* order; the statistical confidence levels were comparatively high, 94/99/1.0 for Maximum Likelihood/Maximum Parsimony/Bayesian inference analyses, respectively, at a node uniting the monotypic class *Mixiomycetes* and the order *Spiculogloeales* (containing only the family *Spiculogloeaceae*). Oberwinkler (cf. Fig. 2 in 2017) adopted the phylogenies (Aime et al. 2014; Wang et al. 2015a, b) in his phylogenetic dendrogram for orders and classes in *Pucciniomycotina*. In the early 2010s, draft genome sequencing was performed by Nishida et al. (2011a) but lacked genomic information, particularly for *Pucciniomycotina* taxa to compare with that for *M. osmundae*. Subsequently, Toome et al. (2014) generated genomic data for *M. osmundae*. Their genome-based phylogeny (Fig. 1 in Toome et al. 2014) showed that "*M. osmundae* is resolved as a sister group to *Microbotrymycetes* rather than *Pucciniomycetes*"; however, the "genomes from only three of the nine classes of *Pucciniomycotina*" were available for genome-based tree. Further notes on the genome-scale phylogenies of *Mixiomycetes*/*Mixiales* will be provided in the "Phylogeny and Evolution" section.

Characters that define the taxa in the order

Bauer et al. (2006) defined *Mixiales* and *Mixiomycetes* as follows: "Members of the Pucciniomycotina having multinucleate hyphae. Multiple spores produced simultaneously on sporogenous cells.) Main characteristics: Multinucleate hyphae, multiple spores produced simultaneously on sporogenous cells (Nishida et al. 1995)." Subsequently, Oberwinkler (2017) interpreted the unique characteristics of both taxa with illustrations and his comments.

Based on the knowledge and findings that have been accumulated (mainly by Nishida 1911; Mix 1947; Kramer 1959, 1987; Nishida et al. 1995, 2011b; Bauer et al. 2006; Sugiyama and Katumoto 2008a; Toome et al. 2014; Sugiyama et al. 2018), a general description of *Mixiales*, *Mixia*, and *M. osmundae* is summarized below.

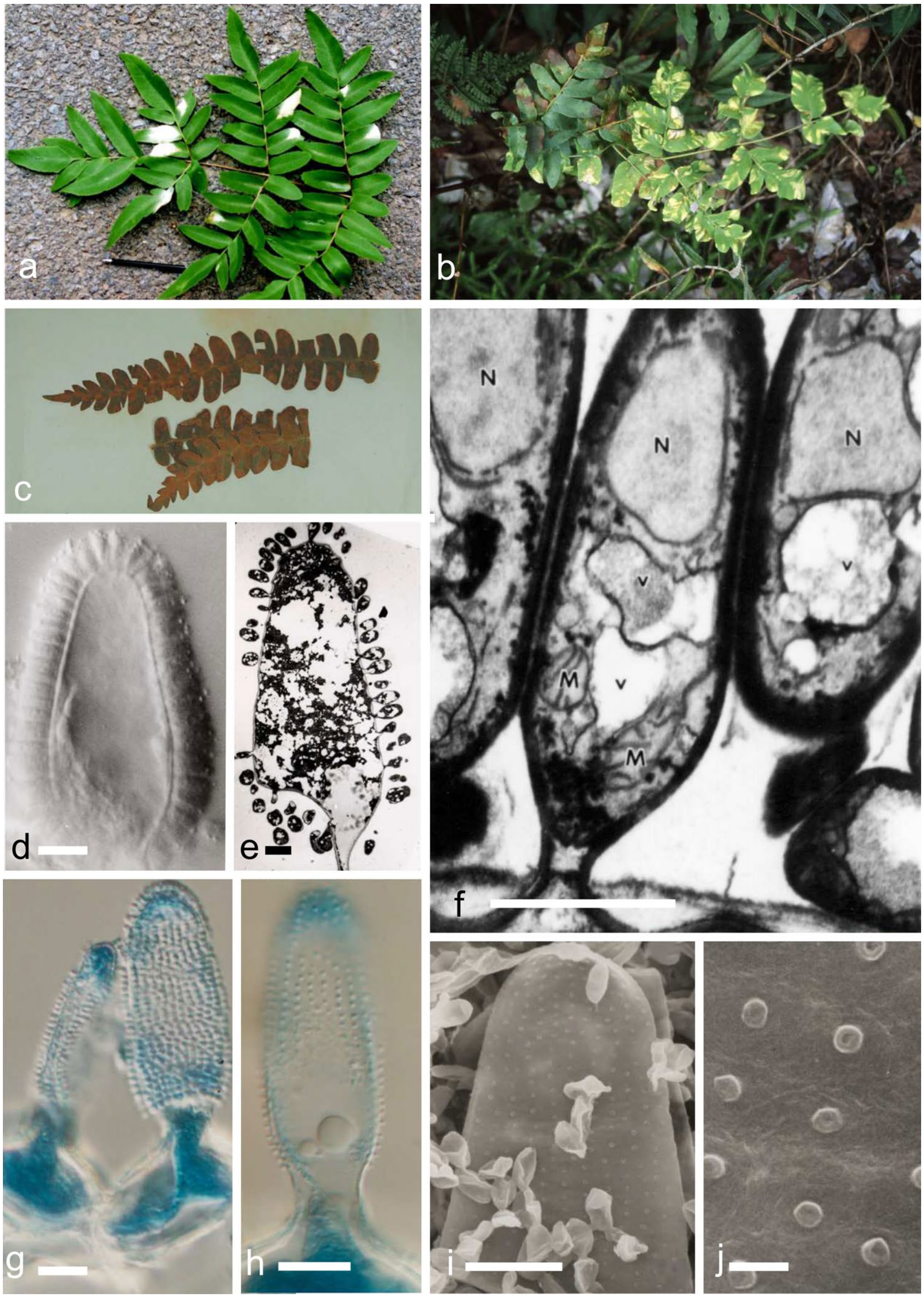
Sexual morph: Based on the analyses of *M. osmundae* genome sequence using the authentic living strain JCM 22182 (=IAM 14324; see Nishida et al. 1995 and Sugiyama et al. 2018), Toome et al. (2014) remarked that "our finding of a complete complement of mating and meiosis genes" suggested the capacity to undergo sexual production." However, the basidiomes or other sexual fructiations are lacking; basidiospores are not seen. Thus, the sexual morph is unknown to date.

Asexual morph: The fungus (e.g., Fig. 40a, b) is biotrophic (proved by genome-based information by Toome et al. 2014), causing necrotic lesions on unthickened fronds of living ferns (*Osmunda* and *Osmundastrum*) and appear as small to large lesion spots, initially yellowish brown but appear as fine white powder with developing mature sporogenous cells covered with numerous spores (Figs. 40d, e, g); naked, sessile or separated by a septum at the base ("stalk cell" in Mix 1947; Kramer 1959; Ito 1964), almost oblong, pyriform, or bacilliform, 32–44 × 17–25 µm (Kumamoto and Niigata, coll. T. Nishida, and K. Yoshino, respectively, Japan, in Nishida 1911 as *Taphrina osmundae* sp. nov.), 50–70 × 20–26 µm (Taichung, Taiwan province, China, coll. K. Sawada, TNS-F-192985, in Sawada 1929 as *Phytoceratiomyxa osmundae* sp. nov.), 40–80 × 13–23 µm (Georgia, USA, coll. B. B. Higgins, in Mix 1947 as *T. higginsii* sp. nov.; subsequently, Georgia, Michigan, USA, coll. B. B. Higgins and C. L. Kramer, in Kramer 1959 as *M. osmundae* comb. nov.), 26–63 × 17–27 µm (Ito 1964 as *T. osmundae*), 24–60 × 9–25.5 µm (Shizuoka, Japan, coll. J. Sugiyama et al., IAM-F 01408 = TNS-F-133689, in Nishida et al. 1995 as *M. osmundae*; Fig. 1d–f), 42.5–97.5 × 25–37.7 µm (Yunnang, China, coll. M. Kakishima, TNS-F-54015, in Sugiyama et al. 2018 as *M. osmundae*; Fig. 40b); putative asexual spores (see Toome et al. 2014) produced exogenously, enteroblastically, and simultaneously from the surface of sporogenous cells ultrastructually confirmed by Nishida et al. (1995; Fig. 40d–f) and subsequently by Bauer et al. (2006) that are hyaline, elliptical or ovate to obovate, no notation (noted only "fine") for size (Nishida 1911), 4.0–6.5 × 2.0–4.0 µm (Sawada 1929), 2–5 × 1.5–4 µm (Mix 1947; Kramer 1959), 3–4 × 2–3.5 µm (Ito 1964), 3–4.5 × 1.5–2.5 µm (Nishida et al. 1995), 2–5 × 1.5–4 µm (cf. Figs 1E, 3E in Sugiyama et al. 2018). After the release of the spores, numerous tiny cuneiform denticles (ca. 0.5 µm in diameter), which are slightly sunken at the center, can be observed at the surface of the sporogenous cells (Fig. 40 i, j; cf. Fig. 3d–f in Nishida et al. 1995). Dimensions of sprogenous cells and spores refer to Table 1 in Sugiyama and Katumoto (2008a). The details on the ontogeny and wall structure of putative asexual spores were illustrated and interpreted based on SEM and TEM observations by Nishida et al. (1995) and confirmed partly by Bauer et al. (2006).

The cultural characteristics as a yeast in culture (Nishida et al. 1995, 2011b): Spores (cells) grow in a yeast-like manner in pure culture; After 10 days at 20 °C, colonies (Fig. 41a, b) on Corn Meal (KM-030) agar were white to cream and became pale pinkish-cream upon age or similar color after twenty days on YM agar at 20 °C (see a colony photo in JCM On-line Catalog of Strains for *M. osmundae*); yeast cells (Fig. 41c, d) are oblong, cylindrical to pyriform, 3–6 × 1–2 µm and reproduce mainly by enteroblastic budding successively with bud scars showing percurrent extension (Fig. 41e; Seifert et al. 2011, cf. "*Taphrina*" *maculans* CBS 427.69 [Fig. 4D, E] and "*T.*" *californica* CBS 374.39 [Fig. 4F] in Sjamsuridzal et al. 1997); neither hyphae nor pseudohyphae are not formed, whereas a few of these form a hypha or pseudohypha in Potato Dextrose (PD) broth after ten days at 20 °C; neither ballistospores nor chlamydospores do not occur; the cell wall is multi-layered (Fig. 41e; cf. Fig. 4D–F in Sjamsuridzal et al. 1997). The ontogeny and wall structure of yeast cells (Fig. 41e) were elucidated based on SEM and TEM observations by Nishida et al. (1995).

Physiological and biochemical (chemotaxonomic) characteristics as a yeast in culture (Nishida et al. 2011b): The growth at 25 °C is variable; no growth at 30 °C and 37 °C. Inositol is assimilated. Fermentation is absent. Soluble starch is weakly assimilated. Extracellular starch-like compounds are not formed. Nitrate is not assimilated. Carotenoid pigments are formed. Staining with diazonium blue B (DBB) is negative, but the colony turns yellowish. Urease activity is present. The primary ubiquinone system: Q-10. Mol% G+C (by High-performance liquid chromatography determination): 53.9 (IAM 14324) and 53.8 (IAM 14511).

Plates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◀ **Fig. 40** Symptom, sporulating structures, and spore morphology of Mixiales. **a** *Osumunda japonica* leaves (fronds) infected with *Mixia osmundae* were collected at Sezawa (ca. 220 m alt.), Nakakawane-cho, Haibara-gun, Shizuoka Prefecture, Japan (photo: J. Sugiyama on May 31, 1993; voucher specimen TNS-F-13368 = IAM-F 0148); the pencil indicates 9 cm in length. **b** *O. japonica* leaves infected with *M. osmundae* at Xiao Cao Ba Forest Nursery (alt. 1760 m), Zhaotong District, Yiliang Co., Yunnan Province, China (photo: M. Kakishima on Sep. 17, 1998). **c** a part of the lectotype specimen (NY barcode 02226172) of *Taphrina higginsii*. **d** a sporogenous cell bearing an exogenously, blastically, and simultaneously produced multiple spores. **e**, **f** TEM of *M. osmundae* on *O. japonica* fronds (voucher specimen IAM-F 0150, now TNS-F-30046: Mitsuma, Nakakawane-cho, Haibara-gun, Shizuoka-ken, June 1, 1994, coll. J. Sugiyama and Y. Ando). The respective ultrathin sections showing the sporogenous cell from which spores were enteroblastically produced; the wall of spore is continuous with an inner layer of sporogenous cell wall. *M* mitochondrion, *N* nucleus, *V* vacuole. **g**, **h** young sporogenous cells exogenously bearing several immature spores; the micrographs taken from a slide preparation from a fresh specimen (det. Y. Harada as *Taphrina osmundae*; voucher specimen TNS-F-99211, donated from HHUF) of *M. osmundae* found on *O. japonica* fronds, 15 June 2002, coll. Y. Hadada et al., in Nishimeya-mura, Nakatsugaru-gun, Aomori, Japan. **i**, **j** SEM showing cuneiform denticles on the surface of sporogenous cells from which mature spores seced. **a**, **d**–**f**, **j**: reproduced from Fig. 3a, c, f and Fig. 4a, c in Nishida et al. (1995); @ Canadian Science Publishing (NRC Research Press). **b**, **c** reproduced from Fig. 1B and Fig. 2E in Sugiyama et al. (2018); @ The Mycological Society of America. **g**, **h**: Micrographs taken by J. Sugiyama on July 29, 2004 from a slide preparation made by Y. Harada on July 17, 2002. **i**: SEM micrograph taken by K. Ando. Scale bars: d = 5 µm, e = 2 µm, f = 1 µm, g, h = 10 µm, i = 5 µm, j = 1 µm

Genera included

Family Mixiaceae C.L. Kramer 1987
Mixia C.L. Kramer 1959
= *Phytoceratiomyxa* Sawada 1929

Phylogeny and evolution

As briefly mentioned in the introductory part, the hypothesized phylogenetic origin of *Mixia*, viz. the *Taphrinales*-*Mixia*- "Phycomycetes" connection, based on the analyses of phenotypic (mainly morphological) characteristics by Savile (1955, 1968) and Kramer (1959, 1987), was rejected due to single-locus data set (SSU gene)-based phylogeny (Nishida et al. 1995; Sjamsuridzal et al. 2002) and multigene (e.g., Schell et al. 2011; Aime et al. 2014; Wang et al. 2015a, b) and genome-based phylogenies (Nishida et al. 2011a; Toome et al. 2014). It was suggested that the sporogenous structure called ascus/asci in *Mixia osumndae* (≡ *Taphrina osmundae*) by Nishida (1911), Mix (1947, 1949), and Kramer (1959, 1987), is not an ascus/asci. Their SSU gene phylogeny suggested the *Mixia*-basidiomycete (the simple-septate basidiomycete/urediniomycete lineage) connection (cf. Sugiyama and Nishida 1995; Sugiyama 1998). Additionally, the specificity of the sporogenous cells of *M. osmundae* was ultrastructually unveiled: if exogenously produced spores are meiospores, the meiosporangium is assignable to holobasidium, which would be unique in Basidiomycota. Subsequently, the SSU sequence-based phylogenetic placement of *Mixia* by Nishida et al. (1995) was reinforced by sequence analyses of a single-locus data set (SSU gene by Sjamsuridzal et al. 1997, 1999 or LSU gene by Sjamsuridzal et al. 2002), and a combined two-locus data set (SSU and LSU genes by Bauer et al. 2006; Aime et al. 2006). In the 2010s, the multigene sequence-based phylogenetic analyses were performed in

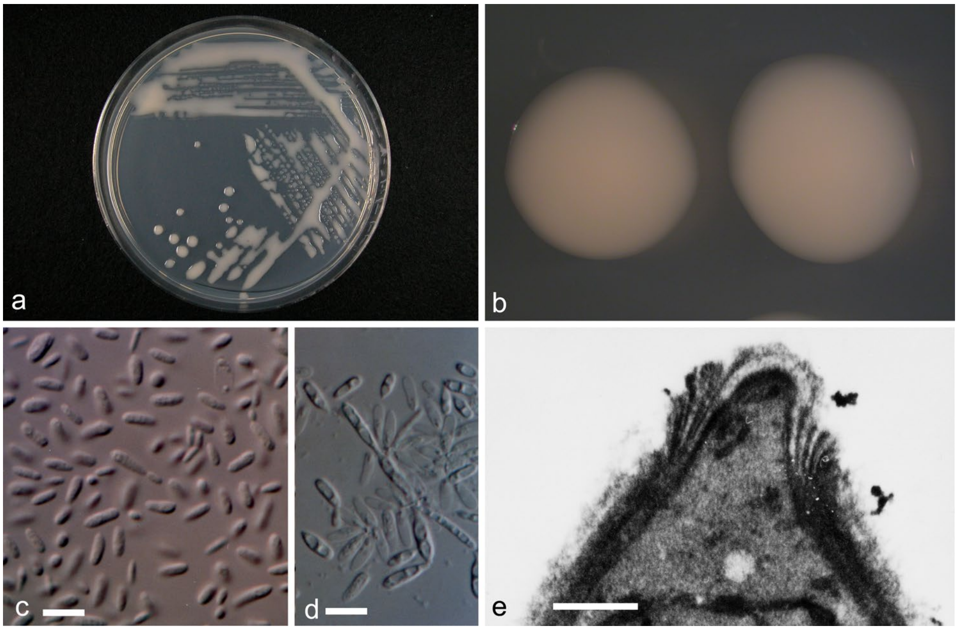

Fig. 41 Colonies and yeast state of *M. osmundae* in culture. **a**, **b** colonies on KM-030. **c** yeast cells on KM-030. **d** yeast cells and a few of these forming a hypha or pseudohypha in PD broth. **e** TEM showing a yeast cell with successive enteroblastic budding with scars (cf. Fig. 4D–F in Sjamsuridzal et al. 1997). **a**–**d** Photographs and micrographs were taken by T. Kiyuna. **e** TEM: Reproduced from Fig. 1b in Nishida et al. (1995); @ Canadian Science Publishing (NRC Research Press). Scale bars: c, d = 5 µm, e = 0.5 µm

fungal molecular systematics. A combined three-locus data set (SSU, LSU, and *TEF1* genes)-based phylogenies (Schell et al. 2011; Aime et al. 2014) showed that *Mixiomycetes* could be a sister clade to *Agaricostilbomycetes* within *Pucciniomycotina* but with weak bootstrapped confidence level (75% of Maximum Likelihood). Wang et al. (2015a) performed a comprehensive phylogenetic analysis of yeasts and yeast-like fungi, including *Mixia*, within *Pucciniomycotina* using a combined multigene data set (i.e., SSU, LSU D1/D2, ITS, *rpb1*, *rpb2*, *tef1*, and *cytb*). A simplified phylogenetic tree (Fig. 4) modified by Sugiyama et al. (2018) from Fig. 1 in Wang et al. (2015a) was illustrated. Their combined seven-locus data set-based phylogeny indicated the phylogenetic placement of *Mixiomycetes*, which appeared as a sister of *Spiculogloeales*, an *Agaricostilbomycete* order. Incidentally *Spiculogloeales* contained *Mycogloea* and *Spiculogloea*, characterized by tremelloid haustorial cells, and the yeast genus *Sporobolomyces* p. p. (Bauer et al. 2006; Oberwinkler 2017), namely seven *Sporobolomyces* spp. that have been accommodated in a new genus *Phyllozyma* within a new class *Spiculogloeomycetes* typified by the order *Spiculogloeales* (Wang et al. 2015b). The statistical confidence levels were comparatively high, 94/99/1.0, for Maximum Likelihood/Maximum Parsimony/Bayesian inference analyses, respectively (Wang et al. 2015a), at a node uniting the monotypic class *Mixiomycetes* and the order *Spiculogloeales*. However, various analyses by Wang et al. (2015a) provided different placements of *Mixiomycetes*, where it was not always as a sister of *Spiculogloeales*. In settling the phylogenetic placement of *Mixia*, the discovery of new taxa within the monotypic class *Mixiomycetes* is indispensable in addition to more taxa and sequences in the subphylum *Pucciniomycotina*, as suggested by Sugiyama et al. (2018).

Concurrently, genome sequencing of *M. osmundae* was performed by Toome et al. (2014) after a draft genome sequencing by Nishida et al. (2011a). Toome et al. (2014) determined and identified 13.63 Mb (204 contigs and 156 scaffolds) and 6,903 genes of the genome of *M. osmundae* strain JCM 22182 (=IAM 14324); incidentally the genome size was the smallest plant pathogenic basidiomycete genome sequenced and almost the same as the dimorphic ascomycete *Taphrina deformans* estimated at 13.3 kb (Cissé et al. 2013). Toome et al. (2014) detected the presence of 87 meiosis-related genes, and a full complement of mating loci, strongly suggesting that *M. osmundae* has the capacity to undergo sexual reproduction. Phylogenetically their consensus tree of RAxML analyses of 71 orthologous proteins (Fig. 1 in Toome et al. 2014) demonstrated that *M. osmundae* (*Mixiomycetes*) appeared as a sister to *Microbotryomycetes* represented by *Microbotryum violaceum* and *Sprobolomyces roseus* rather than *Pucciniomycetes*, with 58 RAxML bootstrap value. A fungal tree of life, namely cladogram of the kingdom *fungi* based on published multigene and genome-scale data sets, generated by Spatafora et al. (2018) classified subphylum *Pucciniomycotina* into eight classes, including *Mixiomycetes* which is sister to *Pucciniomycetes*, the largest class in the subphylum (commonly "rust" fungi) and *Tritirachiomycetes* (no sexual morph, originally classified as ascomycete taxa). On the other hand, a genome-scale phylogeney (Li et al. 2021c) inferred from a combined 290-gene dataset of 1,644 taxon samles (at species level) in *fungi* showed that *Mixiales* formed a cluster with *Agarigostilbales* within *Pucciniomycotina*. The ML tree (Fig. 1) and the topology by Li et al. (2021c) exhibited that *Mixiomycetes*/*Mixiales*/*Mixiaceae* clustered with *Agaricostilbolomycetes*/*Agaricostilbales*/*Chionosphaeraceae* represented by *Cystobasidiopsis lactophila*. The divergence between the two is up to 312 million years ago in the Carboniferous period (see Fig. 1).

Toome et al. (2014) analyzed all publicly available environmental sequences. They discovered several ITS sequences that were congeneric with *Mixia*, namely two from the bamboo plant *Yushania exilis* in China (Zhang et al. 1997) and three from the European beech, *Fagus sylvatica*, in France (Cordier et al. 2012). Toome et al. (2014) hypothesized that "*Mixia* members may exist in other plant hosts and with a broader distribution than previously known [namely Japan, China (Taiwan, Yunnan), and USA (Georgia, Michigan); see Sugiyama et al. 2018]." However, the evidence from living fronds of *Osmunda*/*Osmundastrum* ferns needs to confirm this hypothesis by living *Mixia* isolates, as Sugiyama et al. (2018) remarked. The genome data generated by Toome et al. (2014) suggested that *M. osmundae* lost its basidia in the process of evolution, and this enigmatic fungus is a living fossil that lives clonally in nature.

The authors refered to nomenclatural and biogeographical problems in relation to *M. osmundae*. The conspecificity between *Taphrina higginsii*, lectotypified by Sugiyama et al. (2018), and *M. osmundae* was confirmed by morphological observations of the authentic specimen of *T. higginsii* by Sugiyama et al. (2018) and supported Kramer (1959) taxonomic treatment, as mentioned previously. The geographical discovery of *M. osmundae*, China main land (Yunnan) by Sugiyama et al. (2018) was added as the third locality of the fungus in addition to the known localities, including Japan (Honshu, Kyushu), and North America (Georgia, Michigan). Considering the geographical records of *Osmunda*/*Osmundastrum* ferns by Kato (2007), Metzgar et al. (2008), Bomfleur et al. (2017), and Tsutsumi et al. (2021), Europe (Netherlands, Germany, and Italy), southern Africa (including Madagascar), India, and eastern North America to eastern South America in addition to eastern Asia, it may be fruitful to search for *M. osmundae* in these additional localities. On the other hand, the existence of environmental sequences that are congeneric or possibly conspecific with *M. osmundae* detected by Toome et al. (2014) opens the way for further developments and polyphasic insights into *Mixiomycete* systematics and evolution as commented by Sugiyama et al. (2018).

Justification of order and problems

As mentioned previously, phenotypic and genotypic characteristics of *Mixia*/*M. osmundae* showed that it is an independent taxon with no allied fungi within *Pucciniomycotina*. To construct a robust phylogenetic tree focusing on *Mixiales*/*Mixiomycetes*, the accumulation of multigene and genome sequences based on appropriate taxon sampling in *Pucciniomycotina* is required. Discovering new taxa in *Mixiomycetes* is essential because it leads to unveiling the true identity and evolutionary implications of *Mixia*, and we are able to answer a question "What exactly is *Mixia*?".

For *M. osmundae*, the yeast state showing a basidiomycetous nature is meaningful in the life strategy of the biotrophic fungus. With regard to the identity of the life cycle or history of *M. osmundae* involved with primitive *Osmunda*/*Osmundastrum* ferns dating back to the Late Triassic from 180 million years (Bomfleur et al. 2014; Grimm et al. 2015), very little is currently known. Therefore, it is presumed to be analyzed in the future. Also, the identity of the sporogenous cells and whether the basidium and basidiospore exist in the life cycle still need to be fully unveiled; therefore, it should be analyzed cytologically at nuclear and nuclear chromosome levels soon.

Significance

Ecological and economical roles

Mixia osmundae is a parasite occurring on leaves of *Osmunda* and/or *Osmundastrum* ferns in Japan (Honshu, Kyushu), China (Yunnan), and USA (Georgia, Michigan) (Sugiyama et al. 2018). The yeast (asexual) morph presumably exists in soil, but no evidence has been detected yet.

Chemical diversity

The physiological and biochemical (chemotaxonomic) characterization for *Mixia osmundae* (as a yeast morph) has been summarized under the subheading "Characters that define the taxa in the order" (Nishida et al. 2011b).

Other relevant data and future recommendations

In relation to elucidating the life cycle/strategy of *Mixia* biologically, based on Koch's postulates, inoculation experiments onto *Osmunda* ferns using the isolates have not yet succeeded; it remains a very important issue for the future. Focusing on the taxonomy, phylogeny, and fossils of the host ferns, the taxonomy of *Osmunda* s.l. as the host plant of *M. osmundae* was clarified by phylogenetic analyses of DNA sequences (> 8500 characters) of seven plastid loci, demonstrating the paraphyly or the prevailing concept of the genus (Metzgar et al. 2008). Metzgar et al. (2008) proposed a monophyletic concept for *Osmunda* s.s., consisting of all the traditionally accepted *Osmunda* species except *Osmundastrum cinnamomeum* (formerly *Osmunda cinnamomea*) as its sole extant species. Recent molecular phylogenetic analyses of the molecular clock and fossil records (Grimm et al. 2015; cf. Yatabe et al. 1999; Kato 2007) support the phylogenetic relationships proposed between *Osmunda japonica* and relatives and *Osmundastrum cinnamomeum* (Metzgar et al. 2008). The diversification of *Osmunda* and *Osmundastrum* dates to the Late Triassic, from 180 Myr (Bomfleur et al. 2014; Grimm et al. 2015). Although useful applications of the fungus *M. osmundae* are unknown, young shoots of *Osmunda japonica* ("Zenmai," a Japanese name) sterile fronds are widely served food as one of the wild spring plants in Japan (Iwatsuki 1992; Hashimoto 2003; Ebihara 2016).

Moniliellales Q.M. Wang, F.Y. Bai & Boekhout 2014

Contributed by: Teun Boekhout

Introduction

Moniliella was described by Stolk and Dakin for a black yeast-like fungus that was classified in order Moniliellales of Fungi Imperfecti (Stolk and Dakin 1966). One year later the genus *Sporotrichonoides* was described (Haskins and Spencer 1967), but this was reduced as a synonym under *Moniliella* by Rosa et al. (2008). Thus, only one genus is presently known for the order. Biochemical tests, such as urease activity, and a positive staining with Diazoneum Blue B salt, already early on indicated a basidiomycetous affinity. Wang and coworkers assigned the genus to Ustilaginomycotina, and because of the deep node, they proposed the class Moniliellomycetes, order Moniliellales and family Moniliellaceae to accommodate these fungi (Wang et al. 2014b).

Characters that define the taxa in the order

Development of sexual stages unknown. Colonies smooth to velvety, grayish to olivaceous black. Budding yeast cells present. True hyphae present that form arthroconida. Pseudohyphae and chlamydospores can be present. Hyphal cell walls have a lamellar substructure. Septal pores differ and can have a dolipore-like structure or micropores. Many species ferment glucose, and several also some other sugars. CoQ-9. Xylose and fucose are absent in cell wall (Wang et al. 2014b).

Plates

See figures 150.2–150.10 in de Hoog et al. (2011).

Genera included

Family Moniliellaceae Q.M Wang, F.Y Bai & Boekhout 2014
  Moniliella Stolk & Dakin 1966
  = *Sachsiella* Cif. 1955
  = *Trichosporonoides* Haskins & J.F.T. Spencer 1967
  = *Zygosaccharomyces* B.T.P. Barker

Evolution

The position of Moniliellales, together with Malasseziales, in Ustilaginomycotina may hold some surprises that still have to be unearthed. Members of both these orders are, in contrast, to most members of Ustilaginomycotina, no pathogens on plants, and they do not even have a plant-related ecology. Comparative genomics may hold the answer to explain this apparent contrast between lifestyles and phylogenetic affiliation. For Malasseziales, gross differences were observed in the genomes of *Malassezia* species and those of the, mainly, plant pathogenic Ustilaginomycotina (Xu et al. 2007), and something similar can be expected for Monilielles versus plantpathogenic Ustilaginomycotina. Moniliellales is estimated to have originated 245 million years ago (Zhao et al. 2017), which together with Malasseziales is based on currentl knowledge the earliest diverging lineage of Ustilaginomycotina.

Justification of order and problems

Moniliellales is mainly based on its occurrence as a distinct lineage within Ustilaginomycotina, where it sits, in most analyses next to Malasseziales. Different gene sets provided clear separation of Moniliellomycetes, however, the topology within Ustilaginomycotina differed between the various datasets (Wang et al. 2014b). It is therefore needed to perform a genome-based phylogenetic analysis of the Ustilaginomycotina to better understand the proper position within Ustilaginomycotina.

Significance

Ecological and economical roles

Several species are xerophilic and cause spoilage of food stuffs, e.g. jams and marmalade. Also known from fats, oils or substrates with low water activity, such as honey. Some species are known as producers of erythritol, an artificial sweetener. Other species are known from flowers and insects in tropical rainforests (de Hoog et al. 2011).

Chemical diversity

Most species ferment glucose, and some also galactose, sucrose or raffinose, which is a rare trait amongst Basidiomycota (Wang et al. 2014b).

Naohideales R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw. 2006

Contributed by: Nathan Schoutteten, Teun Boekhout

Introduction

Naohideales contains at present only one genus with one species, *Naohidea sebacea*, which is a dimorphic, nm-fusion pore mycoparasite with an ontogenetic yeast stage (Oberwinkler 1990; Bauer et al. 2006; Sampaio and Chen 2011). So far, no other species are known to belong to this order, which represents the earliest diverging lineage in Cystobasidiomycetes.

History

Naohidea sebacea was initially described as *Dacrymyces sebaceus* by Berkeley and Broome (1871) and was later recombined in the genus *Platygloea* by McNabb (1965a, b, c, d, e, f) based on the presence of transversally septate basidia. Detailed morphological and ultrastructural observations led Oberwinkler (1990) to conclude there are enough arguments to separate this species from the genus *Platygloea* and proposed the genus *Naohidea* to accommodate this species. Based on insights from ultrastructural observations and combined LSU and SSU phylogenetic tree reconstructions, Bauer et al. (2006) proposed the order Naohideales for this monotypic lineage. Several molecular phylogenetic studies demonstrated Naohideales as a member of Cystobasidiomycetes, in which it forms a separate and basal position to

Erythrobasidiales and Cystobasidiales (Weiss et al. 2004a, b; Aime et al. 2006; Bauer et al. 2006; Wang et al. 2015a, b).

Characters that define the taxa in the order

Bauer et al. (2006) delineated the order based on its phylogenetic position as a member of Cystobasidiomycetes and ultrastructural characters, such as 'simple' septal pores without cystosomes, and the presence of 'intracellular' haustoria along the host–parasite interface. A detailed description of *Naohidea sebacea* is provided by Oberwinkler (1990). Basidiomes are minute, pulvinate and gelatinous, overgrowing host stromata. Hyphae thin-walled and with clamp connections. Basidia originate from hyphae, stalked, transversely three-septate, elongated up to 275 µm. Basidial stalk cells reach up to 100 µm long. Sterigmata often curved, sometimes bifurcating. Basidiospores actively discharged from sterigmata, subglobose to broadly naviculate, germinating by secondary spore production or budding yeast cells. In old and soaked specimens, sessile basidiospores are produced by budding directly from the basidial cells. A peculiarity of *N. sebacea* is the endospore formation in hyphal compartments and basidial cells, which originates from an internal budding locus. The specific origin, function and karyological situation of these endospores is not known. The host-parasite interface of *N. sebacea* and its ascomycetous host was investigated by Bauer (2004) and summarized in Bauer et al. (2006). *N. sebacea* produces haustorial cells which invaginate host cells, which are surrounded by a conspicuous electron-transparent layer. Along the host–parasite interface, multiple, several nm-fusion pore channels traverse this layer and establish cytoplasmic contact between host and parasite.

Plates

Fig. 42 *Naohidea sebacea* on wood (7630, Netherlands, credit: N. Schoutteten, Copyright Phragmoproject). Also see Fig. 124.2 in Sampaio and Chen (2011), and Oberwinkler (1990, 2017)

Genera included

Family Naohideaceae Denchev 2009
Naohidea Oberw. 1990

Evolution

Naohideales form a basal lineage to Cystobasidiales and Erythrobasidiales (Aime et al. 2006; Bauer et al. 2006; Wang et al. 2015a). Given the monotypic character of the order, meaningful interpretation of its evolutionary trends awaits the discovery of more species of the order. Zhao et al. (2017) estimated the origin of the order 185 million years ago.

Justification of order and problems

Unfortunately, only a few isolates are available in public culture collections. It is possible that *N. sebacea* constitutes a species complex, with possible species diversity correlated with hosts specialization or different geographic regions. Isolation and description of new species diversity in this order is essential to understand its biological, ecological and evolutionary limits. For instance, are all members mycoparasitic or not?

Significance

Ecological and economical roles

The single species known in this order is a haustorial nm-fusion pore interacting mycoparasite of pyrenomycetous ascomycetes. Several host species have been reported, e.g., *Botryosphaeria* sp., *Botryodiplodia* sp., and *Dothiorella iberica* (Bandoni 1973; Oberwinkler 1990; Akulov et al. 2022). *Naohidea sebacea* seems to have a geographically wide distribution pattern and is currently known from North America, Europe, and Asia (Sampaio and Chen 2011).

Chemical diversity

Unknown.

Pachnocybales R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw. 2006

Contributed by: Nathan Schoutteten, Teun Boekhout

Introduction

The monotypic order Pachnocybales was introduced to accommodate the family Pachnocybaceae with the single genus *Pachnocybe* (Bauer et al. 2006).

History

Pachnocybe was described by Berkeley (1836) to accommodate *P. ferruginosa*, a minute stilboid fungus with holobasidia. The other species that were included by Berkeley mostly belonged to Ascomycota, and the genus is currently regarded as monotypic. The morphology and ultrastructure of *Pachnocybe ferruginea* was investigated in detail by Oberwinkler and Bandoni (1982) and Oberwinkler and Bauer (1989). Early molecular phylogenetic studies identified *Pachnocybe* as a close relative of Helicobasidiales, Platygloeales, Pucciniales, and Septobasidiales (Weiss et al. 2004a, b; Aime et al. 2006; Bauer et al. 2006). Bauer et al. (2006) placed this peculiar fungus in the family Pachnocybaceae in order Pachnocybales (Bauer et al. 2006).

Characters that define the taxa in the order

Pachnocybe is a fungus with stilboid basidiomes that form holobasidia producing sessile, thick-walled brown basidiospores. A yeast stage is not reported. With transmission electron microscopy, mitochondria were found to be connected with a symplechosome-like network of filaments and the SPB is of the rust-type and forms caps with endoplasmic reticulum (Oberwinkler and Bauer 1989; Bauer and Oberwinkler 1990a; Bauer et al. 2006).

Plates

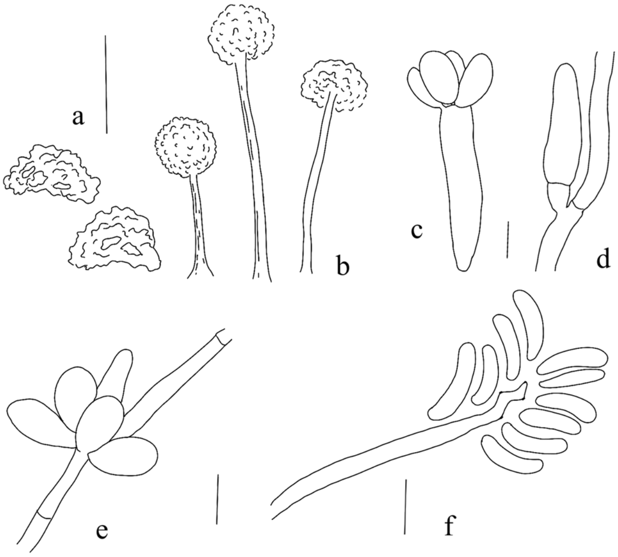

Fig. 43 *Pachnocybe ferruginea*. **a**, **b** conidiophores associated with capitate basidiomes; **c** basidium; **d** youn basidium; **e** clustered chlamydospores; **f** blastic-sym- podially produced conidia. Scale bars: a = 1 mm; c–e = 2 µm; f = 10 µm. Redraw from Kropp and Corden (1986) by Mao-Qiang He. Also See figures in Oberwinkler and Bandoni (1981), Bauer and Oberwinkler (1990a), and Oberwinkler (2017)

Genera included

Family Pachnocybaceae Oberw. & R. Bauer 1989

Pachnocybe Berk. 1836

Evolution

Pachnocybales occurs in a clade with Septobasidiales and Helicobasidiales (Bauer et al. 2006). Members of Helicobasidiales have complex lifecycles alternating between a rust-parasitic haplophase and a dikaryotic phytoparasitic phase and share the SPB-ER caps with *Pachnocybe ferruginea* (Bauer et al. 2006). Members of Septobasidiales are parasites of scale insects (Couch 1938; Bauer et al. 2006). A comparative genomic approach is needed to decipher evolutionary trends between these orders.

Justification of order and problems

Limited studies have been done on the evolutionary relationships between Pachnocybales, Helicobasidiales, Platygloeales, and Septobasidiales. The different lifestyles of fungi belonging to these orders warrant an in depth phylogenomics approach to understand their boundaries and evolutionary history. In addition, more taxa need to be studied by transmission electron microscopy for details on mitosis, meiosis, and hyphal septal pore complexes. Especially, the network connecting the mitochondria needs biochemical and cytological approaches and need to be compared with symplechsomes found in Atractiellomycetes.

Significance

Ecological and economical roles

Pachnocybe ferruginea has a presumed saprotrophic ecology (Bauer et al. 2006).

Chemical diversity

Unknown.

Peribolosporales Witfeld, M. A. Guerreiro, H.D.T. Nguyen, Begerow 2023

Contributed by: Mao-Qiang He

Introduction

Peribolosporales contains only one genus with two species. Species of this order were originally found in the forest soils in Canada, but also possibly exist in Australia, China (Taiwan) and a forest fire region in Portugal based on the molecular data in the public database (Tedersoo et al. 2014a; Buscardo et al. 2015; Witfeld et al. 2023). So far, two species from this order are found to be mesophilic with heat resistance abilities.

History

It is established and found to be a member of Ustilaginomycotina based on the analysis of 38 protein coding genes, orthology, and septal pore type analyses. Accordingly, the class Peribolosporomycetes and family Peribolosporaceae are proposed to accommodate the two species. (Witfeld et al. 2023).

Characters that define the taxa in the order

Peribolosporales is the only order found in Peribolosporomycetes. Species of this order are mesophilic, heat resistant and osmotolerant with slow hyphal growth and high phenotypic variability. Chlamydospores are triangular shaped and distally produced on coiled hyphae. Conidia are ovoid and sympodial, forming simple septal pores, without thickened septum membranes. Parenthesomes, forming distinct septal pore caps are absent, but low contrasted elements indicate non-membranous structures around the pore openings and within the pore (Witfeld et al. 2023).

Plates

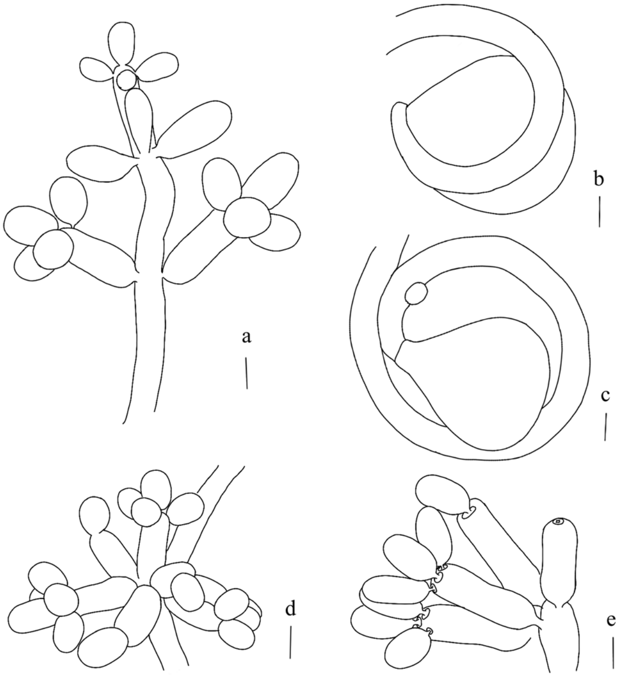

Fig. 44 *Peribolospora*. **a**, **d**, **e** conidiophores producing conidia; **b**, **c** chlamydospores. Scale bars = 2 µm. Redraw from Witfeld et al. (2023) by Mao-Qiang He

Genera included

Family Peribolosporaceae Witfeld, M. A. Guerreiro, H.D.T. Nguyen, Begerow 2023

Peribolospora Witfeld, M. A. Guerreiro, H.D.T. Nguyen, Begerow 2023

Evolution

Species of Peribolosporales have the same traits (e.g., heat resistance, pH growth range) as Geminibasidiales in Wallemiomycotina. But they are not phylogenetically close to each other. Geminibasidiales is in the lineage sister to Agaricomycotina, while Peribolosporales is sister to all other existing Ustilaginomycotina (Spatafora et al. 2017; Naranjo-Ortiz and Gabaldón 2019; Witfeld et al. 2023). Species of Peribolosporales have a unique set of orthologs compare to other species from other classes. The biggest overlap in the individual orthologs set comparisons is found in Exobasiodiomycetes (Witfeld et al. 2023). Further studies of genomic, transcriptomic, and CAZyme analyses could provide insights into the physiological adaptations and the lifestyle of the *Peribolospora* species (Witfeld et al. 2023).

Justification of order and problems

Peribolosporales is a well-defined order with evidences from genetic analyses, morphological observations and the physiological properties. However, divergence time of this new lineage is unresolved. Thus, further comparation of its divergence time with other classes in Ustilaginomycotina is needed.

Phallales E. Fisch. 1898

Contributed by: Larissa Trierveiler-Pereira

Introduction

Phallales is a well supported clade in Agaricomycetidae (Hosaka et al. 2006; Trierveiler-Pereira et al. 2014b; Melanda et al. 2021) which comprises ca. 140 species assigned to 38 genera (He et al. 2019a; Guevara-Guerrero et al. 2021; present study). Members of this order are gasteromycetes with expanded or sequestrate basidiomes (Trierveiler-Pereira et al. 2014b) and some species are famous due to its bizarre, fetid, and uncommon basidiome forms, as the stinkhorns (*Phallus* spp.) and lattice stinkhorns (*Clathrus* spp.) (Spooner and Læssøe 1994).

The taxa are distributed worldwide, found with more diversity and frequency in tropical and subtropical regions (Hosaka et al. 2006), occurring on soil, litterfall or rotten logs, in preserved forests as well as urban areas and gardens (Calonge 1998). Most members are saprotrophic, and at least one genus, *Phlebogaster*, is ectomycorrhizal (Melanda et al. 2021).

History

Phallales E. Fisch. was proposed to accomodate the families Phallaceae Corda and Clathraceae Chevall. (Fischer 1898). Fischer didn't recognize Lysuraceae Corda, proposed by Corda (1842), as an independent family, and instead, included *Lysurus* in Clathraceae. Phallales sensu Fischer included only genera with epigeous species and expanded receptacle (e.g. *Aseroë*, *Clathrus*, *Phallus*).

Cunningham (1931) erected the monogeneric family Claustulaceae G. Cunn., included in Phallales, to accomodate *Claustula* K.M. The author stated that althought the basidiomes were indehiscent, *Claustula* shared important features with other phalloids, as the typical gelatinous peridium, imature receptacle divided into chambers and spores smooth and elliptical. However, latter studies and monographs continued to follow Fischer's two-family concept for the order (e.g. Fischer 1933; Long and Stouffer 1948; Pilát 1958; Dennis 1970; Calonge 1998).

Hysterangiaceae E. Fisch. was also considered in Phallales by some authors (e.g., Dring 1973; Miller and Miller 1988), but most specialists accepted the family in a distinct order, *Hysterangiales* (Fischer 1933; Zeller 1939, 1949; Pilát 1958; Jülich 1981).

The systematics of Phallales became clearer with the phylogenetic studies published by Hosaka et al. (2006). These authors demonstrated that Hysterangiales and Phallales were different clades in the subclass Phallomycetidae (class Agaricomycetes). This study also suggested that Phallales was divided into six families: Clathraceae, Phallaceae, Lysuraceae, Protophallaceae, Claustulaceae and 'Trappeaceae'. The latter, the basal clade included *Trappea darkeri* (Zeller) Castellano and *Phallobata alba* G. Cunn. was tentatively named, and later formally proposed by Kirk et al. (2008).

Gastrosporium Mattir. appeared related to phalloid genera (*Anthurus* Kalchbr. & MacOwan and *Pseudocolus* Lloyd) in the phylogenetic study published by Hibbett and Binder (2002), but it was not included in the phylogenetic analysis conducted by Hosaka et al. (2006). Trierveiler-Pereira et al. (2014b) added new sequences to the Phallales phylogeny and concluded that the family Gastrosporiaceae belongs to Phallales.

Characters that define the taxa in the order

Immature basidiomes are hypogeous or epigeous, consisting of 2–3 layered peridium (usually with a gelatinous layer), usually with thick, white rhizomorphs at base; mature basidiomes usually epigeous, partially hypogeous or hypogeous, expanded or sequestrate (indehiscent), receptaculum pseudostipitate or sessile, pseudostipe pseudoparenchymatous, receptacle bearing the gleba; gleba green, olivaceous to brown, mucilaginous when immature, mucilaginous or rarely pulverulent when mature; basidiospores usually hyaline to greenish, but also golden to brown, bacillarioid, cylindrical to oblong, smooth or rarely ornamented (Trierveiler-Pereira et al. 2014b).

Mature basidiomes could be sequestrated or expanded and show great variability in size, shape and color (Trierveiler-Pereira et al. 2019). The sequestrate species, also called false truffes, are mostly globose, subglobose to cerebriform, but also irregular in form; epigeous (e.g., *Protubera*) or hypogeous (e.g., *Claustula*) (Trierveiler-Pereira et al. 2014a, b), usually externally light-colored or that change color to pink, yellow, or brown in age or if bruised (Sulzbacher et al. 2016a).

The expanded basidiomes erupt from a globose form, also called “eggs”, and usually are embedded in a gelatinous matrix before expansion. The pseudostipe can be light (white, pale yellow or pale pink) or vivid colored (orange, red, bright yellow); simple, not branched (as in *Phallus* and *Mutinus*) or divided into columns or meshes (*Blumenavia* and *Clathrus*) (Calonge 1998). The glebal mass (where the spores are produced) is spred on the pseudoestipe, receptacle or suspended (as in *Laternea* species and *Blumenavia crucis-hellenicae*) (Trierveiler-Pereira et al. 2019; Melanda et al. 2020). Some species exhibit unusual receptacle shapes, as the floriform *Abrachium floriformis* (Cabral et al. 2012) and the coralloid *Lysurus corallocephalus* (Dring 1980).

Plates

Fig. 45 Examples of expanded (**a**–**e**) and sequestrate (**f**–**h**) members of the Phallales. **a** *Phallus aureolatus* (Brazil); **b** *Clathrus* aff. *cristatus* (Brazil); **c** *Mutinus argentinus* (Brazil); **d** *Laternea pusilla* (Brazil); **e** *Pseudocolus fusiformis* (Japan); **f** *Protubera maracuja* (Brazil); **g** *Phallobata alba* (New Zealand); **h** *Trappea darkeri* (U.S.). Photographs: a, Juliano Marcon Baltazar; b, Ronald Péret; c, Giuseppe Estela Dourado; d, e, f, Larissa Trierveiler Pereira; g, Cath Smith h Damon Tighe

Genera included

- Family Clathraceae Chevall. 1826
  - *Abrachium* Baseia & T.S. Cabral 2012
  - *Aseroë* Labill. 1800
  - *Blumenavia* Möller 1895
  - *Clathrus* P. Micheli ex L. 1753
    - =*Anthurus* Kalchbr. & MacOwan 1880
    - =*Aserophallus* Mont. & Lepr. 1845
    - =*Clathrella* E. Fisch. 1898
    - =*Cletria* P. Browne 1756
    - =*Colonnaria* Raf. 1808
    - =*Dycticia* Raf. 1808
    - =*Linderiella* G. Cunn. 1942
  - *Colus* Cavalier & Séchier 1835
  - *Ileodictyon* Tul. & C. Tul. 1844
  - *Laternea* Turpin 1822
  - *Ligiella* J.A. Sáenz 1980
  - *Pseudocolus* Lloyd 1907
- Family Claustulaceae G. Cunn. 1931
  - *Claustula* K.M. Curtis 1926
  - *Gelopellis* Zeller 1939
  - *Kjeldsenia* W. Colgan, Castellano & Bougher 1995
  - *Phlebogaster* Fogel 1980
  - *Pseudogelopellis* K. Tao & B. Liu 1996
- Family Gastrosporiaceae Pilát 1934
  - *Gastrosporium* Mattir. 1903
    - =*Leucorhizon* Velen. 1925
- Family Lysuraceae Corda 1842
  - *Lysurus* Fr. 1823
    - =*Calathiscus* Mont. 1841
    - =*Desmaturus* (Schltdl.) Kalchbr. 1880
    - =*Dictyobole* G.F. Atk. & Long 1902
    - =*Kalchbrennera* Berk. 1876
    - =*Kupsura* Lloyd 1924
    - =*Mycopharus* Petch 1926
    - =*Pharus* Petch 1919
    - =*Schizmaturus* (Corda) Kalchbr. 1880
    - =*Simblum* Klotzsch ex Hook. 1831
    - =*Sinolloydia* C.H. Chow 1936
- Family Phallaceae Corda 1842
  - *Aporophallus* Möller 1895
  - *Aserocybe* Lév. 1855
  - *Echinophallus* Henn. 1898
  - *Endophallus* M. Zang & R.H. Petersen 1989
  - *Itajahya* Möller 1895
    - =*Alboffiella* Speg. 1898
  - *Mutinus* Fr. 1849
    - =*Aedycia* Raf. 1808
    - =*Caromyxa* Mont. 1856
    - =*Corynites* Berk. & M.A. Curtis 1853
    - =*Cynophallus* (Fr.) Corda 1842
    - =*Floccomutinus* Henn. 1895
    - =*Foetidaria* A. St.-Hil. 1835
    - =*Jansia* Penz. 1899
  - *Phallus* Junius ex L. 1753
    - =*Clautriavia* (Pat.) Lloyd 1909
    - =*Cryptophallus* Peck 1897
    - =*Dictyopeplos* Kuhl & Hasselt 1824
    - =*Dictyophallus* Corda 1842
    - =*Dictyophora* Desv. 1809
    - =*Hymenophallus* Nees 1816
    - =*Jaczewskia* Mattir. 1912
    - =*Kirchbaumia* Schulzer 1866
    - =*Morellus* Eaton 1818
    - =*Omphalophallus* Kalchbr. 1883
    - =*Phalloidastrum* Battarra 1755
    - =*Retigerus* Raddi 1829
    - =*Satyrus* Bosc 1811
    - =*Sophronia* Pers. 1827
  - *Staheliomyces* E. Fisch. 1921
  - *Staurophallus* Mont. 1845
  - *Stephanophallus* MacOwan 1880
  - *Xylophallus* (Schltdl.) E. Fisch. 1933
- Family Protophallaceae Zeller 1939
  - *Protubera* Möller 1895
    - =*Kobayasia* S. Imai & A. Kawam. 1958
    - =*Protophallus* Murrill 1910
    - =*Protuberella* S. Imai & A. Kawam. 1958
- Family Trappeaceae P.M. Kirk 2008
  - *Phallobata* G. Cunn. 1926
  - *Pterosporomyces* G. Guevara, Gómez-Reyes & Z.W. Ge 2021
  - *Restingomyces* Sulzbacher, Grebenc & Baseia 2016
  - *Trappea* Castellano 1990
- Phallales genera *incertae sedis*
  - *Calvarula* Zeller 1939
  - *Endoclathrus* B. Liu, Yin H. Liu & Z.J. Gu 2000
  - *Neolysurus* O.K. Mill., Ovrebo & Burk 1991
  - *Pseudoclathrus* B. Liu & Y.S. Bau 1980
  - *Saprogaster* Fogel & States 2001
  - *Vandasia* Velen. 1922

Evolution

The phylogenetic analysis presented by Hosaka et al. (2006) suggested that sequestrate forms were restricted to basal clades. However, Gastrosporiaceae, added later in the order phylogeny by Trierveiler-Pereira et al. (2014b), is not at a basal position, indicating that reversion from expanded to sequestrate forms occurred at least once in the order. Gastrosporiaceae was demonstrated to be sister to Phallaceae with full support, although the morphology of *Gastrosporium* species is different from species included in Phallaceae.

Melanda et al. (2021) stated that only about 20% of all described species in Phallales have DNA sequences available, therefore, more data are still necessary to better understand the species evolution.

Justification of order and problems

Many taxa, including monospecific genera, were not sequenced yet (Trierveiler-Pereira et al. 2014b). Some species are rare or were only found once, which complicates this task. It is expected that with more samples, some genera may be synonymized in the future (for example, *Blumenavia* and *Laternea*) (Melanda et al. 2021).

Although the tropical region has a high diversity of phalloids, with many rare and endemic species, the knowledge of the group in this area is still fragmentary. This fact can be attributed to several reasons, such as ephemeral nature of the basidiomes, especially in tropical rainforests; lack of researchers familiarized with the species in the field; poor field notes of the collected specimens; difficulties in preserving specimens and therefore, badly preserved vouchers in herbaria; publications with poor descriptions and without accurate illustrations or photographs; usage of paleotropical or temperate species names to identify the neotropical species (Dring 1980; Trierveiler-Pereira et al. 2019).

Moreover, many species need further ecological studies about nutritional strategies (saprotrophic, putatively ectomycorrhizal or ectomycorrhizal) (Melanda et al. 2021).

Significance

Ecological and economical roles

Most phalloid species are saprotrophic, therefore, they are important decomposing agents in forests and other ecosystems. Furthermore, they are important food sources for animals, since its fetid odor attracts insects and other arthropods for spore dispersion (entomochory) (Hosaka and Uno 2012). When expanded, basidiomes usually emit a strong, fetid odor that attracts flies, bees, beetles and ants (Nouhra and Dominguéz de Toledo 1994; Burr et al. 1996). Sometimes the attack of insects on these fungi is so intense that they can destroy the basidiomes within a few hours. Sequestrate forms (false truffle) are completely dependent from external agents, including animals, to disperse their spores.

Major reviews on mycophagy by mammals (Fogel and Trappe 1978; Claridge and May 1994) do not report the consumption of phalloid fungi, but there are some reports in literature: Sawada et al. (2013) observed that Japanese macaques (*Macaca fuscata*) consume *Phallus impudicus* L.; in Australia it was observed that the red-necked wallaby (*Macropus rufogriseus*) consume *Ileodictyon gracile* Berk. (Trierveiler-Pereira et al. 2016); and in Brazil, the Azara's agouti (*Dasyprocta azarae*) eats immature basidiomes of *Itajahya galericulata* (Trierveiler-Pereira et al. 2016). Beever and Lebel (2014) discussed that some sequestrate forms of phalloid fungi could also be attractive to birds (*Phallobata alba* and *Claustula fischeri*).

Humans also consume phalloid species (genera *Phallus*, *Lysurus* and *Mutinus*, check a complete list in Li et al. 2021b), and some, as *Phallus* species, are commercially produced in China (Li et al. 2020d).

Chemical diversity

Members of Phallales are gasteroid fungi, therefore, they have lost the ability to forcibly discharge their basidiospores. And since the basidiospores are produced in a sticky, gelatinous mass (gleba), they are also not wind dispersed. Therefore, stinkhorns rely on animals for spore dispersal. To attract these animals, usually arthropods, phalloid fungi produce volatile chemical compounds. The fetid odours, the same ones from putrid odors of feces, urine and decaying materials, attract flies and other insects which normally visit dead animals or dung. For example, the dung-like odor of the fetid lantern stinkhorn *Lysurus mokusin* consists largely of butanoic acid, p-cresol, phenol, pentanoic acid indole, and further aliphatic acids (Kües et al. 2018). Not every phalloid fungi exhale fetid volatile compounds, and some species produce pleasant, sweet odour or fragrances of rotten fruits and flowers (Calonge 2005; Trierveiler-Pereira et al. 2009).

Some chemicals extracted from phalloid fungi also have been tested for medical purposes, as presented by Habtemariam (2019) and Lv et al. (2022).

Other relevant data and future recommendations

Probably many other phalloid species are waiting to be described, especially from tropical regions. Recent molecular studies also have revealed that some morphological groups correspond to complexes of species, as in *Phallus indusiatus* (Cabral et al. 2019), *Xylophallus xylogenus*

(Crous et al. 2018), *Blumenavia rhacodes* (Melanda et al. 2020), and *Staheliomyces cinctus* (Cabral et al. 2022). Therefore, more collections and molecular data are essential to progress with the group knowledge.

On the other hand, some species may be disappearing due to forest fragmentation and other human impacts on the environment (Mueller et al. 2022). In Brazil, three phalloid species were recently assigned as vulnerable, and added to the IUCN Red List of Threatened Species: *Phallus aureolatus*, *Phallus glutinolens*, and *Blumenavia crucis-hellenicae* (https://www.iucnredlist.org/).

Platygloeales R.T. Moore 1990

Contributed by: Nathan Schoutteten, Teun Boekhout

Introduction

Moore (1990) instated the order Platygloeales for those species that were previously classified in Auriculariales based on the presence of transversally septate basidia in their sexual stage and that are characterised by hyphal septa with a 'simple' septal pore organisation.

History

Platygloea was described by Schröter (1889) to accommodate species with transversally septate basidia. The type species is *P. nigricans*, forming pustulate basidiomes on Tillia branches, which is currently known as *Platygloea disciformis*. Donk (1966) discussed the possible synonymy of the genus *Platygloea nigricans* with *Achroomyces tumidus*, which is the type species of the genus *Achroomyces* introduced by Bonorden (1851). Due to the taxonomic confusion that has been established in these early years, both genera *Achroomyces* and *Platygloea* have been used to accommodate many species, which were assigned to the genus only based on the presence of transversally septate basidia. This character is a highly plesiomorphic character in Basidiomycota that can be found in Pucciniomycotina and Agaricomycotina, and it is consequently not surprising that the genus in its present circumscription is highly polyphyletic. Bandoni (1956) performed a taxonomic survey of the genus *Platygloea* based on morphological observations and recognised a high degree of heterogeneity in this morpho-genus and concluded that most species most likely belong to other natural groups. Over the years, several *Platygloea* species were studied in more detail, involving cultivation, transmission electron microscopy and light microscopy, after which they were assigned to other groups of Basidiomycota (e.g., Oberwinkler 1990; Oberwinkler et al. 1990, 1999). Molecular phylogenetic reconstructions have indicated that *Platygloea disciformis*, the type species of the order Platygloeales, belongs to Pucciniomycetes, a clade with Helicobasidiales, Septobasidiales, Pachnocybales and Septobasidiales (Weiss et al. 2004a, b; Aime et al. 2006; Bauer et al. 2006; Wang et al. 2015a, b). So far, no other *Platygloea* species assigned to the genus based on morphological similarities have been genetically confirmed to belong to the same clade as *P. disciformis*. Interestingly, several plant parasitic species characterised by transversally septate basidia were found to be members of Platygloeales, with hosts mainly belonging to mosses and ferns (Oberwinkler and Bandoni 1984).

Characters that define the taxa in the order

Platygloeales is mainly circumscribed by phylogenetic reconstructions. The order comprises species producing pulvinate or clavarioid basidiomes, but some species only produce slimy layers on their plant hosts or even grow inbetween the host cells. Basidia transversally septate, two- to four-celled, producing ballisospores. Germination of basidiospores occurs by repetition or hyphae. Hyphal septa are characterised by 'simple' septal pore complexes.

Plates

Fig. 46 Selected basidiome types of Platygloeales. **a** *Achroomyces disciformis* (ENZ 21-010, Netherlands); **b** *Eocronartium muscicola* (ENZ 22-054, Netherlands, Credit: Roeland Enzlin, Copyright Phragmoproject)

Genera included

Family Eocronartiaceae Jülich 1982
  Eocronartium G.F. Atk. 1902
  = *Protopistillaria* Rick 1933
  Herpobasidium Lind 1908
  Jola Möller 1895
  Platycarpa Couch 1949
  Ptechetelium Oberw. & Bandoni 1984
Family Platygloeaceae Racib. 1909
  Achroomyces Bonord. 1851
  Glomerogloea Doweld 2013
  Glomopsis D.M. Hend. 1961
  = *Glomerularia* Peck 1880
  Insolibasidium Oberw. & Bandoni 1984
  Platygloea J. Schröt. 1887
  = *Collopezis* Clem. 1909
  = *Tachaphantium* Bref. 1888
  = *Tjibodasia* Holterm. 1898

Evolution

Using nuclear ribosomal DNA sequence data, Platygloeales is found as sister to Pucciniales (Bauer et al. 2006; Kumar et al. 2007). An evolutionary pattern towards plant parasitism may be recognised, with Platygloeales mainly infecting mosses and ferns, and the sister group Pucciniales that mainly diverged on Gymnosperms and Angiosperms. This leaves room for interesting comparative studies at the genome and secretome levels. Platygloeales is estimated to have emerged about 187 million years ago (Zhao et al. 2017).

Justification of order and problems

The phylogenetic position of Platygloeales combined with its mainly phytoparasitic lifestyle justifies the order. Many species are regarded as rare, and almost none are available as living cultures. Additional sampling is needed to obtain a better understanding of the true diversity of the order.

Significance

Ecological and economical roles

Mainly plant parasites infecting mosses and ferns, but also some examples are known from seed plants.

Chemical diversity

Unknown.

Polyporales Gäum. 1926

Contributed by: Sergio P. Gorjón, Viktor Papp, Ricardo Valenzuela, Tatiana B. Gibertoni, Chang-Lin Zhao, Milay Cabarroi-Hernández, Alfredo Justo, Laura Guzmán-Dávalos

Introduction

Polyporales is a diverse group of Agaricomycetes with 18 families, 285 genera and 2544 species and it is considered as a strongly supported clade (Binder et al. 2013; Hibbett et al. 2014; Justo et al. 2017; He et al. 2019a; Shen et al. 2019). Binder et al. (2013) included an analysis of a 373-species with nrLSU, 5.8S, nrSSU, rpb1, rpb2 and tef1 and also analyzed ten Polyporales genomes and performed phylogenetic informativeness profiling with 356, 71, and 25-gene datasets. The resulting trees from the phylogenetic analyses of the 25-gene dataset have an identical topology to the 71 and 356-gene analyses and all internal nodes of the Polyporales received full support (100% BS, 1 PP) (Binder et al. 2013). Justo et al. (2017) analyzed the combination of rpb1 and ribosomal RNA genes (ITS, LSU), and found robust resolution of many clades, including 18 were recognized as families, but they mentioned that some nodes remained weakly supported and numerous taxa have yet to be sampled.

The great majority of Polyporales are saprotrophic wood-decay fungi, while around 100 species are plant pathogens causing timber damage (Dai 2012b; Rajchenberg and Robledo 2013), and they produce white-rot (degrade lignin and cellulose compounds) or brown-rot (degrade cellulose and hemicellulose) and play an important role in the carbon cycle (Binder et al. 2013). Surprisingly, the Polyporales has been found as endophytes or are commonly isolated as part of the endophytic communities in woody tissues and roots. Although several ecological roles have been proposed for these fungi, from latent pathogen or saprotroph hypothesis, it is suggested that many endophytic species may invade living trees as a strategy for early substrate colonization as protective agents (Hibbett et al. 2014; Martin et al. 2015). The order includes a wide variety of basidiomes types and hymenophore configurations in bracket-shaped, effused resupinate, stipitate with poroid, lamellate, labyrinthiform, or smooth hymenophores, and few species produce shelf-like or flabellate clusters of overlapping sporomes (Binder et al. 2013). Besides, macroscopic and microscopic characters are variable and are present in several families of Polyporales. Variations of and transitions between basidiome types exist, and there is no morphological synapomorphy that unites Polyporales (Binder et al. 2013). The most common polyporoid basidiome types just mentioned also have evolved convergently in at least 11 additional orders of Agaricomycetes (Binder et al. 2013), therefore, the Polyporales is related only for the molecular characters (Figs. 42, 43, 44, 45, 46, 47, 48, 49, 50, 51, 52, 53, 54, 55, 56, 57, 58, 59, 60, 61, 62, 63, 64, 65, 66, 67, 68, 69, 70).

History

Accommodating polyporoid fungi into a classification scheme has been a difficult work dating back to the earliest attempts by Linnaeus (1753), who included 12 stipitate species with a poroid surface as belonging to *Boletus* (six of them now in Polyporaceae) and other two, as *Agaricus*: *A.* (*Daedalea*) *quercinus* L. and *A.* (*Lenzites*) *betulinus* L., currently also in Polyporales, in Fomitopsidaceae and Polyporaceae, respectively (Overholts 1953; Bernicchia 1990). Micheli (1729) described *Polyporus* as a "plantae genus", in which the lower part, perforate and with holes, cannot be separated from the upper part. Persoon (1801) placed into *Boletus* section *Polyporus*, and later, Persoon (1825) recognized in Hymenomycetes sections: *Porodermei* (with pores), *Odontedermei* (with teeth), and *Agaricini* (with gills). The most accepted classification of fungi for decades among the first mycologists was that carried out by Fries, who in his works Observationes mycologicæ (1815–1818), Systema mycologicum (1821, 1823, 1829), and Epicrisis systematis mycologici (1838) separated many groups according to macroscopic features and the color of the basidiospores. Fries (1821) accommodated the polypores known until then into two genera, *Daedalea* Pers. and *Polyporus*, following the criteria of Micheli (1729), and divided *Polyporus* into three subgenera: *Favolus*, *Microporus*, and *Polystictus*. Later, Fries (1828) recognized *Favolus* Fr. as a distinct genus.

Subsequently, Fries (1838) separated *Trametes* from *Daedalea*, and recognized *Cyclomyces* and *Hexagona* as different genera [all of them as Polyporei or as a subdivision of a family following Donk (1964)]. Corda (1839) proposed Polyporaceae as a family based on Fries' Polyporei, where he included *Polyporus* and *Boletus*. Fries (1851) divided *Polyporus* into three subgenera: *Eupolyporus* (annual, fleshy), *Fomes* (perennial with stratified tubes), and *Poria* (resupinate forms). Also, in this work, *Polystictus* was segregated from *Polyporus* and elevated as genus, mainly due to the coriaceous pileus and the fibrous cuticle. The connection of *Polyporus* with the genera *Boletus* and *Polystictus* was discussed by Fries (1855), considering the features of the pores; also, he divided *Polyporus* in two series: *Eupolyporus* and *Fomes*. According to Cunningham (1947), throughout Fries' work, he generally accepted seven genera in the polypore group: *Cyclomyces*, *Daedalea, Favolus, Hexagona, Polyporus, Polystictus*, and *Trametes*. Then, more species were described, so Fries' classification was not enough to include them in his genera (Cunningham 1947; Donk 1964).

Some authors (e.g., Gillet 1878; Quélet 1886; Patouillard 1900; Murrill 1904; Lloyd 1908) started to re-examine the Friesian classification, incorporating other genera, and elevating some of them to family level. Hennings (1900) divided the subclass Hymenomycetes (Fries 1874) into six orders (at that time using the ending -aceae), among them Polyporaceae, which included the tribes Boleteae, Fistulineae, Merulieae, and Polyporeae. Later, Murrill (1907) suggested some other genera under the tribes Daedaleae, Fomiteae, Polyporeae, and Porieae. In Overholts (1915, 1953) included different characters to segregate the genera in Polyporaceae, like the consistency of the pileus and the separable tube layer. She made a revision of the family and included 16 genera with a key: *Bjerkandera*, *Coriolus, Cryptoporus, Daedalea*, *Favolus, Fomes, Ganoderma*, *Gloeoporus, Ischnoderma, Phaeolus, Phellinus*, *Piptoporus, Polyporus*, *Polystictus, Porodisculus,* and *Trametes*.

Rea (1922), considering the classification system suggested by Patouillard (1900), who incorporated "les Clavaires, les Thélephores, les Hydnes et les Polypores de Fries" under the family "Aphyllophorancés", established Aphyllophorales with two suborders, Clavariineae and Porohydnineae, and placed under the last one the families Cyphellaceae, Fistulinaceae, Hydnaceae, Meruliaceae, Polyporaceae, Polystictaceae, and Thelephoraceae. Polyporaceae contained five genera: *Fomes, Ganoderma, Polyporus, Poria*, and *Sistotrema*. Gäumann (1926) established Polyporales, following Micheli's concept and since that moment the group became one of the largest and most controversial orders of Agaricomycetes. Whether this group constitutes an order, a family, or a tribe was a topic hotly debated among mycologists for decades (Cunningham 1947).

Donk (1964) made a re-evaluation of Aphyllophorales, in which he recognized 21 families, considering different macro and microscopic characteristics, such as the shape and ornamentation of the basidiospores. In his work, the author mentioned that Polyporaceae was like a container for all 'polypores' not assigned to other families, even suggesting that the family was an "artificial assemblage" of different and similar species that develop tubes. Ryvarden (1991) accepted Polyporaceae as the family of polyporoid fungi and, through phenetic analysis, recognized 11 groups of related genera and one more of unknown affinity. The 11 groups were: *Daedalea*, *Fomes*, *Grammothele*, *Junghuhnia*, *Laetiporus*, *Nigroporus*, *Polyporus*, *Perenniporia*, *Rigidoporus*, *Trametes*, and *Tyromyces*. Furthermore, *Australoporus*, *Diacanthodes, Echinoporia, Lenzitella, Murrilloporus, Navisporus, Pachykytospora, Paratrichaptum, Polyporoletus*, and *Pseudopiptoporus* were in the group whose affinities were unknown.

Solving the taxonomic structure of Polyporales has been recognized as a difficult task based on morphological characters, hence different authors (e.g., Binder et al. 2005, 2013; Justo and Hibbett 2011; Miettinen et al. 2011; He et al. 2019a) have tried to elucidate its taxonomic arrangement using ribosomal DNA sequences or protein-coding genes (*rpb1*, *rpb2*, *tef1*). However, the phylogenetic reconstructions have shown the paraphyllia of several families and genera belonging to the Polyporales (Binder et al. 2013).

Hibbett and Thorn (2001) and Binder et al. (2005) found eight monophyletic major clades of Homobasidiomycetes with molecular data, which were given informal names (polyporoid clade, euagarics clade, etc.). Binder et al. (2005) mentioned that the monophyly of the polyporoid clade was controversial. Later, Binder et al. (2013) supported the three lineages of Polyporales previously described by Binder et al. (2005): core polyporoid clade, *Antrodia* clade, and phlebioid clade, but recognized a residual polyporoid clade where the relationships among these lineages were not well resolved (e.g., *Gelatoporia, Grifola, Tyromyces*). Justo et al. (2017) suggested 18 clades corresponding to family names, of which three new families were described (Cerrenaceae, Gelatoporiaceae, Panaceae).

Different authors further divided each of the clades suggested by Binder et al. (2005, 2013) in Polyporales. The core polyporoid clade was divided into three well-supported lineages (polyporus, trametoid, dentocorticium clades) by Justo and Hibbett (2011). Ortiz-Santana et al. (2013) presented a phylogenetic overview of the five main groups recovered into the antrodia clade: fibroporia, laetiporus, postia, laricifomes, and core antrodia groups, although not all these groups received strong support in their analyses. He et al. (2019a, b) considered narrowly defined families as synonyms of Polyporaceae, including Ganodermataceae, as a strategy to avoid introducing taxonomic problems by establishing too many families into the core polyporoid clade. Robledo et al. (2020) suggested that the basidiospore features are correlated with lineages of the core polyporoid clade and, in this sense, revealed *Diacanthodes*, a genus with ornamented and dextrinoid basidiospores, whose phylogenetic position had remained elusive, belongs to the polyporoid clade.

Characters that define the taxa in the order

Polyporales constitutes a very diverse group of organisms, without exclusive morphological features to clearly define the order. A majority have a tubular or poroid hymenophore, with no typical lamellae, but with numerous exceptions. They often form leathery and hard basidiomes, which do not rot easily. There is no way to define the group strictly based on morphology, even one can easily recognize the majority of polypore fungi belonging to the Polyporales.

Basidiomes generally have a gymnocarpic development, without protective structures of the hymenium (except some genera such as *Cryptoporus*). They can range from resupinate (most corticioid species in Phanerochaetaceae, Meruliaceae Hyphodermataceae, etc.) to the more commonly pileate (most polypores in Polyporaceae and other poroid families), and in some cases, forming stipitate basidiomes (e.g., *Amauroderma*, *Polyporus*). We can also find some representatives that produce hydnoid and clavarioid processes (*Hydnopolyporus*, *Sparassis*), or some groups that form stipitate stereoid fructifications (Podoscyphaceae). The hymenophore configuration is highly variable, from smooth to tuberculate, phlebioid to merulioid, aculate to more typically poroid with circular, irregular, or sometimes pseudolamellar elongated pores. In some cases, a laminar configuration can rarely be found (*Lentinus*).

From a micromorphological point of view we can find a wide variability as well. The hyphal system varies from monomitic to dimitic and trimitic, presenting more or less sclerified vegetative hyphae depending on the structural complexity of the basidiomes. Generative hyphae have simple septa or clamped septation, and in some species a mixture of both is found in the same hyphae, and more rarely, some species can produce hyphae with verticillate clamps. Basidia are usually clavate, bearing four sterigmata, with some exceptions. A diverse number of cystidia are found in the hymenial and subhymenial layer, and these sterile elements are more commonly present among the corticioid species. The basidiospores (ballistospores) are not repetitive. Their morphology may be extremely variable and can take almost any shape such as: globose, subglobose, obovate, ellipsoid, cylindrical, fusiform, sigmoid, allantoid, navicular, amygdaliform, sub-angular, or tetrahedral. Most basidiospores are hyaline, more rarely pigmented and then in general yellowish or brownish. The basidiospore surface is usually smooth, more rarely ornamented and then asperulate, tuberculate, echinulate, striate, warted, reticulate or punctulate appearance. Their wall is usually thin, but can also be thick-walled and rarely with a double wall, the inner thick-walled and ornamented, the outer hyaline and smooth. Usually, they do not react in Melzer's reagent, but with some exceptions (Donk 1964; Ryvarden 1991; Bernicchia 2005; Wang et al. 2021b, 2022b). All the abovementioned macro- and micromorphological characteristics are important for the taxonomy of the group and some of them, such as chemical reactions and morphology of the basidiospores, are considered of evolutionary significance.

Plates


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◂ **Fig. 47** Selected basidiome types of Polyporales. **a** *Antrodia heteromorpha* (RV 11112, Oaxaca State, Mexico); **b** *Coriolopsis byrsina* (RV 17992, Cozumel Island, Mexico); **c** *Podoscypha venustula* (SPG 4793, Ecuador); **d** *Flavodon flavus* (RV 17965, Yucatan State, Mexico); **e** *Hexagonia tenuis* (RV 17892, Campeche State, Mexico); **f** *Irpex lacteus* (RV 17796, Mexico); **g** *Laetiporus sulphureus* (RV 13314, Hidalgo Satate, Mexico); **h** *Lamelloporus americanus* (RV 16314, Oaxaca State, Mexico); **i** *Lentinus arcularius* (RV 16193, Hidalgo State, Mexico); **j** *Panus rudis* (RV 18256, Veracruz State, Mexico); **k** *Ceriporia viridans* (SPG 1394, Spain); **l** *Dacryobolus karstenii* (SPG 253, Spain); **m** *Hypochnicium albostramineum* (SPG 643, Spain); **n** *Picipes badius* (RV 16191, Hidalgo State, Mexico); **o** *Daedaleopsis confragosa* (SPG 5386, Spain); **p** *Favolus tenuiculus* (SPG 4850, Ecuador); **q** *Fomes inzengae* (SPG 143, Spain); **r** *Hypoderma setigerum* (SPG 683, Spain); **s** *Sparassis crispa* (ZRL2080315, Yunnan province, China); **t** *Phanerochaete sordida* (SPG 527, Spain); **u** *Phlebia tuberculate* (SPG 402, Spain); **v** *Phlebiopsis crassa* (SPG 5363, Spain); **w** *Rigidoporus mutabilis* (SPG 5806, Ecuador); **x** *Trametes maxima* (RV 12140, Campeche State, Mexico); **y** *Vitreoporus dichrous* (RV 18536, Michoacan State, Mexico)

Genera included

Family Adustoporiaceae Audet 2018
 = Amyloporiaceae Audet 2018
 = Caloporaceae Bondartseva 1983
 = Lentoporiaceae Audet 2018
 = Rhodoniaceae Audet 2018
  Adustoporia Audet 2017
  Amyloporia Singer 1944
  Lentoporia Audet 2017
  Resinoporia Audet 2017
  Rhodonia Niemelä 2005
 = *Caloporus* P. Karst. 1881
Family Auriporiaceae B.K. Cui, Shun Liu & Y.C. Dai 2022
  Auriporia Ryvarden 1973
Family Cerrenaceae Miettinen, Justo & Hibbett 2017
  Cerrena Gray 1821
  = *Phyllodontia* P. Karst. 1883
  Irpiciporus Murrill 1905
  Pseudolagarobasidium J.C. Jang & T.Chen 1985
  Pseudospongipellis Y.C. Dai & Chao G. Wang 2022
  Radulodon Ryvarden 1972
Family Climacocystaceae B.K. Cui, Shun Liu & Y.C. Dai 2023
  Climacocystis Kotl. & Pouzar 1958
  Diplomitoporus Domański 1970
  = *Fabisporus* Zmitr. 2001
Family Dacryobolaceae Jülich 1982
  Dacryobolus Fr. 1849
  = *Gloeocystidium* P. Karst. 1889
Family Fibroporiaceae Audet 2018
  Fibroporia Parmasto 1968
  Pseudofibroporia Yuan Y. Chen, B.K. Cui & Y.C. Dai 2017
Family Fomitopsidaceae Jülich 1982
 = Daedaleaceae Jülich 1982
 = Piptoporaceae Jülich 1982
  Amyloporiella A. David & Tortič 1984
  Anthoporia Karasiński & Niemelä 2016
  Antrodia P. Karst. 1879
  = *Amyloporia* Singer 1944
  = *Amyloporiella* A. David & Tortič 1984
  = *Coriolellus* Murrill 1905
  Antrodiopsis Audet 2017
  Brunneoporus Audet 2017
  Buglossoporus Kotl. & Pouzar 1966
  Cartilosoma Kotl. & Pouzar 1958
  Daedalea Pers. 1801
  = *Agarico-suber* Paulet 1793
  = *Striglia* Adans. 1763
  = *Hypogaea* E. Horak 1964
  = *Spelaeomyces* Fresen. 1863
  Daedalella B.K. Cui & Shun Liu 2022
  Dentiporus Audet 2017
  Flavidoporia Audet 2017
  Fomitopsis P. Karst. 1881
  = *Pilatoporus* Kotl. & Pouzar 1990
  = *Piptoporus* P. Karst. 1881
  = *Placoderma* (Ricken) Ulbr. 1928
  = *Ungularia* Lázaro Ibiza 1916
  Fragifomes B.K. Cui, M.L. Han & Y.C. Dai 2016
  Melanoporia Murrill 1907
  Neoantrodia Audet 2017
  Neolentiporus Rajchenb. 1995
  Niveoporofomes B.K. Cui, M.L. Han & Y.C. Dai 2016
  Parmastomyces Kotl. & Pouzar 1964
  = *Phaeodaedalea* M. Fidalgo 1962
  Pseudoantrodia B.K. Cui, Yuan Y. Chen & Shun Liu 2022
  Pseudofomitopsis B.K. Cui & Shun Liu 2022
  Ranadivia Zmitr. 2018
  Rhizoporia Audet 2017
  Rhodoantrodia B.K. Cui, Y.Y. Chen & Shun Liu 2022
  Rhodofomes Kotl. & Pouzar 1990
  Rhodofomitopsis B.K. Cui, M.L. Han & Y.C. Dai 2016
  Rubellofomes B.K. Cui, M.L. Han & Y.C. Dai 2016
  Subantrodia Audet 2017
  Ungulidaedalea B.K. Cui, M.L. Han & Y.C. Dai 2016
Family Fragiliporiaceae Y.C. Dai, B.K. Cui & C.L. Zhao 2014
  Fragiliporia Y.C. Dai, B.K. Cui & C.L. Zhao 2014
Family Gelatoporiaceae Miettinen, Justo & Hibbett 2017
  Cinereomyces Jülich 1982
  Gelatoporia Niemelä 1985

Obba Miettinen & Rajchenb. 2012
Sebipora Miettinen 2012
Family Gloeoporellaceae B.K. Cui, Shun Liu & Y.C. Dai 2023
Gloeoporellus Zmitr. 2018
Family Grifolaceae Jülich 1982
Aegis Gómez-Montoya, Rajchenb. & Robledo 2017
Grifola Gray 1821
= *Cautinia Maas* Geest. 1967
= *Cladodendron* Lázaro Ibiza 1916
= *Polypilus* P. Karst. 1881
Family Hyphodermataceae Jülich 1982
Hyphoderma Fr. 1833
= *Mutatoderma* (Parmasto) C.E. Gómez 1976
= *Pycnodon* Underw. 1898
Family Incrustoporiaceae Jülich 1982
Incrustoporia Domanski 1963
Piloporia Niemelä 1982
Skeletocutis Kotl. & Pouzar 1958
= *Leptotrimitus* Pouzar 1966
Tyromyces P. Karst. 1881
= *Leptoporellus* Spirin 2001
= *Persooniana* Britzelm. 1897
Family Irpicaceae Spirin & Zmitr. 2003
Byssomerulius Parmasto 1967
= *Ceraceomerulius* (Parmasto) J. Erikss. & Ryvarden 1973
Candelabrochaete Boidin 1970
Ceriporia Donk 1933
Crystallicutis El-Gharabawy, Leal-Dutra & G.W. Griff. 2021
Cytidiella Pouzar 1954
Emmia Zmitr., Spirin & Malysheva 2006
Flavodontia C.L. Zhao 2022
Gloeoporus Mont. 1842
= *Meruliporia* Murrill 1942
= *Vitreoporus* Zmitr. 2018
Irpex Fr. 1825
= *Cystidiophorus* Bondartsev & Ljub. 1963
= *Efibula* Sheng H. Wu 1990
= *Flavodon* Ryvarden 1973
= *Hydnopolyporus* D.A.Reid 1962
Leptoporus Quél. 1886
Meruliopsis Bondartsev 1959
Phanerochaetella C.C. Chen & Sheng H. Wu 2021
Raduliporus Spirin & Zmitr. 2006
Resiniporus Zmitr. 2018
Trametopsis Tomšovský 2008
Family Ischnodermataceae Jülich 1982
Ischnoderma P. Karst. 1879
= *Lasiochlaena* Pouzar 1990
Family Laetiporaceae Jülich 1982
Kusaghiporia J. Hussein, S. Tibell & Tibuhwa 2021
Laetiporus Murrill 1904
= *Cladoporus* (Pers.) Chevall. 1826
= *Pseudophaeolus* Ryvarden 1975
Macrohyporia I. Johans. & Ryvarden 1979
Wolfiporiella B.K. Cui & Shun Liu 2022
Wolfiporiopsis B.K. Cui & Shun Liu 2022
Family Laricifomitaceae Jülich 1982
Gilbertsonia Parmasto 2001
Laricifomes Kotl. & Pouzar 1957
Ryvardenia Rajchenb. 1994
Family Meripilaceae Jülich 1982
= Rigidoporaceae Jülich 1982
Meripilus P. Karst. 1882
= *Flabellopilus* Kotl. & Pouzar 1957
= *Leucofomes* Kotl. & Pouzar 1957
= *Porodon* Fr. 1851
Family Meruliaceae Rea 1922
= Climacodontaceae Jülich 1982
= Phlebiaceae Jülich 1982
Allophlebia C.R.S. de Lira, Gibertoni & K.H. Larss. 2022
Aurantiopileus Ginns, D.L. Lindner & T.J. Baroni 2010
Aurantiporus Murrill 1905
Ceriporiopsis Domański 1963
Ceriporiopsoides C.L. Zhao 2023
Climacodon P. Karst. 1881
Crustodontia Hjortstam & Ryvarden 2005
Geesterania Westphalen, Tomšovský & Rajchenb. 2018
Hermanssonia Zmitr. 2018
Hydnophanerochaete Sheng H. Wu & C.C. Chen 2018
Hydnophlebia Parmasto 1967
Lilaceophlebia (Parmasto) Spirin & Zmitr. 2004
Luteochaete C.C. Chen & Sheng H. Wu 2021
Luteoporia F. Wu, Jia J. Chen & S.H. He 2016
Merulius Fr. 1821
Mycoacia Donk 1931
Mycoaciella J. Erikss. & Ryvarden 1978
= *Ceraceohydnum* Jülich 1978
Noblesia Nakasone 2021
Odoria V. Papp & Dima 2017
Pappia Zmitr. 2018
Phlebia Fr. 1821
= *Caloporia* P. Karst. 1893
= *Jacksonomyces* Jülich 1979
= *Ricnophora* Pers. 1825
= *Trabecularia* Bonord. 1857
Phlebicolorata C.L. Zhao 2023
Phlebiodontia Motato-Vásq. & Westphalen 2022
Phlebiporia Jia J. Chen, B.K. Cui & Y.C. Dai 2014
Physisporinus P. Karst. 1889
Pseudonadsoniella T.O. Kondr. & S.Y. Kondr. 2015
Pseudophlebia C.L. Zhao 2023

Sarcodontia Schulzer 1866
= *Oxydontia* L.W. Mill. 1933
Scopuloides (Massee) Höhn. & Litsch. 1908
Stereophlebia Zmitr. 2018
Family Panaceae Miettinen, Justo & Hibbett 2017
Cymatoderma Jungh. 1840
= *Actinostroma* Klotzsch 1843
= *Beccariella* Ces. 1879
= *Cladoderris* Pers. ex Berk. 1842
Panus Fr. 1838
= *Lentinopanus* Pilát 1941
Family Phaeolaceae Jülich 1982
Melanoporella Murrill 1907
Phaeolus (Pat.) Pat. 1900
= *Choriphyllum* Velen. 1922
= *Spongiosus* Lloyd ex Torrend 1920
Wolfiporia Ryvarden & Gilb. 1984
= *Pachyma* Fr. 1822
Family Phanerochaetaceae Jülich 1982
= Hapalopilaceae Jülich 1982
= Bjerkanderaceae Jülich 1982
Alboefibula C.C. Chen & Sheng H. Wu 2021
Bjerkandera P. Karst. 1879
= *Geotrichopsis* Tzean & Estey 1991
= *Myriadoporus* Peck 1884
Callosus C.L. Zhao 2022
Cremeoderma Sheng H. Wu & C.C. Chen 2021
Crepatura C.L. Zhao 2019
Donkia Pilát 1937
Efibulella Zmitr. 2018
Gelatinofungus Sheng H. Wu, C.C. Chen & C.L. Wei 2021
Geliporus Yuan Yuan, Jia J. Chen & S.H. He 2017
Hapalopilus P. Karst. 1881
Hyphodermella J. Erikss. & Ryvarden 1976
Odontoefibula C.C. Chen & Sheng H. Wu 2018
Oxychaete Miettinen 2016
Phaeophlebiopsis D. Floudas & Hibbett 2015
Phanerina Miettinen 2016
Phanerochaete P. Karst. 1889
= *Atheliachaete* Spirin & Zmitr. 2011
= *Grandiniella* P. Karst. 1895
= *Hjortstamia* Boidin & Gilles 2003
= *Xerocarpus* P. Karst. 1881
Phlebiopsis Jülich 1978
= *Castanoporus* Ryvarden 1991
Pirex Hjortstam & Ryvarden 1985
Porostereum Pilát 1937
Quasiphlebia C.C. Chen & Sheng H. Wu 2021
Rhizochaete Gresl., Nakasone & Rajchenb. 2004
Riopa D.A. Reid 1969
= *Miainomyces* Corda 1833.
= *Sporotrichum* Link 1809
Roseograndinia Hjortstam & Ryvarden 2005
Terana Adans. 1763
= *Pulcherricium* Parmasto 1968
Family Piptoporellaceae B.K. Cui, Shun Liu & Y.C. Dai 2022
Piptoporellus B.K. Cui, M.L. Han & Y.C. Dai 2016
Family Podoscyphaceae D.A. Reid 1965
Abortiporus Murrill 1904
= *Heteroporus* Lázaro Ibiza 1916
= *Irpicium* Bref. 1912
= *Sporotrichopsis* Stalpers 2000
Podoscypha Pat. 1900
= *Stereogloeocystidium* Rick 1940
Pouzaroporia Vampola 1992
Family Polyporaceae Fr. ex Corda 1839
= Ganodermataceae (Donk) Donk 1948
= Coriolaceae Singer 1961
= Cryptoporaceae Jülich 1982
= Echinochaetaceae Jülich 1982
= Fomitaceae Jülich 1982
= Grammotheleaceae Jülich 1982
= Haddowiaceae Jülich 1982
= Microporaceae Jülich 1981
= Pachykytosporaceae Jülich 1982
= Perenniporiaceae Jülich 1982
= Sparsitubaceae Jülich 1982
= Lophariaceae Boidin et al. 1998
= Trametaceae Boidin et al. 1998
Abundisporus Ryvarden 1999
Amauroderma Murrill 1905
= *Lazulinospora* Burds. & M.J. Larsen 1974
= *Magoderna* Steyaert 1972
Amaurodermellus Costa-Rezende, Drechsler-Santos & Góes-Neto 2020
Amylosporia B.K. Cui, C.L. Zhao & Y.C. Dai 2019
Atroporus Ryvarden 1973
Aurantioporia B.K. Cui & Xing Ji 2023
Australoporus P.K. Buchanan & Ryvarden 1988
Bresadolia Speg. 1883
Cerarioporia F. Wu, L.W. Zhou & J. Si 2016
Cerioporus Quél. 1886
= *Grandinioides* Banker 1906
= *Melanopus* Pat. 1887
= *Mycobonia* Pat. 1894
= *Petaloides* Lloyd ex Torrend 1920
Cinereomycetella Zmitr. 2018
Citrinoporia B.K. Cui & Xing Ji 2023
Colospora Miettinen & Spirin 2015
Coriolopsis Murrill 1905
Crassisporus B.K. Cui & Xing Ji 2019
Cristataspora Robledo & Costa-Rezende 2020
Cryptoporus (Peck) Shear 1902
Cystidioporia B.K. Cui & Xing Ji 2023

Daedaleopsis J. Schröt. 1888
= *Apoxona* Donk 1969
Datroniella B.K. Cui, Hai J. Li & Y.C. Dai 2014
Dendroporia B.K. Cui & Xing Ji 2023
Dentocorticium (Parmasto) M.J. Larsen & Gilb. 1974
= *Dendrodontia* Hjortstam & Ryvarden 1980
= *Fuscocerrena* Ryvarden 1982
Dextrinoporus H.S. Yuan 2018
Dichomitus D.A. Reid 1965
Donkioporia Kotl. & Pouzar 1973
Donkioporiella L.W. Zhou 2016
Earliella Murrill 1905
Echinochaete D.A. Reid 1963
= *Dendrochaete* G. Cunn. 1965
Endopandanicola Tibpromma & K.D. Hyde 2018
Epithele (Pat.) Pat. 1900
Epithelopsis Jülich 1976
Favolus Fr. 1828
Flammeopellis Y.C. Dai, B.K. Cui & C.L. Zhao 2014
Fomes (Fr.) Fr. 1849
= *Elfvingiella* Murrill 1914
= *Xylopilus* P. Karst. 1882
Fomitella Murrill 1905
Foraminispora Robledo, Costa-Rezende & Drechsler-Santos 2017
Funalia Pat. 1900
Furtadoa Costa-Rezende, Robledo & Drechsler-Santos 2017
Furtadomyces Leonardo-Silva, Cotrim & Xavier-Santos 2022
Ganoderma P. Karst. 1881
= *Elfvingia* P. Karst. 1889
Globifomes Murrill 1904
= *Placodes* Quél. 1886
= *Ungulina* Pat. 1900
Grammothele Berk. & M.A. Curtis 1868
Grammothelopsis Jülich 1982
Haddowia Steyaert 1972
Haploporus Bondartsev & Singer 1944
Hexagonia Fr. 1835
Hirticrusta Matozaki, T. Hatt. & Sotome 2020
Hornodermoporus Teixeira 1993
Humphreya Steyaert 1972
Jorgewrightia Gibertoni & C.R.S. Lira 2021
Laccocephalum McAlpine & Tepper 1895
Leifiporia Y.C. Dai, F. Wu & C.L. Zhao 2016
Lentinus Fr. 1825
= *Lentodiellum* Murrill 1915
= *Lentodium* Morgan 1895
= *Leucoporus* Quél. 1886
= *Polyporellus* P. Karst. 1879
Lignosus Lloyd ex Torrend 1920
Lopharia Kalchbr. & MacOwan 1881
= *Licentia* Pilát 1940
= *Lloydella* Bres. 1901
= *Thwaitesiella* Massee 1892
Luteoperenniporia B.K. Cui & Xing Ji 2023
Macroporia B.K. Cui & Xing Ji 2023
Macrosporia B.K. Cui & Xing Ji 2023
Mariorajchenbergia Gibertoni & C.R.S. Lira 2021
= *Megasporoporiella* B.K. Cui, Y.C. Dai & Hai J. Li 2013
Megasporia B.K. Cui, Y.C. Dai & Hai J. Li 2013
Megasporoporia Ryvarden & J.E. Wright 1982
Melanoderma B.K. Cui & Y.C. Dai 2011
Microporellus Murrill 1905
= *Cystostiptoporus* Dhanda & Ryvarden 1975
Microporus P. Beauv. 1805
Minoporus B.K. Cui & Xing Ji 2023
Mollicarpus Ginns 1984
Murinicarpus B.K. Cui & Y.C. Dai 2019
Myriothele Nakasone 2013
Navisporus Ryvarden 1980
Neoganoderma B.K. Cui & Y.F. Sun 2022
Neodatronia B.K. Cui, Hai J. Li & Y.C. Dai 2014
Neodictyopus Palacio, Robledo, Reck & Drechsler-Santos 2017
Neofavolus Sotome & T. Hatt. 2013
Neofomitella Y.C. Dai, Hai J. Li & Vlasák 2014
Neoporia B.K. Cui & Xing Ji 2023
Niveoporia B.K. Cui & Xing Ji 2023
Pachykytospora Kotl. & Pouzar 1963
Perenniporia Murrill 1942
= *Dextrinosporium* Bondartsev 1972
= *Loweporus* J.E. Wright 1976
= *Physisporus* Chevall. 1826
= *Poroptyche* Beck 1888
Perenniporiella Decock & Ryvarden 2003
Perenniporiopsis C.L. Zhao 2017
Phaeotrametes Lloyd ex J.E. Wright 1966
= *Phaeotrametes* Lloyd 1915
Picipes Zmitr. & Kovalenko 2016
Podofomes Pouzar 1966
= *Datronia* Donk 1966
Polyporopsis Audet 2010
Polyporus [P. Micheli ex Adans.] Fr. 1821
= *Cladomeris* Quél. 1886
= *Dendropolyporus* (Pouzar) Jülich 1982
= *Mycelithe* Gasp. 1841
Poriella C.L. Zhao 2021
Porogramme (Pat.) Pat. 1900
= *Tinctoporia* Murrill 1907
Poronidulus Murrill 1904
Pseudofavolus Pat. 1900
Pseudomegasporoporia X.H. Ji & F. Wu 2017
Pseudopiptoporus Ryvarden 1980

Pyrofomes Kotl. & Pouzar 1964
Rhizoperenniporia B.K. Cui & Xing Ji 2023
Royoporus A.B. De 1996
Rubroporus Log.-Leite, Ryvarden & Groposo 2002
Sanguinoderma Y.F. Sun, D.H. Costa & B.K. Cui 2020
Sinoganoderma B.K. Cui, J.H. Xing & Y.F. Sun 2022
Sparsitubus L.W. Hsu & J.D. Zhao 1980
Szczepkamyces Zmitr. 2018
Theleporus Fr. 1847
Tinctoporellus Ryvarden 1979
Tomophagus Murrill 1905
= *Thermophymatospora* Udagawa, Awao & Abdullah 1986
Trachydermella B.K. Cui & Y.F. Sun 2022
Trametes Fr. 1836
= *Artolenzites* Falck 1909
= *Cellularia* Bull. 1788
= *Cellulariella* Zmitr. & Malysheva 2014
= *Coriolus* Quél. 1886
= *Cubamyces* Murrill 1905
= *Leiotrametes* Welti & Courtec. 2012
= *Lenzites* Fr. 1836
= *Pherima* Raf. 1819
= *Pilatotrama* Zmitr. 2018
= *Pogonomyces* Murrill 1904
= *Pseudotrametes* Bondartsev & Singer 1944
= *Pycnoporus* P. Karst. 1881
= *Sclerodepsis* Cooke 1890
= *Tomentoporus* Ryvarden 1973
= *Trametella* Pinto-Lopes 1952
Tropicoporia B.K. Cui & Xing Ji 2023
Truncospora Pilát 1953
Truncatoporia B.K. Cui & Xing Ji 2023
Vanderbylia D.A. Reid 1973
Vanderbyliella B.K. Cui & Xing Ji 2023
Xanthoperenniporia B.K. Cui & Xing Ji 2023
Yuchengia B.K. Cui & K.T. Steffen 2013
Family Postiaceae B.K. Cui, Shun Liu & Y.C. Dai 2022
Amaropostia B.K. Cui, L.L. Shen & Y.C. Dai 2019
Amylocystis Bondartsev & Singer ex Singer 1944
Aurantipostia B.K. Cui & Shun Liu 2022
Calcipostia B.K. Cui, L.L. Shen & Y.C. Dai 2019
Cyanosporus McGinty 1909
Cystidiopostia B.K. Cui, L.L. Shen & Y.C. Dai 2019
Fuscopostia B.K. Cui, L.L. Shen & Y.C. Dai 2019
Jahnoporus Nuss 1980
Nothofagiporus B.K. Cui & Shun Liu 2022
Oligoporus Bref. 1888
= *Strangulidium* Pouzar 1967
Osteina Donk 1966
Postia Fr. 1874
= *Hemidiscia* Lázaro Ibiza 1916
= *Podoporia* P. Karst. 1892
Ptychogaster Corda 1838
Spongiporus Murrill 1905
Tenuipostia B.K. Cui & Shun Liu 2022
Family Pycnoporellaceae Audet 2018
Crustoderma Parmasto 1968
Pycnoporellus Murrill 1905
= *Aurantiporellus* Murrill 1905
Family Sarcoporiaceae Audet 2018
Sarcoporia P. Karst. 1894
Family Sparassidaceae Herter 1910
Sparassis Fr. 1819
= *Masseeola* Kuntze 1891
Family Steccherinaceae Parmasto 1968
= Mycorraphiacaceae Jülich 1982
Antella Miettinen 2016
Antrodiella Ryvarden & I. Johans. 1980
Atraporiella Ryvarden 2007
Austeria Miettinen 2016
Butyrea Miettinen 2016
Cabalodontia Piątek 2004
Caudicicola Miettinen, M. Kulju & Kotir. 2017
Citripora Miettinen 2016
Elaphroporia Z.Q. Wu & C.L. Zhao 2018
Etheirodon Banker 1902
Flabellophora G. Cunn. 1965
Flaviporus Murrill 1905
= *Baeostratoporus* Bondartsev & Singer 1944
Frantisekia Spirin & Zmitr. 2007
Junghuhnia Corda 1842
= *Chaetoporus* P. Karst. 1890
Lamelloporus Ryvarden 1987
Loweomyces (Kotl. & Pouzar) Jülich 1982
Metuloidea G. Cunn. 1965
Mycorrhaphium Maas Geest. 1962
Niemelaea Zmitr., Ezhov & Khimich 2015
Nigroporus Murrill 1905
Rhomboidia C.L. Zhao 2020
Steccherinum Gray 1821
= *Odontina* Pat. 1887
Trullella Zmitr. 2018
Xanthoporus Audet 2010
Family Taiwanofungaceae B.K. Cui, Shun Liu & Y.C. Dai 2022
Taiwanofungus Sheng H. Wu, Z.H. Yu, Y.C. Dai & C.H. Su 2004
Polyporales genera *incertae sedis*
Aegeritopsis Höhn. 1903
Amaurohydnum Jülich 1978
Amauromyces Jülich 1978
Amethicium Hjortstam 1983
Aquascypha D.A. Reid 1965
Australicium Hjortstam & Ryvarden 2002
Australohydnum Jülich 1978

Austrolentinus Ryvarden 1991
Aegerita Pers. 1794
= *Bulbillomyces* Jülich 1974
= *Crocysporium* Corda 1837
= *Dermosporium* Link 1816
Bourdotiella Duhem & Schultheis 2011
Columnodontia Jülich 1979
Conohypha Jülich 1975
Coralloderma D.A. Reid 1965
Cordochaete Sanyal, Samita, Dhingra & Avn.P. Singh 2013
Cryptomphalina R. Heim 1966
Crystallocystidium (Rick) Rick 1940
Cyanodontia Hjortstam 1987
Dendrophlebia Dhingra & Priyanka 2011
Diacanthodes Singer 1945
= *Bornetina* L. Mangin & Viala 1903
Erastia Niemelä & Kinnunen 2005
Faerberia Pouzar 1981
= *Geopetalum* Pat. 1887
Globosomyces Jülich 1980
Gyrophanopsis Jülich 1979
= *Hyphodermopsis* Jülich 1982
Henningsia Möller 1895
Hymenogramme Mont. & Berk. 1844
Hyphodontiastra Hjortstam 1999
Hypochnicium J. Erikss. 1958
= *Nodotia* Hjortstam 1987
Inflatostereum D.A. Reid 1965
Irpicochaete Rick 1940
Laetifomes T. Hatt. 2001
Meruliophana Duhem & Buyck 2011
Mycoleptodonoides Nikol. 1952
Mycorrhaphoides Hembrom, K. Das & Hallenb. 2017
Nigrohydnum Ryvarden 1987
Phanerodontia Hjortstam & Ryvarden 2010
Phaneroites Hjortstam & Ryvarden 2010
Repetobasidiopsis Dhingra & Avn.P. Singh 2008
Rickiopora Westphalen, Tomšovský & Rajchenb. 2016
Roseofavolus T. Hatt. 2003
Skeletohydnum Jülich 1979
Sparassiella Schwarzman 1964
Spathulina Pat. 1900
Spongioides Lázaro Ibiza 1916
Spongipellis Pat. 1887
Stegiacantha Maas Geest. 1966
Uncobasidium Hjortstam & Ryvarden 1978

Evolution

Studies on the evolution of Polyporales have focused mostly on: (i) taxonomy, including the limits and composition of the order and translation of the phylogenies into a formal taxonomic framework of families and genera (Binder and Hibbett 2002; Binder et al. 2005, 2013; Justo et al. 2017; Liu et al. 2023a); (ii) morphological evolution, especially transitions between basidiome types, hymenophore types and evaluating the taxonomic significance of morphological features (e.g. Binder et al. 2005; Justo and Hibbett 2011; Floudas and Hibbett 2015; Costa-Rezende et al. 2020; Robledo et al. 2020) (iii) evolution of the wood-decay enzymatic apparatus from a phylogenomics perspective, especially origins, transitions and differences between white-rot and brown-rot fungi in the order.

As phylogenomic data has accumulated, support for the Polyporales as a monophyletic, well-supported clade has increased. In the analysis presented here (Fig. 2) 73 indidual genomes of Polyporales are recovered with full support (100% bootstrap) as monophletic group. Our analyses also recover a well-supported sister-taxa relationship between Polyporales (exclusively saprotrophic or parasitic) and Thelephorales (predominantly ectomycorrhizal).

Justification of order and problems

Notwithstanding the extensive phylogenetic research conducted on the classification of Polyporales (e.g., Binder et al. 2013; Justo et al. 2017; Liu et al. 2023a), unresolved issues persist concerning the systematic placement of certain families and taxa. Currently, one of the most pressing issues concerns the delineation of the Polyporaceae, which represents the largest family within the order. While recent studies generally adopt the broad Polyporaceae concept proposed by Binder et al. (2013) and Justo et al. (2017), ganodermatoid species are often excluded from this monophyletic clade and recognized as in a separate family, Ganodermataceae. Therefore, the classification of Ganodermataceae remains a controversial issue and is debated even today. The traditional morphological delimitation of the ganodermatoid taxa in subgeneric (Patouillard 1889), generic (Steyaert 1972), and higher levels (Donk 1933, 1948; Jülich 1981) was based upon the characteristics of the basidiospore. This approach continues to play a significant role in the systematical concepts of recent phylogenetic studies (e.g., Costa-Rezende et al. 2017, 2020; Sun et al. 2020, 2022).

While the double-walled basidiospores with ornamented endospores are a defining characteristic of ganodermatoid species, the utility of this morphological feature for taxonomic delineation at family level remains a topic of debate. While recent taxonomic and systematic studies have provided evidence for the monophyly of ganodermatoid clade (e.g., Costa-Rezende et al. 2020; Luangharn et al. 2021), the joint examination of the phylogenetically closest taxa in Polyporaceae remains unexplored (Ji et al. 2023). For instance, the taxonomic classifications proposed by Binder et al. (2013) and Justo et al. (2017) considered Polyporaceae as the core polyporoid clade was also followed by Cui et al. (2019) with one exception. Cui et al. (2019) excluded ganodermatoid taxa from Polyporaceae due to discrepancies in basidiospore characteristics, and thus did not include this group in their phylogenetic analysis. However, in accord to several former multi-gene phylogenetic analysis (e.g. Justo et al. 2017; Costa-Rezende et al. 2020) our phylogenomic tree (Figs. 1, 2) have demonstrated that the exclusion of Ganodermataceae from the core polyporoid clade results in paraphyletic Polyporaceae family. If Polyporaceae is split into smaller families, currently the systematic position of several non-ganodermatoid genera (e.g. *Cryptoporus*, *Dichomitus*, *Perenniporia* s. lato, etc.) will remain unclear. Therefore, in the present work Ganodermataceae is not accepted as an independent family, and the suggested 14 ganodermatoid genera (vid. *Amauroderma*, *Amaurodermellus*, *Cristataspora*, *Foraminispora*, *Furtadomyces*, *Ganoderma*, *Haddowia*, *Humphreya*, *Magoderna*, *Neoganoderma*, *Sanguinoderma*, *Sinoganoderma*, *Tomophagus*, *Trachydermella*) are discussed in Polyporaceae, until it will have not been split into smaller families (e.g. Ganodermataceae, Grammotheleaceae, Coriolaceae, etc.). However, creating many narrowly defined families within Polyporaceae would cause a domino effect and increase the number of problematic taxonomic scenarios. If taxonomists want to distinguish a monophyletic group within Polyporaceae s. lato, it would be worth considering describing these groups below the family level to avoid ambiguous taxonomic cases.

Significance

Species of Polyporales are mainly saprobes on dead wood, but many are parasites, especially in economically important tree species (Alexopoulos et al. 1996; Deacon 2006). They are considered the major wood decomposers, especially species of Polyporaceae, thus, playing a crucial role in nutrient cycling, releasing among other things carbon originally removed from the atmosphere by autotrophic organisms in arboreous and shrubby ecosystems (Ryvarden 1991; Alexopoulos et al. 1996; Deacon 2006). The saprotrophic species are generally divided in two major groups, those which cause white rot and those causing brown (cubical) rot. Species in the first group are the majority and are the only organisms known to be able to degrade lignin, a complex polymer present in the plant cell wall, by strong oxidants produced by few enzymes (lignin and manganese peroxidase, H_2O_2-generating enzymes, and laccase) in well oxygenised environments. They also remove cellulose and hemicelluloses from wood, leaving the substrate with a whitish and spongy aspect. The brown-rot fungi are able only to degrade cellulose and hemicelluloses, reducing the substrate to a brownish residuum of lignin. Since the decay of the lignin is irregular, being stronger in some cell groups, the wood cracks in cubic pieces. The cellulose and hemicelluse decay are also due to oxidative processes, involving the production of hydrogen peroxide (H_2O_2) possibly using the hemicellulose as substrate (Ryvarden 1991; Deacon 2006).

Some species of some genera [e.g., *Fomes* (Fr.) Fr., *Fomitopsis* P. Karst., *Ganoderma* P. Karst., *Laetiporus* Murrill, *Meripilus* P. Karst., *Phaeolus* (Pat.) Pat.] (Schmidt 2006; Jayawardena et al 2020) are able to penetrate lesions or similar openings caused by animal chewing, branch breaks, broken tops, lighting, mechanized wood harvest, etc. in living trees, then attack the heartwood and, in the end, causing tree weakening or death (Alexopoulos et al. 1996; Schmidt 2006). On the other hand, arthropods commonly use the basidiomes of several species as food and as reproduction sites (Lunde et al. 2022).

Many Polyporales species can be used as indicators of changes in biodiversity or ecosystem quality, mostly due to their close association with trees, including climate change (eg. Norstedt et al. 2001; Andrew et al. 2019; Runnel et al. 2021).

Some species of Polyporales are edible, such as *Grifola frondosa* (Dicks.) Gray, *Sparassis latifolia* Y.C. Dai & Zheng Wang and *Laetiporus* spp. (Boa 2004; Dai et al. 2010; Wei et al. 2022; He et al. 2023b), while others are known to have medicinal values, such as *Bjerkandera adusta* (Willd.) P. Karst., *B. fumosa* (Pers.) P. Karst., *Climacodon septentrionalis* (Fr.) P. Karst., *Ganoderma lingzhi* Sheng H. Wu, Y. Cao & Y.C. Dai, *Irpex hydnoides* Y.W. Lim & H.S. Jung, *Perenniporia robiniophila* (Murrill) Ryvarden, *Phlebia tremellosa* (Schrad.) Nakasone & Burds. and *Wolfiporia hoelen* (Fr.) Y.C. Dai & V. Papp (Dai et al. 2009; Wu et al. 2019b; Quintero-Cabello et al.

2021; Li and Dong 2022; Shankar and Sharma 2022; Zhang et al. 2023a). Some are already commercialized for medicinal purposes [eg. *Trametes versicolor* (L.) Lloyd, *Ganoderma lingzhi*]. Clinically, a few species in Polyporales have recently emerged as important human pathogens, including *B. adusta*, *I. laceratus*, and *I. lacteus* (Chowdhary et al. 2014).

Others have potential industrial applications for biodegradation and bioconversion, due to their efficient enzymatic system, such as *Bjerkandera adusta*, *Irpex laceratus*, *I. lacteus*, and *Phanerochaete chrysosporium* Burds. (Kumar et al. 2009; Kumar and Sharma 2017; Sandargo et al. 2019; Xiao and Kondo 2019). In agriculture and forestry, most species of the order Polyporales, such as *Phlebiopsis gigantean* (Fr.) Jülich, has been utilized as a biological control agent against conifer root and butt rot caused by *Heterobasidion* spp. (Pratt et al. 2000), and *Irpex latemarginatus* has been reported to produce volatile compounds that control fruit decay (Lee et al. 2009). More recently, some species are being tested in the development of biomaterials, several of them based in traditional use of these fungi (Gandia et al. 2021).

Pucciniales Caruel 1881

Contributed by: Makoto Kakishima, Merje Toome-Heller

Introduction

Rust fungi (Pucciniales) are one of the largest orders of fungi, with about 8000 described species. They are obligate parasites of vascular plants and have been reported worldwide. Each species is known to be parasitic on taxonomically narrow groups of plants (host specificity), which is the result of the co-evolution between rust fungi and their host plants. Many species cause serious plant diseases in agriculture and forestry. Therefore, their biology, life cycle, host-parasite interaction and epidemiology have been investigated intensively. They have unique characteristics and produce five types of morphologically and functionally different spores (spermatium, aeciospore, urediniospore, teliospore, basidiospore). Thick-walled urediniospore called amphispore is also produced in many species for wintering. Depending on the types of spores produced, six different rust fungi life cycles have been recognized. Furthermore, heteroecious species need two taxonomically different host plants to complete their life cycles, whereas autoecious species complete their life cycles on a single host plant (Cummins and Hiratsuka 2003; Aime et al. 2017; Aime and McTaggart 2021).

History

After scientific descriptions of rust fungi by P. A Micheli and C. H. Persoon in the eighteenth century, many species were found and included in the regional floras around the world. In these publications, two familiess (Melampsoraceae and Pucciniaceae) were widely accepted, mainly based on the morphological characteristics of the telial stage. Additional families, Zhagouaniaceae, Pucciniastraceae, Cronartiaceae, Chrysomyxaceae and Coleosporiaceae were later proposed (Cummins and Hiratsuka 2003; Aime et al. 2017). For these families, more than 300 genera were proposed mainly based on sorus structures and spore morphology. When Cummins and Hiratsuka (2003) revised families of rust fungi, their emphasis was on spermogonial structures, resulting in proposing 13 families.

After applying molecular phylogenetic approach to rust fungi systematics, many new genera and changes to existing genera have been proposed. Aime and McTaggart (2021) proposed seven new suborders and 18 family system mainly based on phylogenetic analyses. Zhao et al. (2021) also proposed an additional 3 families. These new family systems are different from the systems based on morphology, whereas still partially supported by morphological characters.

Characters that define the taxa in the order

The new family level classification of rust fungi is based on phylogeny, with consideration of morphology, host plant, and life cycle. At the genus level, qualitative morphological differences in spore stages (structure of spermogonia, aecia, uredinia and telia) and mode of teliospore germination (basidial structure) are used as significant criteria for genus delimitation (Cummins and Hiratsuka 2003), supported by phylogenetic data. For species level identification, quantitative morphological data of spores, host plants, and life cycle are mainly used, with phylogenetic data becoming essential for identification.

Plates

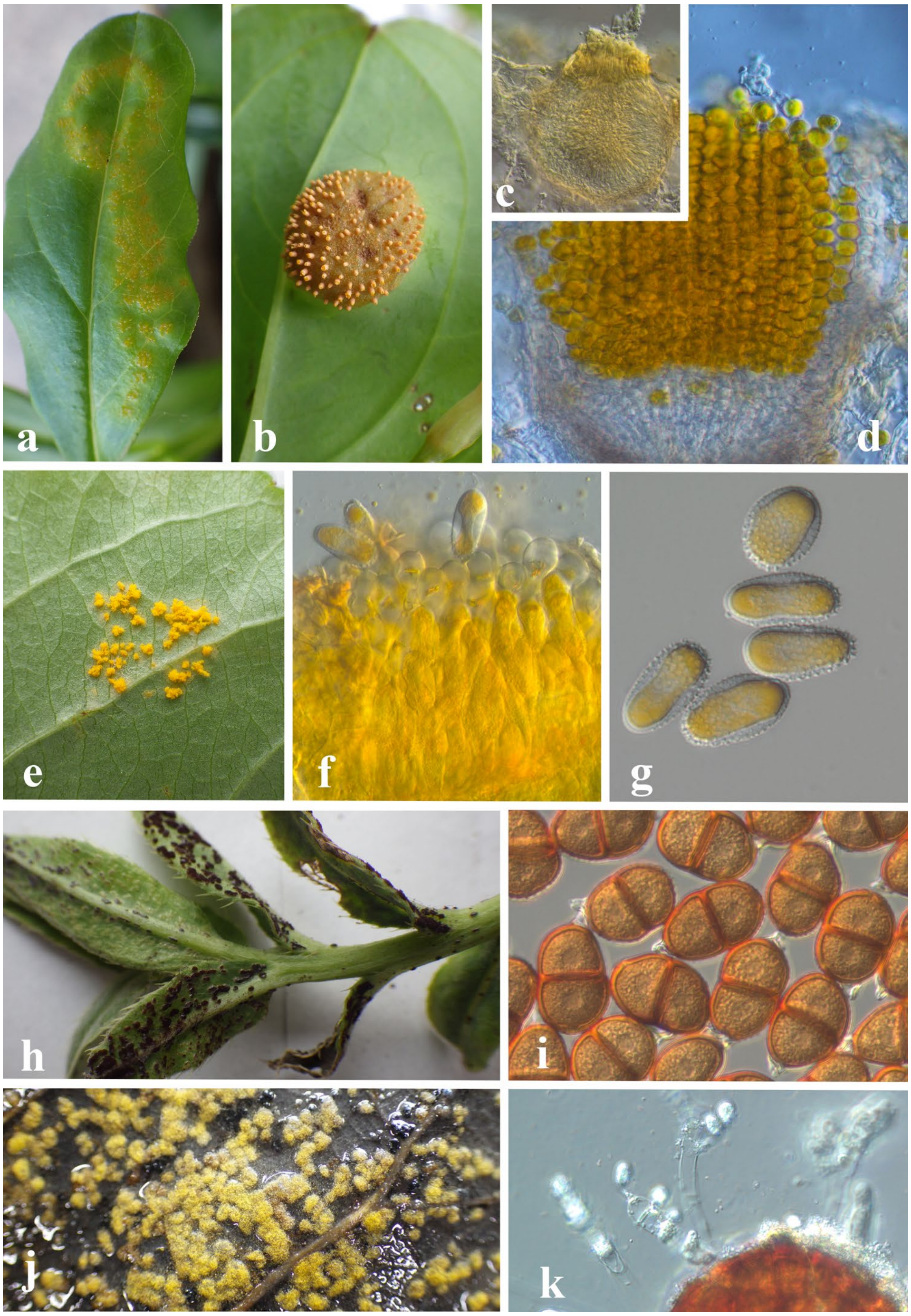


Fig. 48 Morphological characters of Pucciniales. **a** spermogonia of *Puccinia klugkistiana* on *Ligustrum obtusifolium*; **b** aecia of *Puccinia caricis-smilacis* on *Smilax china*; **c** vertical section of a spermogonium of *Puccinia caricis-smilacis* on *Smilax china*; **d** vertical section of an aecium of *Puccinia caricis-smilacis* on *Smilax china*; **e** uredinia of *Melampsora laricis-populina* on *Populus x canadensis*; **f** vertical section of uredinium of *Melampsora laricis-populina* on *Populus x canadensis*; **g** urediniospores of *Melampsora laricis-populina*; **h** telia of *Puccinia punctiformis* on *Cirsium arvense*; **i** teliospores of *Puccinia punctiformis*; **j** germination of teliospores of *Melampsora laricis* on a dead leaf of *Populus alba*; **k** germination of teliospores of *Nothoravenelia japonica* (basidia and basidiospores)

Genera included

Family Araucariomycetaceae Aime & McTaggart 2020
  Araucariomyces Aime & McTaggart 2020
Family Coleosporiaceae Dietel 1900
  Aculeastrum M. Scholler, U. Braun & Bubner 2022
  Ceropsora B.K. Bakshi & Suj. Singh 1960
  Chrysomyxa Unger 1840
  = *Barclayella* Dietel 1890
  = *Coleosporium* subgen. *Melampsoropsis* J. Schröt. 1879
  = *Hiratsukaia* Hara 1948
  = *Melampsoropsis* (J. Schröt.) Sacc. 1888
  = *Melampsoropsis* (J. Schröt.) Arthur 1906
  = *Stilbechrysomyxa* M.M. Chen 1984
  Coleosporium Lév. 1847
  = *Erannium* Bonord. 1860
  = *Stichopsora* Dietel 1899 [1900]
  = *Synomyces* Arthur 1924
  Cronartium Fr. 1815
  = *Endocronartium* Y. Hirats. 1969

Diaphanopellis P.E. Crane 2005
Gallowaya Arthur 1906
Rossmanomyces Aime & McTaggart 2020
Thekopsora Magnus 1875
Quasipucciniastrum X.H. Qi, P. Zhao & L. Cai 2019
Family Crossopsoraceae Aime & McTaggart 2020
Angiopsora Mains 1934
Catenulopsora Mundk. 1943
Crossopsora Syd. & P. Syd. 1919
Kweilingia Teng 1940
= *Dasturella* Mundk. & Khesw. 1943
Neoolivea Aime & McTaggart 2020
Stomatisora J.M. Yen 1971
Family Endoraeciaceae P. Zhao & L. Cai 2021
Endoraecium Hodges & D.E. Gardner 1984
= *Racospermyces* J. Walker 2001
Family Gymnosporangiaceae Chevall. 1826
Gymnosporangium R. Hedw. ex DC. 1805
= *Ceratitium* Rabenh. 1851
= *Ceratitium* Ces. 1879
= *Ciglides* Chevall. 1826
= *Podisoma* Link 1809
Gymnotelium Syd. 1921
Peridiopsora Kamat & Sathe 1969
Family Melampsoraceae Dietel 1897
Ceropsora B.K. Bakshi & Suj. Singh 1960
Melampsora Castagne 1843
= *Chnoopsora* Dietel 1906
= *Mesopsora* Dietel 1922
= *Necium* Arthur 1907
= *Podocystis* Fr. 1849
= *Podosporium* Lév. 1847
Family Milesinaceae Aime & McTaggart 2020
Milesia F.B. White 1878
Milesina Magnus 1909
Naohidemyces S. Sato, Katsuya & Y. Hirats. 1993
Uredinopsis Magnus 1893
Family Ochropsoraceae Aime & McTaggart 2020
Aplopsora Mains 1921
Ceraceopsora Kakish., T. Sato & S. Sato 1984
Ochropsora Dietel 1895
Family Phakopsoraceae Cummins & Hirats. f. 1983
Arthuria H.S. Jacks. 1931
Bubakia Arthur 1906
Cerotelium Arthur 1906
= *Catenulopsora* Mundk. 1943
= *Tunicopsora* Suj. Singh & P.C. Pandey 1971
Dicheirinia Arthur 1907
Monosporidium Barclay 1888
= *Kulkarniella* Gokhale & Patel 1952 [1951]
Masseeëlla Dietel 1895
Nothoravenelia Dietel 1910
Phakopsora Dietel 1895
= *Angiopsora* Mains 1934
= *Batistopsora* Dianese, R.B. Medeiros & L.T.P. Santos 1993
= *Malupa* Y. Ono, Buriticá & J.F. Hennen 1992
= *Physopella* Arthur 1906
= *Stakmania* Kamat & Sathe 1968
= *Uredostilbe* Buriticá & J.F. Hennen 1994
= *Uredendo* Buriticá & J.F. Hennen 1994 [nom. inval.]
Phragmidiella Henn. 1905
= *Santapauella* Mundk. & Thirum. 1945
Pucciniostele Tranzschel & K.L. Kom. 1899
= *Klastopsora* Dietel 1904
= *Phragmostele* Clem. 1909
Scalarispora Buriticá & J.F. Hennen 1994
Uredopeltis Henn. 1908
Family Neophysopellaceae P. Zhao & L. Cai 2021
Neophysopella Jing X. Ji & Kakish. 2019
Family Nyssopsoraceae Sanjay & Raghv. Singh 2023
Nyssopsora Arthur 1906
= *Oplophora* Syd. 1921
Family Phragmidiaceae Corda 1837
Gerwasia Racib. 1909
= *Mainsia* H.S. Jacks. 1931
Gymnoconia Lagerh. 1894
= *Kunkelia* Arthur 1917
Hamaspora Körn. 1877
= *Hamasporella* Höhn. 1912
Joerstadia Gjaerum & Cummins 1982
Kuehneola Magnus 1898
= *Spirechina* Arthur 1907
Phragmidium Link 1816
= *Ameris* Arthur 1906
= *Aregma* Fr. 1815
= *Earlea* Arthur 1906
= *Epitea* Fr. 1832
= *Frommea* Arthur 1917
= *Frommeëlla* Cummins & Y. Hirats. 1983
= *Lecythea* Lév. 1847
= *Phragmidium* A *Phragmidiopsis* G. Winter 1881 [1884]
= *Phragmidiopsis* (G. Winter) Mussat 1901
= *Teloconia* Syd. 1921
= *Trolliomyces* Ulbr. 1938
Trachyspora Fuckel 1861
= *Trachysporella* Syd. 1921
Triphragmium Link 1825
Xenodochus Schltdl. 1826
Family Pileolariaceae Cummins & Y. Hirats. 1983
Pileolaria Castagne 1842
= *Discospora* Arthur 1907
Family Pucciniaceae Chevall. 1826
Baeodromus Arthur 1905

Ceratocoma Buriticá & J.F. Hennen 1991
Cerradoa J.F. Hennen & Y. Ono 1978
Chardoniella F. Kern 1939
Chrysella Syd. 1926
Chrysocelis Lagerh. & Dietel 1914
= *Stomatisora* J.M. Yen 1971
Chrysocyclus Syd. 1925
= *Holwayella* H.S. Jacks. 1926
Chrysopsora Lagerh. 1892
Cionothrix Arthur 1907
Cleptomyces Arthur 1918
Coleopucciniella Hara ex Hirats. 1937
= *Coleopucciniella* Hara 1936
Corbulopsora Cummins 1940
Cumminsiella Arthur 1933
Desmella Syd. & P. Syd. 1919 [1918]
Didymopsora Dietel 1899
Dietelia Henn. 1897
= *Endophylloides* Whetzel & Olive 1917
= *Jacksonia* J.C. Lindq. 1970
= *Jacksoniella* J.C. Lindq. 1972
= *Jacksoniella* Kamat & Sathe 1972
= *Thirumalachariella* Sathe 1975 [1974]
Dipyxis Cummins & J.W. Baxter 1967
Edythea H.S. Jacks. 1931
Endophyllum Lév. 1826
Hapalophragmium Syd. & P. Syd. 1901
= *Hapalophragmiopsis* Thirum. 1950
= *Triactella* Syd. 1921
Kernella Thirum. 1949
= *Kernia* Thirum. 1946
Macruropyxis Azbukina 1972
Miyagia Miyabe ex Syd. & P. Syd. 1913
= *Peristemma* Syd. 1921
Novopuccinia Y.M. Liang & Yun Liu 2021
Polioma Arthur 1907
Pseudocerradoa M. Ebinghaus & Dianese 2022
Puccinia Pers. 1794
= *Argomyces* Arthur 1912
= *Argotelium* Arthur 1906
= *Bullaria* DC. 1805
= *Coronotelium* Syd. 1921
= *Cutomyces* Thüm. 1878
= *Dicaeoma* Gray 1821
= *Eriosporangium* Bertero ex Ruschenb. 1831
= *Hemipuccinia* Sacc. & De Toni 1889
= *Jackya* Bubák 1902
= *Leptinia* Juel 1897
= *Leptopuccinia* (G. Winter) Rostr. 1902
= *Lindrothia* Syd. 1922
= *Linkiella* Syd. 1921
= *Lysospora* Arthur 1906
= *Micropuccinia* Rostr. 1902
= *Persooniella* Syd. 1922
= *Pleomeris* Syd. 1921
= *Poliomella* Syd. 1922
= *Puccinia* subgen. *Leptopuccinia* G. Winter 1881 [1884]
= *Puccinidia* Mayr 1890
= *Rostrupia* Lagerh. 1889
= *Schroeterella* Syd. 1922
= *Sclerotelium* Syd. 1921
= *Solenodonta* Castagne 1845
= *Trailia* Syd. 1922
Pucciniosira Lagerh. 1892
= *Aecidiella* Ellis & Kelsey 1897
= *Didymosira* Clem. 1909
= *Schizospora* Dietel 1895
Sphenospora Dietel 1892
Stereostratum Magnus 1899
Trichopsora Lagerh. 1892
Uromyces (Link) Unger 1833
= *Alveomyces* Bubák 1914
= *Capitularia* Rabenh. 1851
= *Coeomurus* Gray 1821
= *Dichlamys* Syd. & P. Syd. 1920 [1919]
= *Groveola* Syd. 1921
= *Haplopyxis* Syd. & P. Syd. 1920 [1919]
= *Haplotelium* Syd. 1922
= *Hypodermium* subgen. *Uromyces* Link 1816 [1815]
= *Klebahnia* Arthur 1906
= *Nielsenia* Syd. 1921
= *Ontotelium* Syd. 1921
= *Poliotelium* Syd. 1922
= *Puccinella* Fuckel 1860
= *Pucciniola* L. Marchand 1829
= *Teleutospora* Arthur & Bisby 1921
= *Telospora* Arthur 1906
= *Trochodium* Syd. & P. Syd. 1920 [1919]
= *Uromycopsis* Arthur 1906
Xenostele Syd. & P. Syd. 1921
Family Pucciniastraceae Gäum. ex Leppik 1972
Coleopuccinia Pat. 1889
= *Coleoma* Clem. 1909
Hyalopsora Magnus 1902
Melampsorella J. Schröt. 1874
Melampsoridium Kleb. 1899
Pucciniastrum G.H. Otth 1861
= *Calyptospora* J.G. Kühn 1869
= *Phragmopsora* Magnus 1875
= *Pomatomyces* Oerst. 1864
Family Raveneliaceae Leppik 1972
Allotelium Syd. 1939
Anthomyces Dietel 1899
Anthomycetella Syd. & P. Syd. 1916
= *Reyesiella* Sacc. 1917

Apra J.F. Hennen & F.O. Freire 1979
Atelocauda Arthur & Cummins 1933
Bibulocystis J. Walker, Beilharz, Pascoe & Priest 2006
Cephalotelium Syd. 1921
Chaconia Juel 1897
= *Bitzea* Mains 1939
= *Desmotelium* Syd. 1937
Crossopsorella E.S.C. Souza, Aime, Galvão-Elias & Dianese 2018
Cystomyces Syd. 1926
Diabole Arthur 1922
Diorchidiella J.C. Lindq. 1957
Diorchidium Kalchbr. 1882.
= *Diphragmium* Boedijn (1960) [1959]
Esalque J.F. Hennen, Figueiredo & A.A. Carvalho 2000
Hennenia Buriticá 1995
Kernkampella Rajendren 1970
Lipocystis Cummins 1937
Maravalia Arthur 1922
= *Acervulopsora* Thirum. 1945
= *Angusia* G.F. Laundon 1964
= *Argomycetella* Syd. 1922
= *Scopella* Mains 1939
= *Scopellopsis* T.S. Ramakr. & K. Ramakr. 1947
Mimema H.S. Jacks. 1931
Newinia Thaung 1973
Olivea Arthur 1917
= *Tegillum* Mains 1940
Phragmopyxis Dietel 1897
= *Tricella* Long 1912
Porotenus Viégas 1960
Prospodium Arthur 1907
= *Coinostelium* Syd. 1939
= *Nephlyctis* Arthur 1907
Ravenelia Berk. 1853
= *Cystingophora* Arthur 1907
= *Cystotelium* Syd. 1921
= *Dendroecia* Arthur 1906
= *Haploravenelia* Syd. 1921
= *Longia* Syd. 1921
= *Neoravenelia* Long 1903
= *Pleoravenelia* Long 1903
Sorataea Syd. 1930
= *Allopuccinia* H.S. Jacks. 1931
Spumula Mains 1935
Tegillum Mains 1940
Triphragmiopsis Naumov 1914
= *Nyssopsorella* Syd. 1921
Uromycladium McAlpine 1905
= *Macalpinia* Arthur 1906
Uropyxis J. Schröt. 1875
= *Calliospora* Arthur 1905
Ypsilospora Cummins 1941

Family Rogerpetersoniaceae Aime & McTaggart 2020
Rogerpetersonia Aime & McTaggart 2020
Family Skierkaceae Aime & McTaggart 2020
Skierka Racib. 1900
= *Ctenoderma* Syd. & P. Syd. 1919
Family Sphaerophragmiaceae Cummins & Y. Hirats. 1983
Austropuccinia Beenken 2017
Dasyspora Berk. & M.A. Curtis 1854
= *Sartvellia* Berk. 1857
Puccorchidium Beenken 2015
Sphaerophragmium Magnus 1891
Sphenorchidium Beeken 2015
Family Tranzscheliaceae Aime & McTaggart 2020
Leucotelium Tranzschel 1935
Tranzschelia Arthur 1906
= *Polythelis* Arthur 1906
= *Lipospora* Arthur 1942
Family Uncolaceae Buriticá 2000
Calidion Syd. & P. Syd. 1919
Uncol Buriticá & P.A. Rodr. 2000
Family Uromycladiaceae P. Zhao & L. Cai 2021
Uromycladium McAlpine 1905
Family Zaghouaniaceae P. Syd. & Syd. 1915
Achrotelium Syd. 1928
Blastospora Dietel 1908
= *Pelastoma* M. Salazar, A.A. Carvalho & J.F. Hennen 2012
Botryorhiza Whetzel & Olive 1917
Botryosorus Jing X. Ji, Okane & Kakish. 2023
Desmosorus Ritschel, Oberw. & Berndt 2005
Elateraecium Thirum., F. Kern & B.V. Patil 1966
= *Hiratsukamyces* Thirum., F. Kern & B.V. Patil 1975
Hemileia Berk. & Broome 1869
= *Hemileiopsis* Racib. 1900
= *Wardia* J.F. Hennen & M.M. Hennen 2003
Mikronegeria Dietel 1899
Zaghouania Pat. 1901
= *Cystopsora* E.J. Butler 1910
Pucciniales genera *incertae sedis*
Aecidiconium Vuill. 1892
Aecidiolum Unger 1833
Aecidium Pers. 1796
= *Sphaerotheca* Desv. 1817
= *Symperidium* Klotzsch 1843
Aeciure Buriticá & J.F. Hennen 1994
Allodus Arthur 1906
Alveolaria Lagerh. 1892
Arthuriomyces Cummins & Y. Hirats. 1983
Caeoma Link 1809
= *Hypodermium* Link 1815
Caetea Salazar-Yepes & A.A. Carvalho 2012
Campanulospora Salazar-Yepes, Pardo-Card. & Buriticá 2007

Canasta A.A. Carvalho & J.F. Hennen 2010
Cumminsina Petr. 1955
Desmellopsis J.M. Yen 1969
Diabolidium Berndt 1995
Didymopsorella Thirum. 1950
= *Gymnopuccinia* K. Ramakr. 1951
Flaminia Sacc. & P. Syd. 1902
Gambleola Massee 1898
Intrapes J.F. Hennen & Figueiredo 1979
= *Kamatomyces* Sathe 1966
Kimuromyces Dianese, L.T.P. Santos, R.B. Medeiros & Furlan. 1995
Macabuna Buriticá & J.F. Hennen 1994
Masseeella Dietel 1895
Mehtamyces Mundk. & Thirum. 1945
Morispora Salazar-Yepes, Pardo-Card. & Buriticá 2007
Neopuccinia A. Martins 2019
Peridermium (Link) J.C. Schmidt & Kunze 1817
Phragmotelium Syd. 1921
Physonema Lév. 1847
Poliomopsis A.W. Ramaley 1987
Ramakrishnania Ramachar & Bhagyan. 1979
Roestelia Rebent. 1804
= *Cancellaria* Brongn. 1825
= *Centridium* Chevall. 1826
Schroeteriaster Magnus 1896
= *Uromycodes* Clem. 1909
Scutelliformis Salazar-Yepes, Pardo-Card. & Buriticá 2007
Uraecium Arthur 1933
Uredo Pers. 1801
= *Mapea* Pat. 1906
= *Nigredo* (Pers.) Roussel 1806
= *Peridipes* Buriticá & J.F. Hennen 1994
= *Rubigo* (Pers.) Roussel 1806
= *Trichobasis* Lév., in Orbigny 1849
= *Uredo* ** *Nigredo* Pers. 1801
Goplana Racib. 1900
Telomapea G.F. Laundon 1967

Evolution

The co-evolution between the rust fungi and their host plants has been considered to be the major factor driving rust fungi speciation and diversification. Recently, host jumps or host shifts to taxonomically unrelated host plants have also been reported to be important (Aime et al. 2017).

Ferns have been hypothesized to have been the original host plants, and rust fungi on ferns (*Uredinipsis, Milesina* and *Hyalopsora*) have been considered as primitive genera (Cummins and Hiratsuka 2003). Aime et al. (2018a) completed phylogenetic analyses using rust fungi on a wide range of host plants and revealed that the timing of diversification in the Pucciniales correlated with the diversification of their gymnosperm and angiosperm hosts. The host reconciliation analyses suggested that systematic relationships of hosts from the aecial stage of the Pucciniales life cycle better reflected the systematic relationships among the Pucciniales. These results demonstrate the importance of the aecial spore stage on the overall evolution of the Pucciniales and supported hypotheses made by Leppik (1953, 1965, 1967, 1972) over half a century ago. The findings of Aime et al. (2018a, b, c, d) were also supported by Ji et al. (2022a, b) in phylogenetic analyses of *Puccinia* species on Poaceae and Carex.

Justification of order and problems

A significant hurdle in molecular systematics and taxonomy of Pucciniales has been the limited sampling of taxa, especially type species of genera. Two recent studies have made significant steps to overcome these limitations by performing a massive sampling of rust fungi. Aime and McTaggart (2021) analyzed 80% of the rust genera by including 86 type species and 22 type species proxies using three loci (SSU, LSU and COX3) of 314 species. Based on phylogeny, morphology, host range and life cycle, they proposed a taxonomical arrangement with seven suborders and 18 families that differed considerably relative to earlier classifications. A later study also found similar results based on the molecular data (ITS, SSU and LSU) of 1,654 collections gathered in 86 natural sites in China (Zhao et al. 2021). They confirmed the main families described in Aime and McTaggart 2021 and proposed three new families. Considerable improvements have been made in the past few years in rust taxonomy that genome sequencing projects could further boost in the future. In our analyses, the existence of Pucciniaceae, Sphaerophragmiaceae, Zaghouaniaceae, Coleosporiaceae and Melampsoraceae was confirmed with the same taxonomical relationships as in Aime and McTaggart (2021).

Significance

Ecological and economical roles

Many rust fungi are suspected to adapt their environmental conditions (host plant, climate condition) with their survival strategies. Many types of spores and complicated life cycles are considered as the results of their survival strategies. However, we are still unknown how they ecologically adapt in nature and how they affect ecological conditions.

Many rust fungi are known as economically important pathogens of cultivated plants like wheat (*Puccinia graminis, P. triticina*), corn (*Puccinia sorghi, P. polysora*), coffee (*Hemileia vastatrix*) and pine (*Cronartium* spp.). Therefore, protection of crops from them are important subjects for our life and have been paid much efforts for developing effective control methods. Cummins and Hiratsuka (2003) listed about 50 internationally important rust fungi causing damage to agricultural and horticultural crops, and forest trees.

Other relevant data and future recommendations

General aspects of rust fungi are described in most mycology and plant pathology textbooks, which generally provide good teaching resources to introduce the biology and significance of rust fungi. Videos covering the biology of economically important rust fungi have also been generated, providing a visual demonstration of different spore stages formed in rust fungi life cycle. Regional flora's or lists of rust fungi have been published in many countries. While these are useful for species identification, there is a need for books or review papers summarising the current systematic treatment of rust fungi. To understand the traditional morphology-based approach to rust fungi taxonomy, "Illustrated Genera of Rust Fungi 3rd Edition" by Cummins and Hiratsuka (2003) is recommended as an important and useful publication. For more recent taxonomy including molecular phylogeny, papers published by Aime et al. (2017, 2018a) and Aime and McTaggart (2021) are useful resources.

Quasiramulariales R. Kirschner, M. Kolařík & M. Piepenbr. 2021

Contributed by: Teun Boekhout, Nathan Schoutteten

Introduction

A Ramularia-like anamorphic filamentous fungus was isolated from rust sori on a leaf of plants in various cities in Taiwan province in China and sequence analysis of multiple gene loci identified this as a member of Ustilaginomycotina. Due to its isolated phylogenetic position a new genus *Quasiramularia*, a new family Quasiramulariaceae, and a new order Quasiramulariales was proposed (Kolařík et al. 2021).

History

Quasiramulariales was described in 2021 from materials isolated from rust sori on plants in Taiwan province of China (Kolařík et al. 2021).

Characters that define the taxa in the order

Taken from Kolařík et al. (2021). Colonies whitish, subeffuse to powdery. Hyphae present, without clamp connections. Conidiophores emerging from rust sori and on agar plates, erect to decumbent, hyaline to subhyaline, smooth to finely verruculose, simple or with short branches. Conidiogenous cells are usually terminal, but also subterminal or lateral, with slightly thickened and slightly darkened conidiogenous loci. Conidia catenate, ellipsoid-ovoid to subcylindric-fusiform, hyaline to subhyaline, smooth to rough, with thickened, slightly darkened hila. Molecular phylogenies identified Quasiramulariales as a lineage in Ustilaginomycotina where it sits basal to Ustilaginales and Urocystidales (Kolařík et al. 2021).

Plates

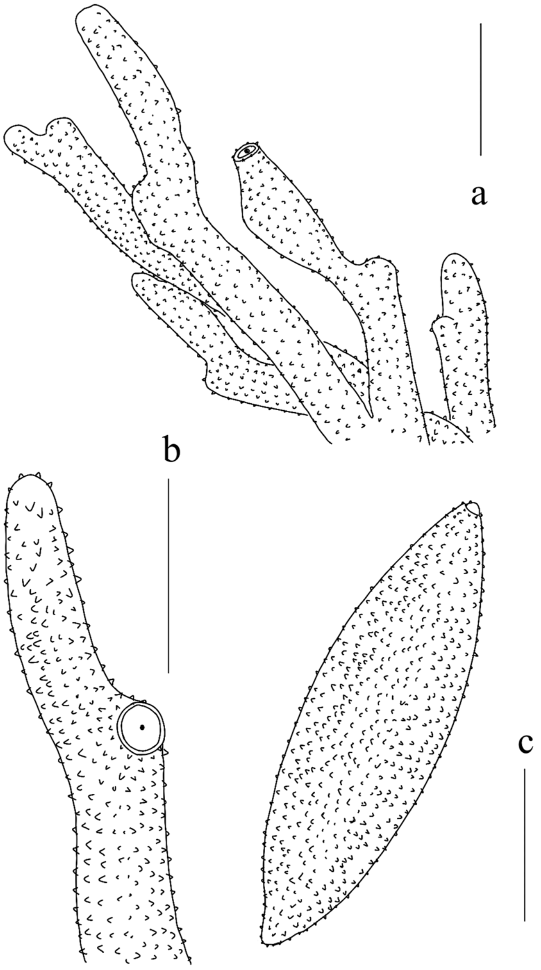


Fig. 49 *Quasiramularia phakopsoricola*. **a** conidiogenous cells with terminal geniculations and conidiogenous loci; **b** Conidiogenous cell with a central pore; **c** fusiform conidium with hilum. Scale bars: a,c = 5 µm; b = 3 µm. Redraw from Kolařík et al. (2021) by Mao-Qiang He

Genera included

Family Quasiramulariaceae R. Kirschner, M. Kolařík & M. Piepenbr. 2021
    Quasiramularia I-Chin Wei & R. Kirschner 2021

Evolution

Within Ustilaginomycotina this order seems to have a basal position to Ustilaginales and Urocystidales (Kolařik et al. 2021). It remains to be seen if a sexual state is present and, if so, how this does compare to those of other representatives of Ustilaginomycotina. Also, the fungicolous lifestyle needs further investigation as it has been suggested that *Quasiramularia* evolved from saprotrophic plant parasitic fungi into a colonizer of specific rust species (Kolařik et al. 2021). It is the first mycoparasitic representative to be discovered in Ustilaginomycotina. Another group of basidiomycetous rust parasites is Helicobasidiales (Pucciniomycotina), but other than the same host group there are no obvious similarities between these two mycoparasitic orders. Interestingly, ITS sequences of *Quasiramularia* have a very low GC content, but, likely, do not represent a psudogene (Kolařik et al. 2021).

Justification of order and problems

Although only based on a single species this order seems justified by its phylogenetic position in Ustilaginomycotina (Kolařik et al. 2021). However, a whole genome analysis and a phylogenomic analysis will show more lights into the evolutionary trends of this and related fungi.

Significance

Ecological and economical roles

Only known from uredinia of *Phakopsora ampelopsidis* occurring on leaves of *Ampelopsis brevipeduculata* and *Parthenocissus tricuspidata* in cities in Taiwan province, China (Kolařik et al. 2021).

Chemical diversity

Not known, but the ITS sequences have a very low GC content (Kolařik et al. 2021).

Robbauerales Boekhout, Begerow, Q.M. Wang & F.Y. Bai 2015

Contributed by: Martin Kemler, Cvetomir M. Denchev, Dominik Begerow, Teodor T. Denchev

Introduction

Robbauerales was erected to accommodate the species *Robbauera albescens* (Gokhale) Boekhout et al. previously residing in the genus *Tilletiopsis* (Wang et al. 2015d). The order was erected purely on phylogenetic evidence, it is monotypic and only contains the family Robbaueraceae with the sole genus *Robbauera.* The single described species *R. albescens* is ecologically not well characterized and has been recovered from a plethora of habitats, including human urinary tracts (Liu et al. 2022d), sporocarps of other fungi (Sa’diyah et al. 2021), or the plant phyllosphere (Boekhout 2011). A further species is assumed (Richter et al. 2019).

Currently, one family, one genus, and one species are included in this order.

Characters that define the taxa in the order

Robbauera albescens is only known in its yeast stage and is characterized by whitish or whitishcream to yellowish-cream colored yeast colonies (Boekhout 1991a). The yeast stage proliferates via budding. Sexual reproduction is unknown. Hyphal growth is known on artificial media. Septate, regular branching hyphae are formed, which can produce ballistocondidia (Boekhout 2011). Chlamydospores are formed intercalary or terminal. Although *R. albescens* grows on a wide range of carbon sources, it only does so in the presence of oxygen and fermentation is not known (Boekhout 1991a, 2011).

Plates

For illustrations, see Boekhout (1991a, b: Fig. 48) and Boekhout (2011: Fig. 160.2 & Fig. 160.3).

Genera included

Family Robbaueraceae Boekhout, Begerow, Q.M. Wang & F.Y. Bai 2015
    Robbauera Boekhout, Begerow, Q.M. Wang & F.Y. Bai 2015

Evolution and justification of order

Robbauerales is only phylogenetically characterized and the species used to be part of the anamorphous genus *Tilletiopsis*. Together with the Golubeviales (nom. inval.), they may form a sister group to the rest of the Exobasidiomycetes (Richter et al. 2019). In other phylogenetic studies, Robbauerales is the sister lineage to a group containing Tilletiales, Golubeviales, and Microstromatales within Exobasidiomycetes (McTaggart et al. 2020).

Economic importance

Despite *Robbauera albescens* seemingly occurring in many habitats (see e.g., Boekhout 2011; Liu et al. 2022d; Sa'diyah et al. 2021), nearly nothing is known about its ecology or its impact on economy. A lineage most likely closely related to *R. albescens* has been recovered from apple fruits, where it causes "white haze" (Boekhout et al. 2006; Richter et al. 2019). This post-harvest disorder has some economic impact on apple fruit production.

Rosettozymales Q.M. Wang & F.Y. Bai 2020

Contributed by: Teun Boekhout

Introduction

Molecular phylogenetic studies made it possible to place both asexually and sexually reproducing yeasts in a phylogenetic context and translate this in a formal taxonomic classification. The order Rosettozymales is such an example (Li et al. 2020b).

History

In 2020, the genus *Rosettozyma*, family Rosettozymaceae, and order Rosettozymales was described in Microbotryomycetes, Pucciniomycotina, to accommodate three newly described species (Li et al. 2020b).

Characters that define the taxa in the order

Rosettozymales is mainly characterized by its phylogenetic position in a multigene-based phylogeny in which it appeared as a sister lineage to *Oberwinklerozyma* and *Phenoliferia* species. No sexual state is known. Asexual reproduction is by polar budding, and the buds may form rosetta-like clusters (Li et al. 2020b).

Plates

See Figs. 5 and 16 in Li et al. (2020b).

Genera included

Family Rosettozymaceae Q.M. Wang & F.Y. Bai 2020
  Rosettozyma Q.M. Wang & F.Y. Bai 2020

Evolution

No studies available.

Justification of order and problems

Rosettozymales was recently described based on molecular phylogenetic studies (Li et al. 2020b). Given the limited taxon sampling of that study, further studies are needed to explore the relationships within the order and between Rosettozymales and related taxa.

Significance

Ecological and economical roles

All known species were obtained from leaf surfaces (Li et al. 2020b).

Chemical diversity

Unknown.

Russulales Kreisel ex P.M. Kirk, P.F. Cannon & J.C. David 2001

Contributed by: Guo-Jie Li, Ricardo Valenzuela, Ruben De Lange, Bin Cao, Mao-Qiang He, Rui-Lin Zhao

Introduction

Russulales is a significant group within the Basidiomycota, consisting of a total of 4436 species, 98 genera, and 11 families (He et al. 2019a, b). The concept of Russulales was initially proposed by Kreisel (1969) and later accepted and amended by Kirk et al. (2001). Members of the Russulales exhibit diverse basidiome structures which can range from agaricoid to discoid, clavarioid, polyporoid, corticiod, and even gasteroid. Furthermore, hymenophore types among the Russulales encompass lamellate, hydnoid, poroid, labyrinthoid, grandinioid and a smooth configuration (Miller et al. 2006; Kirk et al. 2008). Many species within the Russulales share two key morphological features. Firstly, their spore walls exhibit an amyloid reaction combined with an ornamented outline (although there are a few exceptions that have non-amyloid or smooth walls). Secondly, many of these species possess gloeoplerous hyphae or gloeocystidia containing sesquiterpenes that can be stained by sulphuric benzaldehydes. However, it is worth noting that in some genera within this order, these elements may be absent or transformed into homologous structures like lactiferous hyphae (Larsson and Larsson 2003). In the past few decades, evidence supporting the monophyly of Russulales has been gathered through both morphological characteristics and DNA sequence phylogenetic analyses (Hibbett and Donoghue 1995; Hibbett et al. 1997; Miller et al. 2001, 2006; Binder et al. 2005; He et al. 2019a). Members of Russulales exhibit a wide range of ecological strategies including saprotrophic wood rotting, tree root and heartwood pathogens, ectomycorrhizal, and association with insects as entomogenous fungi (Hibbett et al. 2014).

History

Persoon (1794a) introduced the genera *Hericium* and *Stereum*, now recognized as members of Russulales. Later, Persoon (1796) also recognized the genera *Russula* and *Lactarius*. Fries (1821) included *Russula* and *Lactarius* as tribes, called *Russula* and *Galorrheus* respectively, in the genus *Agaricus*. Whereas, Gray (1821) classified, *Hericium*, *Lactarius*, *Russula*, and *Stereum* into their own respective genera within a group known as Hymenotheceae; additionally, he described two new genera *Albatrellus* and *Auriscalpium* in that same group. These classifications have persisted remarkably well until now with notable continuity. Karsten (1879) contributed to this classification by establishing *Gloiodon* as a genus for three wood-inhabiting species with hydnoid hymenophores (*Hydnum strigosum* Sw.: Fr., *H. hirtum* Fr., and *H. pudorinum* Fr.), but narrowed it down in 1882 to only include *G. strigosus* (Sw.:Fr.) P.Karst. Until the mid- to late twentieth century, classification systems in the homobasidiomycetes were primarily based on Friesian concepts that emphasized the physical appearance of sporophores. This meant that fungi with a similar sporophore type were considered to be more closely related. It was difficult to conceive that taxa with different sporophore morphologies could be grouped together (Miller et al. 2006). However, Donk (1971) was the first to suggest a possible relationship between the family Hericiaceae and other Basidiomycetes based on shared micromorphological features such as gloeoplerous hyphae and amyloid basidiospore ornamentations. These similarities may indicate the presence of an unrecognized large order encompassing various sporophore types. Singer and Smith (1960) questioned the necessity of maintaining a separation between agarics and gasteroid taxa in the Hymenogastrales. This aspect had already been questioned prior to the application of molecular phylogenetic methods in fungal taxonomy (Oberwinkler 1977; Pegler and Young 1979). In the past, differentiating between agaricoid and gasteroid basidiome forms was considered significant evidence for classifying higher categories within Basidiomycota (Hawksworth et al. 1995). Oberwinkler put forth Russulales as an example of a closely related group of fungi that encompassed all known types of sporocarps among homobasidiomycetes (Miller et al. 2006). The concept of Russulales was not accepted until the ninth edition of Dictionary of Fungi (Kirk et al. 2001). This is because the initial publication (Kreisel 1969) was not conform to the rules outlined in the International Code for algae, fungi, and plants. However, support for recognizing a new russuloid lineage within Basidiomycota has been reinforced through molecular phylogenetic analyses (Hibbett and Donoghue 1995; Hibbett et al. 1997). Further clarification on the diversity of Russulales came from Hibbett and Thorn (2001). More recently, this classification has expanded with the proposal of a new member called Terrestriporiaceae based on the discovery of a new genus called *Terrestriporia* (Wu et al. 2020a). Larsson and Larsson (2003) have suggested that two major clades exist within Russulales: peniophorales and enrussuloid suborders. However, subsequent analyses conducted by have failed to provide consistent support for this distinction (He et al. 2019a; Wu et al. 2020a).

Characters that define the taxa in the order

The morphology of the basidiome and hymenophore, together with habitat, are often regarded as important characters for the taxonomy of the Russulales (Larsson and Larsson 2003; Miller et al. 2001, 2006). Resupinate basidiomes are common in Echinodontiaceae, Peniophoraceae, Stereaceae, Terrestriporiaceae and Xenasmataceae, and rarely present in Hericiaceae and Russulaceae. Pileate basidiomes are predominantly found in Albatrellaceae, Auriscalpiaceae, Bondarzewiaceae, Hericiaceae and Russulaceae. Gasteroid basidiomes are mainly present in Hybogasteraceae and Russulaceae, rarely in Albatrellaceae. Clavarioid basidiomes are present in Auriscalpiaceae, Bondarzewiaceae and Peniophoraceae. Effused-reflexed basidiomes are infrequently scattered in Auriscalpiaceae, Echinodontiaceae, Hericiaceae, Peniophoraceae and Stereaceae (Miller et al. 2006; Kirk et al. 2008). The family Russulaceae was proposed legally and validly by Dutch botanist Johannes P. Lotsy. Only *Lactarius*, *Russula*, and *Russulina* (synonym of *Russula*) were included as members of the family at that time. Synonyms of this group are Asterosporaceae, Elasmomycetaceae, and Lactariaceae (Pegler and Young 1979). Gasteroid Russulaceae members were once classified in *Arcangeliella*, *Bucholtzia*, *Cystangium*, *Elasmomyces*, *Gymnomyces*, *Martellia*, and *Zelleromyces* (Bucholtz 1901, 1903). Most of these taxa have been revised as *Lactifluus*, *Lactarius*, and *Russula* (Elliott and Trappe 2018).

Albatrellaceae Nuss is characterized by annual, resupinate, pileate-stipitate or gasteroid basidiomes, poroid or locular (gasteroid fungi) hymenophore, monomitic hyphal system, with or without clamp connections, inamyloid or amyloid hyphae, smooth or appearing slightly rough, with a double wall separated by interwall pillar or aleveolate, hyaline, inamyloid or amyloid basidisopores. Ectomycorrizal fungi.

Auriscalpiaceae Maas Geest. is characterized by annual, resupinate, effused-reflexed, pileate-sessile, pileate-stipitate to clavarioid basidiomes, hydnoid, poroid, labyrinthine to daedaleoid, meruloid and lamellate hymenophore. Monomitic to dimitic hyphal system, generative hyphae with clamp-connections, inamyloid or amyloid, skeletal hyphae when present dextrinoid (*Amylonotus*), gloeoplerous hyphae and gloeocystidia present or absent, with asperulate, spinulose, verrucose, hyaline to pigmented, amyloid basidiospores. Wood decay or ectomycorrizal fungi.

Bondarzewiaceae Kotl. & Pouzar is characterized by annual to perennial, resupinate, effused-reflexed, pileate-sessile, pileate-stipitate to clavarioid basidiomes, smooth, tuberculate, poroid, hydnoid hymenophore. Monomitic, pseudodimitic to dimitic hyphal system, generative hyphae with or without clamp-connections, inamyloid, skeletal hyphae inamyloid or dextrinoid (*Amylosporus*), gloeoplerous hyphae and gloeocystidia present or absent, with asperulate, spinulose, verrucose, echinulate, ridges or crests, hyaline to pigmented, amyloid basidiospores. Wood decay fungi.

Echinodontiaceae Donk is characterized by annual to perennial, resupinate, effused-reflexed to pileate-sessile basidiomes, smooth, poroid to hydnoid hymenophore. Monomitic, pseudodimitic to dimitic hyphal system, generative hyphae with or without clamp-connections, inamyloid, skeletal hyphae inamyloid or dextrinoid (*Larssoniporia*), gloeocystidia present or incrusted cystidia absent or present, with smooth, asperulate, spinulose, verrucose, hyaline to pigmented, amyloid basidiospores. Wood decay fungi.

Hericiaceae Donk is characterized by annual, resupinate, effused-reflexed, pileate-sessile to flabelliform basidiomes, smooth, poroid to hydnoid hymenophore. Monomitic or dimitic hyphal system, generative hyphae with clamp-connections, inamyloid or amyloid, skeletal hyphae inamyloid or dextrinoid (*Pseudowrightoporia, Wrightoporiopsis*), gloeoplerous hyphae and gloeocystidia present or abscent, with asperulate, spinulose or echinulate, hyaline, amyloid basidiospores. Wood decay fungi.

Hybogasteraceae Jülich is characterized by gasteroid epigeus basidiomes, tuberiform, lobulate-gibbous, more or less irregularly umbilicate above, almost cerebriform, at base constricted into a stipe-like extension where the columella originates. Dimitic? hyphal system (Singer 1964 said "hyphal walls inamyloid, clamp connections not seen, but septa rare and difficult to observe"), gloeoplerous hyphae present (Singer 1964 called "laticifers"), echinulate, amyloid basidiospores. Wood decay fungi.

Peniophoraceae Lotsy is characterized by annual, resupinate, orbicular, discoid, effused-reflexed, to clavarioid basidiomes, smooth, grandinioid, tuberculate or raduloid hymenophore. Monomitic to dimitic hyphal system, generative hyphae with or without clamp-connections, inamyloid or dextrinoid skeletal hyphae or dichohyphae when present dextrinoid (*Baltazaria*) or inamyloid binding hyphae as 'bovista-type" (*Licrostroma*), dextrinoid asterosetae (*Asterostroma*), gloeoplerous hyphae and gloeocystidia present or absent, lamprocystidia present or absent with smooth, asperulate, spinulose, verrucose, hyaline to pigmented, inamyloid (*Dendrophora*, *Entomocorticium*, *Licrostroma, Peniophora*, *Sceptrulum*, *Vararia*) or with amyloid suprahilar plage (some species of *Vararia*) or amyloid basidiospores. Wood decay fungi. Leal-Dutra et al. (2018) demsotrated the inclusión of *Parapterulicium* and *Baltazaria* in the family Peniophoraceae based on morphological and molecular characters.

Russulaceae Lotsy is characterized by annual, resupinate, corticioid, pleurotoid, canthareloid (*Multifurca*), agaricoid, gasteroid (secuestrate) and some with veiled basidiomes, with or without milk, smooth, lamellate, regularly forked and globular or irregular hymenophore, Monomitic to dimitic hyphal system, generative hyphae with or without clamp-connections, heteromerous trama in context, lamellae and stipe with sphaerocysts and hyphae mixed (*Lactarius*, *Russula* and some secuestrate fungi), gloeoplerous hyphae and gloeocystidia present or absent, lamprocystidia present or absent, pseudocystidia and macrocuystidia present or absent, with asperulate, spinulose, verrucose, echinulate, ridges or crests,subreticulate to reticulate, amyloid basidiospores. Wood decay or ectomycorrizal fungi.

Stereaceae Pilat is characterized by annual, resupinate, discoid, cupulate, stereoid, auricularioid (gelatinous to fleshy, *Gloeosoma*) pulvinate, disciform, effused-reflexed, pileate-sessile to flabelliform basidiomes, smooth, rugose to tubrculate hymenophore. Monomitic to dimitic hyphal system, generative hyphae with or without clamp-connections, amyloid (*Amylohyphus*) or inamyloid; skeletal hyphae occasionally branched, nonamyloid, nondextrinoid or binding hyphae distributed in the subiculum (*Gloeomyces*); gloeoplerous hyphae and gloeocystidia present or absent, pseudocystidia present or absent, Skeletocystidia present or not, amyloid (*Amylohyphus*), dextrinoid (*Dextrinocystidium*) or not, acanthophyses present or absent, acanthobasidia present or absent, botryophyses with tips amiloid present in *Aleurobotrys*; with smooth, asperulate, spinulose, verrucose, echinulate, aculeate, ridges or crests,subreticulate to reticulate, inamyloid (*Amylohyphus*) or amyloid basidiospores.

Terrestriporiaceae Y.C. Dai, B.K. Cui, F. Wu, Y. Yuan & Jia J. Chen is characterized by annual, resupinate basidioma, poroid hymenophore, monomitic hyphal system, generative hyphae mostly simple septate, but occasionally having clamp connections, gloeoplerous hyphae present, with hyaline, thin-walled, smooth, amyloid basidiospores.

Xenasmataceae Oberw. is characterized by annual, resupinate, ceraceous to geletinous basidioma, smooth hymenophore, monomitic hyphal systems, generative hyphae with clamp connections; cystidia present or abscent, gloeoplerous hyphae and gloeocystidia not observed; basidia pleural usually with 4 sterigmata and a basal clamp connection, with warted, striate to angular (tetrahedral), hyaline, inamilod to weakly dextrinoid basidiospores.

Plates

Fig. 50 Selected basidiome types of Russuales. **a** *Russula formula* (ZRL20220518, Xizang Autonomous Region, China); **b** *Peniophora albobadia* (RV 21832, San Luis Potosi, Mexico); **c** *Albatrellopsis ellisii* (RV 12781, Durango State, Mexico); **d** *Aleurodiscus amorphous* (RV 17163, Hidalgo State, Mexico); **e** *Artomyces pyxidatus* (RV 15093, Oaxaca State, Mexico); **f** *Auriscalpium* sp. (ZRL20221251, Hubei province, China); **g** *Bondarzewia mesofila* (RV 13824, Hidalgo State, Mexico); **h** *Hericium erinaceus* (RV 12609, Sonora State, Mexico); **i** *Lactarius deliciosus* (ZRL20238102, Chongqing municipality, China); **j** *Scutiger pes-capre* (RV 12720, Durango State, Mexico); **k** *Stereum ostrea* (RV 11526, Hidalgo State, Mexico); **l** *Stereum sanguinolentum* (RV 12805, Durango State, Mexico)

Genera included

- Family Albatrellaceae Nuss 1980
  - *Albatrellopsis* Teixeira 1993
  - *Albatrellus* Gray 1821
  - = *Ovinus* (Lloyd) Torrend 1920
  - *Byssoporia* M.J. Larsen & Zak 1978
  - *Leucogaster* R. Hesse 1882
  - *Leucophleps* Harkn. 1899
  - = *Cremeogaster* Mattir. 1924
  - *Mycolevis* A.H. Sm. 1965
  - *Polyporoletus* Snell 1936
  - *Scutiger* Paulet 1808
- Family Auriscalpiaceae Maas Geest. 1963
  - *Amylonotus* Ryvarden 1975
  - *Artomyces* Jülich 1982
  - *Auriscalpium* Gray 1821
  - = *Pleurodon* Quél. ex P. Karst. 1881
  - *Dentipratulum* Domański 1965
  - *Lentinellus* P. Karst. 1879
  - = *Hemicybe* P. Karst. 1879
  - *Stalpersia* Parmasto 2001
- Family Bondarzewiaceae Kotl. & Pouzar 1957
- = Hybogasteraceae Jülich 1982
  - *Amylaria* Corner 1955
  - *Amylosporus* Ryvarden 1973
  - = *Rigidoporopsis* I. Johans. & Ryvarden 1979
  - *Bondarzewia* Singer 1940
  - = *Hybogaster* Singer 1964
  - *Gloiodon* P. Karst. 1879
  - = *Leaia* Banker 1906
  - = *Sclerodon* P. Karst. 1889
  - *Heterobasidion* Bref. 1888
  - = *Spiniger* Stalpers 1974
  - *Laurilia* Pouzar 1959
  - *Lauriliella* Nakasone & S.H. He 2017
  - *Stecchericium* D.A. Reid 1963
  - *Wrightoporia* Pouzar 1966
- Family Echinodontiaceae Donk 1961
- = Amylostereaceae Boidin et al. 1998
  - *Amylostereum* Boidin 1958
  - = *Lloydellopsis* Pouzar 1959
  - = *Trichocarpus* P. Karst. 1889
  - *Echinodontiellum* S.H. He & Nakasone 2017
  - *Echinodontium* Ellis & Everh. 1900
  - = *Hydnofomes* Henn. 1900
  - = *Hydnophysa* Clem. 1909
  - *Larssoniporia* Y.C. Dai, Jia J. Chen & B.K. Cui 2015
- Family Hericiaceae Donk 1964
  - *Dentipellicula* Y.C. Dai & L.W. Zhou 2013
  - *Dentipellis* Donk 1962
  - = *Amylodontia* Nikol. 1967
  - *Hericium* Pers. 1794
  - = *Creolophus* P. Karst. 1879
  - = *Friesites* P. Karst. 1879
  - = *Hericium* Schrank 1786
  - = *Hericius* Juss. 1789
  - = *Martella* Endl. 1836
  - = *Medusina* Chevall. 1826
  - *Laxitextum* Lentz 1956
  - *Pseudowrightoporia* Y.C. Dai, Jia J. Chen & B.K. Cui 2015
  - *Wrightoporiopsis* Y.C. Dai, Jia J. Chen & B.K. Cui 2015
- Family Peniophoraceae Lotsy 1907
  - = Lachnocladiaceae D.A. Reid 1965
  - *Amylofungus* Sheng H. Wu 1996
  - *Asterostroma* Massee 1889
  - *Baltazaria* Leal-Dutra, Dentinger & G.W. Grif 2018
  - *Dendrophora* (Parmasto) Chamuris 1987
  - *Dichostereum* Pilát 1926
  - *Duportella* Pat. 1915
  - *Entomocorticium* H.S. Whitney, Bandoni & Oberw. 1987
  - *Gloiothele* Bres. 1920
  - *Lachnocladium* Lév. 1846
  - = *Eriocladus* Lév. 1846
  - = *Stelligera* R. Heim 1938
  - = *Stelligera* R. Heim ex Doty 1948
  - *Licrostroma* P.A. Lemke 1964
  - = *Michenera* Berk. & M.A. Curtis 1868
  - *Metulodontia* Parmasto 1968
  - *Parapterulicium* Corner 1952
  - *Peniophora* Cooke 1879
  - = *Cryptochaete* P. Karst. 1889
  - = *Gloeopeniophora* Höhn. & Litsch. 1907
  - = *Sterellum* P. Karst. 1889
  - *Sceptrulum* K.H. Larss. 2014
  - *Scytinostroma* Donk 1956
  - *Vararia* P. Karst. 1898
  - = *Asterostromella* Höhn. & Litsch. 1907
  - = *Denrophysellum* Parmasto 1968
  - *Vesiculomyces* E. Hagstr. 1977
- Family Russulaceae Lotsy 1907
  - *Boidinia* Stalpers & Hjortstam 1982
  - *Gloeopeniophorella* Rick 1934
  - *Lactarius* Pers. 1797
  - = *Arcangeliella* Cavara 1900
  - = *Galorrheus* (Fr.) Fr. 1825
  - = *Gastrolactarius* R. Heim 1971
  - = *Gastrolactarius* R. Heim ex J.M. Vidal 2005
  - = *Gloeocybe* Earle 1909

=*Lactariella* J. Schröt. 1889
=*Zelleromyces* Singer & A.H. Sm. 1960
Lactifluus (Pers.) Roussel 1806
=*Lactariopsis* Henn. 1901
=*Pleurogala* Redhead & Norvell 1993
Multifurca Buyck & V. Hofst. 2008
Pseudoxenasma K.H. Larss. & Hjortstam 1976
Russula Pers. 1796
=*Bucholtzia* Lohwag 1924
=*Cystangium* Singer & A.H. Sm. 1960
=*Dixophyllum* Earle 1909
=*Elasmomyces* Cavara 1897
=*Gymnomyces* Massee & Rodway 1898
=*Lactarelis* Earle 1909
=*Macowanites* Kalchbr. 1882
=*Martellia* Mattir. 1900
=*Omphalomyces* Battarra ex Earle 1909
=*Phaeohygrocybe* Henn. 1901
=*Russulina* J. Schröt. 1889
Family Stereaceae Pilát 1930
Acanthobasidium Oberw. 1965
Acanthofungus Sheng H. Wu, Boidin & C.Y. Chien 2000
Acanthophysellum Parmasto 1967
Acanthophysium (Pilát) G. Cunn. 1963
Aleurobotrys Boidin 1986
Aleurodiscus Rabenh. ex J. Schröt. 1888
=*Aleurodiscus* Rabenh. 1874
=*Aleurodiscus* Cooke 1885
Aleuromyces Boidin & Gilles 2002
Amylohyphus Ryvarden 1978
Amylosporomyces S.S. Rattan 1977
Conferticium Hallenb. 1980
Coniophorafomes Rick 1934
Dextrinocystidium Sheng H. Wu 1996
Gloeocystidiellum Donk 1931
Gloeocystidiopsis Jülich 1982
Gloeomyces Sheng H. Wu 1996
Gloeosoma Bres. 1920
Megalocystidium Jülich 1978
Neoaleurodiscus Sheng H. Wu 2010
Scotoderma Jülich 1974
Stereodiscus Rajchenb. & Pildain 2021
Stereum Hill ex Pers. 1794
=*Haematostereum* Pouzar 1959
Xylobolus P. Karst. 1881
Family Terrestriporiaceae Y.C. Dai, B.K. Cui, F. Wu, Y. Yuan & Jia J. Chen 2020
Terrestriporia Y.C. Dai, B.K. Cui, F. Wu, Y. Yuan & Jia J. Chen 2020
Family Xenasmataceae Oberw. 1966
Xenasma Donk 1957
Xenosperma Oberw. 1965
genera *incertae sedis*
Aleurocystidiellum P.A. Lemke 1964
Dentipellopsis Y.C. Dai & L.W. Zhou 2013
Dichantharellus Corner 1966
Dichopleuropus D.A. Reid 1965
Gloeoasterostroma Rick 1938
Gloeodontia Boidin 1966
Gloeohypochnicium (Parmasto) Hjortstam 1987
Haloaleurodiscus N. Maek., Suhara & K. Kinjo 2005
Laeticutis Audet 2010
Neoalbatrellus Audet 2010
Perplexostereum Ryvarden & S. Tutka 2014
Polypus Audet 2010
Scopulodontia Hjortstam 1998
Scytinostromella Parmasto 1968
=*Confertobasidium* Jülich 1972
Xeroceps Audet 2010

Evolution

In the Basidiomycota, there has been a clear evolutionary trend in the development of different types of basidiomes. This evolution is marked by a shift from simple crust-like and resupinate forms to more complex morphologies (Hibbett and Binder 2002; Hibbett 2004; Binder et al. 2005). The ancestral resupinate types have given rise to a wide range of morphological variations in basidiomes. These include clavarioid forms, characterized by club-shaped structures; agaricoid or pileate-stipitate forms with distinctive caps and stalks; polyporoid or bracket fungi that grow horizontally on substrates; gasteroid or puffball-like species that release spores internally through rupturing; as well as reduced cup-shaped cyphelloid taxa among others. This diversification demonstrates how distinct adaptations within the Basidiomycota lineage have led to an array of basidiomes morphologies (Nagy et al. 2017). In the Russulales, the ancestral traits in general basidiomes type and hymenophoral configuration are the resupinate habit and smooth hymenophore. The ancestral resupinate habit can be found in 10 families within Russulales, with only Hybogasteraceae exhibiting a gasteroid habit. Two families exclusively possess the resupinate habit, while eight families have evolved into more complex morphologies ranging from resupinate to pileate-stipitate forms. As for hymenophoral configuration, seven families retain the ancestral smooth hymenophore, which is not present in Albatrellaceae, Auriscalpiaceae, Hybogasteraceae and Terrestriporiaceae. Xenasmataceae is the only family in which only the smooth hymenophore configuration can be found. The major diversification of the hymenophoral configuration occurred in Auriscalpiaceae, Bondarzewiaceae, and Russulaceae. Furthermore, the resupinate habit gave rise to clavarioid habits, while on the other hand, the resupinate habit led to various morphological forms such as discoid, cupulate, orbicular, stereoid, auricularioid, pulvinate, disciform, effused-reflexed, pileate-sessile to flabelliform and gasteroid basidiomes with smooth, to grandinioid, rugose, tuberculate, raduloid, poroid or hydnoid hymenophore. The clavariod habit also led to agaricoid and gasteroid basidiomes with lamellar, regularly forked and globular or irregular hymenophores.

Molecular analyses have elucidated the evolutionary relationships (Larsson and Larsson 2003; Miller et al. 2006; He et al. 2019a; Wu et al. 2020a). The findings demonstrate significant morphological changes occurring at both the family and genus levels. Previous investigations utilizing only a single or few gene loci yielded inconclusive results regarding the phylogenetic relationship (Larsson and Larsson 2003; Miller et al. 2006). However, more recent multi-locus analyses have provided more definitive insights into the evolutionary relationships (He et al. 2019a; Wu et al. 2020a). The occurrence of gasteroid basidiomes in the Russulaceae family has been documented in various regions around the world, including Australia, China (Li et al. 2013b, 2018; Xu et al. 2019b), Spain (Martín et al. 1999; Calonge and Martín 2000), Patagonia, Southeast Asia (Verbeken et al. 2014) and USA (Zeller and Dodge 1919; Singer and Smith 1960). The development of gasteroid structures, often as hypogeous basidiomes, is believed to be an adaptation to dry climates (Miller and Miller 1988; Hibbett et al. 1997; Verbeken et al. 2014). Highly supported lineages of *Lactifluus*, *Lactarius*, and *Russula* often exhibit a combination of agaricoid and gasteroid species (Lebel and Tonkin 2007; Wilson et al. 2011). This challenges the idea that gasteroid genera within Russulaceae are distinct and independent from each other. The presence of scattered gasteroid species indicates that this transition to gasteroid forms has occurred multiple times in evolutionary history. Furthermore, there are notable similarities between closely related agaricoid and gasteroid species in their ITS regions (Li et al. 2013b, 2018), suggesting recent evolutions from agaricoid to gasteroid basidiome forms.

Justification of order and problems

Bondarzewiaceae vs. Hybogasteraceae

Hybogaster displays similar characteristics to the genus *Bondarzewia*, such as its overall appearance, structure, colors, spore characters, hyphal structure, as well as its habitat. However, it is uncertain whether this similarity indicates true affinity or convergence of traits. This distinction holds significant importance for making phylogenetic and systematic conclusions. Singer (1964) refrains from providing an opinion on this matter until additional data regarding the cultural characters and individual development of both *Hybogaster* and the Bondarzewiaceae become available. In a more recent study Palfner et al. (2020) propose that *Hybogaster giganteus* Singer should be considered synonymous with *Bondarzewia guaitecasensis* fa. *gigantea* Palfner, Galleguillos & E. Horak.

Russulaceae

Classification of Russulaceae within Russulales has not been fully elucidated due to its examination alongside other agaricoid species in the Agaricales order. Previous studies suggest that the amyloid spore ornamentations indicate a close relationship between this group and certain resupinate and effused-reflexed taxa (Donk 1971; Oberwinkler 1977; Pegler and Young 1979). Molecular analyses have provided evidence that several agaricoid, gasteroid, and corticioid species cluster together as a well-supported lineage and revealed an independent branch consisting of polymorphic Russulaceae species (Hibbett and Thorn 2001; Larsson and Larsson 2003). Further investigations into the phylogeny of Russulaceae were conducted following proposals for new genera such as *Lactifluus* and *Multifurca* in recent years. The genera *Boidinia*, *Gloeopeniophorella*, and *Pseudoxenasma* are characterized by corticioid (Hjortstam and Larsson 1976; Maekawa 1994; Larsson and Larsson 2003; Hjortstam and Ryvarden 2007b). On the other hand, *Lactifluus*, *Lactarius*, *Multifurca* and *Russula* exhibit agaricoid and gasteroid basidiomes. A common feature among these genera is the presence of sphaerocytes in their context. Historically, distinguishing between *Lactarius* species from *Russula* was based on the presence or absence of latex-exuding hyphae (Wang 2008, 2020; Li and Wen 2009; Li et al. 2015). However, the introduction of *Multifurca* blurred the boundaries between these two genera (Buyck et al. 2008). The type genus of the Russulaceae is Russula, with ca 1100 known species also the largest genus of the family (www.indexfungorum.org).

Significance

Ecological and economical roles

Ecological functions performed by members of Russulales include mycorrhizal symbiosis and wood decay. The predominant form of mycorrhizal symbiosis is ectomycorrhizal, with a large number of species from the Albatrellaceae and Russulaceae families forming mutualistic ectomycorrhizas with trees and shrubs (Miller et al. 2006; Wang 2008; Looney et al. 2016). Within the Russulaceae family, the most common genera involved in ectomycorrhizal symbiosis are *Lactifluus*, *Lactarius*, and *Russula*. This group is often referred to as the "russula-lactarius clade" (Tedersoo and Nara 2010). These well-known mycorrhizal associations occur between various plant families including Pinaceae (gymnosperms) and Betulaceae, Cyperaceae, Fagaceae, Nyctaginaceae, Polygonaceae, Rosaceae and Salicaceae (angiosperms) (Haug et al. 2005; Tedersoo et al. 2009, Tedersoo and Põlme 2012; Bâ et al. 2011; Li et al. 2015; Looney et al. 2016). Furthermore, the symbiotic association known as monotropoid mycorrhiza can be observed between certain members of the Russulaceae family and plants belonging to the Ericaceae subfamily Monotropoideae (Richard et al. 2005; Mühlmann and Göbl 2006; Smith and Read 2008). Another type of symbiosis exhibited by Russulaceae is orchid mycorrhiza. Orchids display different nutritional strategies, such as mycoheterotrophy or mixotrophy, which determine whether their relationship with Russulaceae is mutualistic or epiparasitic (Taylor et al. 2004; Girlanda et al. 2005; Roy et al. 2009). The diverse habitats occupied by Russlaceae correspond to a wide range of mycorrhizal plant species found in arctic and alpine tundra, boreal and Alpine forests, temperate forests, and tropical rainforests (Gardes and Dahlberg 1996; Li et al. 2020c, 2021a; Wang 2008; Wang et al. 2009). Wood-decaying behavior is frequently observed in resupinate taxa of Russulales (Larsson and Larsson 2003). By engaging in mycorrhizal symbioses and the process of wood decay, Russulales plays important role in nutrient cycling and decomposition within forest ecosystems.

Heterobasidion abietinum, *H. annosum* and *H. parviporum* have been recognized in Europe and *H. irregulare* and *H. occidentale* were described from North America and all are aggressive pathogens of managed coniferous forests (Yuan et al. 2021). *Echinodontium tinctorium* and *E. tsugicola* (P. Henn. & Shirai) Imaz. cause white heartrot of living Pinaceae in USA and Japan, respectively (Gilbertson and Ryvarden 1986).

Russulales is known for its rich abundance of wild edible mushrooms, particularly those belonging to the Russulaceae family. Numerous species of *Lactarius*, *Lactifluus*, and *Russula* are well-regarded as edible mushrooms in various regions across the globe. Examples include the *Lactarius deliciosus* complex, *Russula griseocarnosa* complex and *Russula* cf. *virescens* in China (Wang et al. 2009; Li et al. 2010; Deng et al. 2020; Wang 2020), *Russula vesca* in Europe, and *Lactifluus edulis* in tropical Africa (https://www2.muse.it/russulales-news). One of the other genera within Russulales that contain well-known edible fungi is *Hericium*. Two species in particular, *H. erinaceus* (commonly known as "monkey-head", "tree hedgehog", or "lion's mane") and *H. coralloides* (coral tooth fungus), are widely cultivated and consumed in China and North America (Dai and Yang 2008; Feng et al. 2023). Additionally, there are members of the family Albatrellaceae such as *Albatrellopsis confluens*, *A. ellisii*, *Polyporus dispansus*, and *Xeroceps yunnanensis* that are also consumed as edible fungi in China, North America, and Mexico (Gilbetrson and Ryvarden 1986; Zheng and Liu 2008; Díaz-Moreno et al. 2005). *Albatrellus subrubescens* was also found to be sold at a market located in Veracruz state, Mexico where it is considered an edible mushroom.

Chemical diversity

Some members of Russulaceae exhibit an acrid taste due to the presence of sesquiterpenes (Kobata et al. 1995; Vidari and Vita-Finzi 1995; Wang et al. 2005). Ingesting basidiomes mistakenly can lead to various gastrointestinal symptoms caused by a complex mixture of natural compounds. A notable species within this family, *Russula subnigricans*, is known for its lethal consequences as it can induce rhabdomyolysis. This is attributed to the presence of russuphelin A and cycloprop-2-ene carboxylic acid in the fungus (Takahashi et al. 1992; Matsuura et al. 2009b). Chemical analyses of members belonging to the Russulaceae family also focus on studying aroma and pigment compounds. The pleasant fragrance emitted by basidiomes of some Russulaceae can be attributed to sotolon and quabalactone III (Rapior et al. 2000; Wood et al. 2012). The vivid reddish, yellowish, and bluish tinges found on the surface of the pileus correspond to pteridine, sesquiterpenes, and methyl stearate (Harmon et al. 1979; Fröde et al. 1995). *Hericium erinaceus* is highly valued for its edible and medicinal properties due to various bioactive components it possesses such as terpenoids, phenolics, fatty acids, steroids, and alkaloids. These constituents contribute towards activities like anti-tumor effects, influence over immune-modulation responses, antihyperglycemic activity, antihypercholesterolemic impacts, neuroprotective roles alongside antimicrobial activity, and antioxidant and anti-ageing activities (Wang et al. 2015c; Thongbai et al. 2015).

Other relevant data and future recommendations

Numerous taxa belonging to Russulales exhibit an ectomycorrhizal lifestyle, resulting in their distribution being closely tied to specific biogeographic regions (Wang 2008; Li 2014; Li et al. 2015; Looney et al. 2016; Buyck et al. 2018). The genera *Lactarius*, *Lactifluus*, and *Russula* exemplify this relationship as they form obligatory symbiotic associations with plants; thus, indicating the significance of associated tree species for the accurate identification and taxonomy of these fungal groups. Neglecting the consideration of biogeography may lead to misidentification errors within this taxonomic group (Teng 1963; Tai 1979; Li 2014). It should be noted that certain closely related species may showcase morphological similarities despite occupying different forest forms or habitat factors such as altitude and climate zone (Wang 2008, 2020; Li et al. 2023a).

Sakaguchiales R.L. Zhao & K.D. Hyde 2017

Contributed by: Teun Boekhout

Introduction

Sakaguchiales, a monotypic order, was recently proposed based on estimated time of divergence (Zhao et al. 2017).

History

Sakaguchia dacryoidea was originally described in the genus *Rhodosporidium* (Fell et al. 1973). However, early molecular phylogenetic analysis showed that the species did not belong to *Rhodosporidium*, but rather to a separate genus (Yamada et al. 1994). This was confirmed by more recent phylogenetic studies that placed *Sakaguchia* in Cystobasidiomycetes (Fell et al. 2000; Scorzetti et al. 2002; Bauer et al. 2006; Wang et al. 2015a, b). Bauer et al. (2006) did not place *Sakaguchia* in any order of Cystobasidiomycetes, but Zhao et al. (2017) created Sakaguchiales based on time of divergence within Cystobasidiomycetes.

Characters that define the taxa in the order

Asexual reproduction by budding. Pseudohyphae or true hyphae may be present. Ballistoconidia are not produced. Heterothallic or self-sporulating. Conjugation results in true, binucleate hyphae with clamp connections. Teliospores occur laterally or terminally on hyphae, germinating with transversely septate, two- to four-celled basidia on which laterally and terminally basidiospores are formed. Presence of Coenzyme Q-10. Xylose absent in cell walls. Main distinction is the clustering in rDNA-based phylogenies in which *Sakaguchia* emerged as a distinct branch (Fell et al. 2000; Bauer et al. 2006; Zhao et al. 2017).

Plates (make sure characters of order are shown).

See Fig. 128.2 (Fell 2011)

Genera included

Family Sakaguchiaceae Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout 2015

Sakaguchia Y. Yamada, K. Maeda & Mikata 1994

Evolution

The monotypic character makes it impossible to infer evolutionary relationships within the order. A multigene phylogenetic analysis added a number of sexual yeast morphs to the genus that now has five species (Wang et al. 2015b). Zhao et al. (2017) estimated the time of origin 122 million years ago.

Justification of order and problems

As all molecular phylogenetic studies have demonstrated the isolated position of *Sakaguchia* among Cystobasidiomycetes, the order seems justified. Adding more taxa is needed to fully understand the biological and evolutionary potential of the order.

Significance

Ecological and economical roles

Members of Sakaguchiales are widespread in marine waters, including those of Antarctica and deep trenches, but also in glacial meltwater, and the phylloplane (Fell 2011).

Sebacinales M. Weiss, Selosse, Rexer, A. Urb. & Oberw. 2004

Contributed by: Leho Tedersoo

Introduction

Sebacinales is a recently described but well-delimited order among the early-diverging Agaricomycetes (Weiss and Oberwinkler 2001; Oberwinkler et al. 2014). It has a few tens of described species, but eDNA analyses suggest the presence of thousands of species associated with plant roots in endophytic and ectomycorrhizal interactions (Weiss et al. 2016).

History

The first species belonging to Sebacinales were initially described as *Corticium incrustans* and *Tremella epigaea* that were later transferred to the newly erected genus *Sebacina*. *Sebacina vermifera* with nematode-like spores was transferred to a separate genus Serendipita (reviewed in Oberwinkler et al. 2013a). Based on the criterion of monophyly, the anamorph genus *Piriformospora* was merged to *Serendipita* (Weiss et al. 2016). Based on micro- and macromorphological characters consistent with phylogeny and ecology, the genus *Sebacina* was divided into several genera (Oberwinkler et al. 2014).

Sebacinales is one of the earliest diverging groups of Agaricomycetes that was separated from Auriculariales based on molecular analysis (Weiss and Oberwinkler 2001; Weiss et al. 2004a, b). It remains a strongly supported, monophyletic group in single- and multi-gene phylogenetic analyses. Additionally, its two families, Serendipitaceae and Sebacinaceae, are well-supported (Weiss et al. 2016).

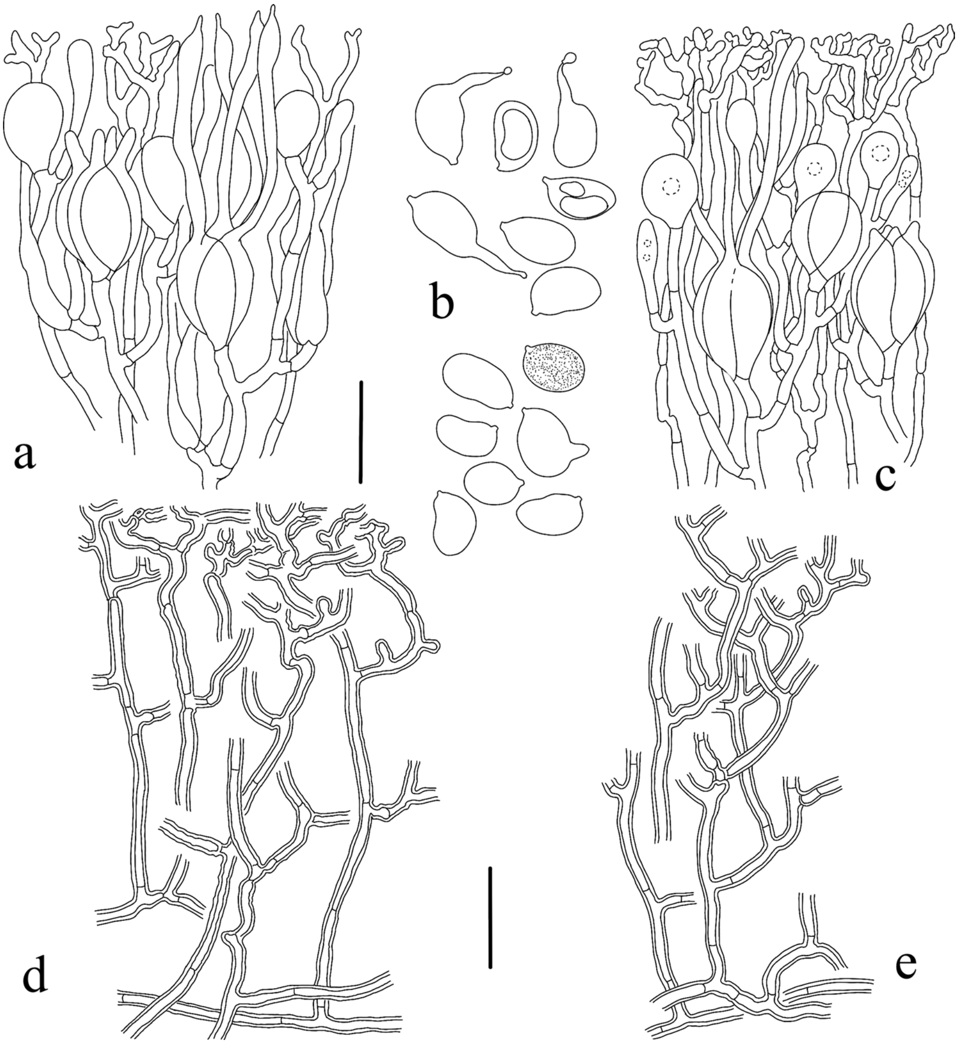
Characters that define the taxa in the order

Species of Sebacinales share multiple cellular features with other early-diverging Agaricomycetes. As in Cantharellales, parenthesomes of Sebacinales are continuous and imperforate (Oberwinkler et al. 2013a). However, their longitudinally septate meiosporangia (phragmobasidia) rather resemble the features of Auriculariales.

Representatives of all genera of Sebacinaceae (except *Paulisebacina*) form fruitbodies, whereas *Serendipita* form no fruit-bodies and sexual structures are rare (Oberwinkler et al. 2013a, 2014). Species of *Serendipita* and *Piriformospora* were initially described based on the teleomorph (Warcup and Talbot 1967), presence and morphology of chlamydospores (Verma et al. 1998) and monilioid cells (Riess et al. 2014). Genera and species of Sebacinaceae have been described based on fruit-body micromorphology, the presence of dikaryophyses and cystidia (Oberwinkler et al. 2014).

Plates

Fig. 51 Microscopic characters of *Sebacina incrustans*. **a**, **c** hymenia with basidia in different developmental stages and dikaryophyses; **b** basidiospores, three germinating with secondary spores; **d**, **e** thick-walled subhymenial hyphae. Scale bars = 20 µm. Redraw from Oberwinkler et al. (2014) by Mao-Qiang He



Genera included

Order Sebacinales M. Weiss, Selosse, Rexer, A. Urb. & Oberw. 2004
  Family Sebacinaceae K. Wells & Oberw. 1982
    Chaetospermum Sacc. 1892
    Ditangium P. Karst. 1867
    = *Craterocolla* Bref. 1888
    = *Poroidea* Göttinger ex G. Winter 1885
    Efibulobasidium K. Wells 1975
    Globulisebacina Oberw., Garnica & K. Riess 2014
    Helvellosebacina Oberw., Garnica & K. Riess 2014
    Paulisebacina Oberw., Garnica & K. Riess 2014
    Sebacina Tul. & C. Tul. 1871
    = *Atkinsonia* Lloyd 1916
    = *Collodendrum* Clem. 1909
    = *Corticioides* Lloyd 1908
    = *Cristella* Pat. 1887
    = *Opadorhiza* T.F. Andersen & R.T. Moore 1996
    = *Soppittiella* Massee 1892
    = *Tremellodendron* G.F. Atk. 1902
    Tremelloscypha D.A. Reid 1979
    = *Tremellostereum* Ryvarden 1986
  Family Serendipitaceae M. Weiss, Waller, A. Zuccaro & Selosse 2016
    Serendipita P. Roberts 1993
    = *Piriformospora* Sav. Verma, Aj. Varma, Rexer, G. Kost & P. Franken 1998

Evolution

Based on molecular dating, Sebacinales evolved between 230 and 250 Myr (Tedersoo et al. 2014b; Garnica et al. 2016), with a present estimate of 290 Myr. The split between the Sebacinaceae and Serendipitaceae families dates back to roughly 145 Myr (Tedersoo et al. 2014b) or 105 Myr (Garnica et al. 2016). The common ancestor of Sebacinales probably had no fruitbody and saprophytic lifestyle. Early in their evolution, the endophytic lifestyle in plant roots became prominent in Sebacinales, given the broad phylogenetic distribution of these ecological features at present. In the Sebacinaceae family, ectomycorrhizal lifestyle evolved once between 45 Myr (Tedersoo et al. 2014b) and 65 Myr (Garnica et al. 2016), covering the currently circumscribed genera *Sebacina*, *Helvellosebacina* and *Tremelloscypha*. In this ectomycorrhizal group, certain species produce large gelatinous, thelephoroid or ramarioid fruit-bodies (Riess et al. 2013). Ectomycorrhizal habit also seems to have evolved at least twice in the genus Serendipita (Tedersoo and Smith 2013), but probably within 20 Myr (Garnica et al. 2016). In a broader group of *Serendipita*, multiple species also establish ericoid mycorrhizal symbiosis with species of Ericaceae (Selosse et al. 2007) and colonize thalli of liverworts (Kottke et al. 2003). Along with Tulasnellaceae and Ceratobasidiaceae (Cantharellales), *Serendipita* species commonly associate with orchids, forming *rhizoctonia*-type root symbiosis. Also, the ectomycorrhizal *Sebacina* and *Helvellosebacina* species associate with orchids, but mainly with (partly) mycoheterotrophic groups (e.g. *Neottia* and *Hexalectis* spp.), playing an essential role in carbon transfer from trees (McKendrick et al. 2002; Taylor et al. 2003; Oja et al. 2015).

Justification of order and problems

Sebacinales is a morphologically and phylogenetically well-delimited order of Agaricomycetes. Also, the families and genera of Sebacinales are well justified. Species delimitation by morphological characters remains the main issue in taxonomy of both Sebacinaceae and Serendipitaceae. Here, the ITS region provides a suitable barcode with good resolution at 97–98% sequence similarity. Genomes of three cultures of *Serendipita* have been sequenced, but representatives of Sebacinaceae face issues because of uncultivability.

Ecological and economical roles

Despite the small size of Sebacinales, this group has important ecological roles and beneficial plant symbionts and providers of a mutualistic niche. The endophytic *Serendipita* species effectively act like arbuscular mycorrhizal symbionts in vascular plants and certain liverworts, with similar benefits in terms of nutrition and protection from abiotic and biotic stress. Serendipita spp. may sometimes act as dominant ericoid or orchid mycorrhizal fungi. Similarly, the ectomycorrhizal Sebacina spp. may sometimes dominate root symbiotic fungal communities and act as the sole mutualistic partners of *Neottia* and *Hexalectis* orchids. One of the ectomycorrhizal lineages of *Serendipita* is commonly associated with early developmental stages of wintergreens—partly mycoheterotrophic members of Pyrolaceae, probably sustaining their early development (Hashimoto et al. 2012).

Economically, Serendipita spp. can be considered important root symbionts of agricultural plants by providing nutritional benefits, inducing systemic resistance to root and leaf pathogens and enhancing tolerance of host plants to drought and salt stress (Weiss et al. 2016). Within the Sebacinaceae family, fruitbodies of a single species, *Tremelloscypha gelatinosa*, are consumed for food in Mexico (Bandala et al. 2014).

Chemical diversity

The chemical properties of Sebacinaceae species are poorly studied. *Serendipita* indica mycelial properties as well as genome and transcriptome are surveyed for the production of plant growth stimulating compounds (e.g., Venneman et al. 2020; Ntana et al. 2021).

Other relevant data and future recommendations

Unlike genus- and family-level taxonomy, the alpha taxonomy and ecology of both Sebacinaceae and Serendipitaceae are poorly known. Given the high ecological importance of Sebacinales, the following questions need answers: (1) What is the relative phylogenetic breadth of *Serendipita* species that are capable of forming mycorrhizal associations with orchids, liverworts and ericoid plants, and what are the genetic mechanisms enabling these structurally different associations; (2) what are the relative nutritional sources and benefits to plants in species of *Sebacina* and *Serendipita* compared with other fungal mutualists in ecto-, ericoid and orchid mycorrhizal and endophytic symbioses; and (3) what is the pharmacological potential of Sebacinales spp.

Septobasidiales Couch ex Donk 1964

Contributed by: Ricardo Valenzuela

Introduction

Septobasidiales is an order in Pucciniomycetes with 240 species, six genera classified in the family Septobasidiaceae, nearly all of which belong to the genus *Septobasidium* (Aime et al. 2006; He et al. 2019a, b). It is the only order in Basidiomycota that are enthomopathogens in scale insects and in Pucciniomycetes, they are the only dimorphic fungi, forming a yeast phase in the haploid state (Bauer et al. 2006). The morphology of Septobasidiales is variable, with corticioid, pteruloid, clavarioid, auricularioid, and amorphous basidiomes, but with phragmobasidia the auricularioid type, transversely septate, originating from thin to thick walled cells (called teleutospores by Couch 1941, probasidia by Aime et al. 2006, 2014) and they have clampless hyphae as all Pucciniomycetes. In Septobasidiales and *Platygloea disciformis*, the septal pores differ from the typical puccinialean septal pore with an organelle-free zone, delimited by microbodies, surrounds each side of the pore, rather in Septobasidiales have microbodies surrounding the septal pores in a more or less circular arrangement appear to be lacking, but the pores are often associated with nonmembrane-bounded electronopaque globules and bands (Bauer et al. 2006). These fungi are found as mats of hyphae covering infected scale insects on plants and they rarely kill their hosts, but use them as nutrients providers, while keeping them alive (Aime et al. 2006; Humber 2008). The fungus eventually kills the infected scale insect and subsequently, dikaryotic hyphae with basidia arise from the insect body to reproduce and disperse the basidiospores or conidia (Bauer et al. 2006), although the true nature of the association may be more commensal than truly parasitic (Henk and Vilgalys 2007). Septobasidiales have a cosmopolitan distribution, living in tropical and temperate zones of Europe, Asia, Africa, North America and South America.

History

Septobasidiales was proposed by Couch in 1938, but was not validated because he did not include a diagnosis in latin, but Donk (1964) considered Couch's description and described and validated the order. Patouillard (1892) described the genus *Septobasidium* with *S. velutinum* Pat. as the type species in the class Hymenomycetes with heterobasidia. Later, Raciborski (1909) proposed the family Septobasidiaceae to include the genera, *Ordonia* Racib., *Mohortia* Racib., and *Septobasidium* Pat., the first two genera have been synonymized with *Septobasidium*, but some species of both genera are validated in Index Fungorum page, so it is necessary obtain sequences of DNA to corroborate their synonymy or validity of taxonomic position of this species. *Uredinella* was described by Couch as an intermediate fungus between *Septobasidium* and the rust fungi (Couch 1941). Hughes and Cavalcanti (1983) described *Johncouchia* S. Hughes & Cavalc., the only asexual genus of Septobasidiales with the unique species *J. manguiferae* (Bat.) S. Hughes & Cavalc. with its sexual morph *Septobasidium pilosum* Boedijn & B.A. Steinm. The genus *Auriculoscypha* was first described and classified in the order Auriculariales but the authors mentioned its very close conections to Septobasidiales by having the non-gelatinous brown fibrous context, thick-walled brown septate hyphae devoid of clamp-connexions, circinate basidia with two fertile segments and enormous septate spores (Reid and Manimohan 1985), and later, Lalitha and Leelavathy (1990) discovered that the fungus is associated to a coccid, and *Auriculoscypha* must be included in Septobasidiales. Henk and Vilgalys (2007) mentioned that Oberwinkler in 1989 suggested that *Septobasidium* is an overly broad generic concept, and erected a new genus *Coccidiodictyon* Oberw. and argued for the resurrection of the genus *Ordonia*. *Coccidiodictyon* was accepted in Septobasidiales, and *Ordonia* is synonymed with *Septobasidium*, because there are not sequences of DNA to corroborate this proposal of Oberwinkler.

Henk and Vilgalys (2007) include two families in Septobasidiales, Septobasidiaceae are parasitic on scale insects (*Coccoidea*), while *Pachnocybe*, the only genus in the family Pachnocybaceae, is found in wood as saprothoph. *Pachnocybe* has been linked to the Septobasidiaceae based on weakly supported phylogenetic inference and the reported presence of microscala, cross-linking membranas between mitochondria and sometimes endoplasmic reticulum only found in the few species examined of *Septobaidium*. However, Bauer et al (2006) mentined that the mitochondrial complexes might thus represent an apomorphy for *Pachnocybe* and the Septobasidiales are phylogenetically separate in monophyletic clades (Kumar et al. 2007).

Characters that define the taxa in the order

Septobasidiales includes the family Septobasidiaceae and they form a well supported monophyletic clade. Septobasidiaceae include six accepted genera: *Aphelariopsis*, *Auriculoscypha*, *Coccidiodictyon*, *Johncouchia*, *Septobasidium* and *Uredinella*.

Aphelariopsis Jülich is characterized by its basidiomes erect, thelephoroid or clavarioid to pteruloid, simple or branched, dark brown, coriaceous, hyphae brown, cylindrical, clampless, somewhat thick-walled. Probasidia broadly ellipsoid or globose, thin- or slightly thick-walled. Phragmobasidia hyaline or yellowish, cylindrical or sinuous, thin- or slightly thick-walled, transversely septate, with 3–4 sterigmata. Basidiospores hyaline, cylindrical or slightly curved, smooth, thin-walled, inamyloid. This genera is validated, but it need phylogenetic studies with molecular data, because Index fungorum considered the type species as *insertae sedis*. One species described from Colombia.

Auriculoscypha D.A. Reid & Manim. was described with basidiomes dependent, cupulate, with central and dorsally attached stipe and consitence woody. Context golden-brown, cottony-fibrillose with hyphae hyaline toward the margin, elsewhere pale brown to brown with thickened refractive walls, and septate and clampless. Probasidia not observed. Phragmobasidia auricularioid, thin-walled or with slightly thickened wall in basal region, hyaline, varying from clavate to circinate, transversely septate, 1–2-septate, but with only two fertile segments. Basidiospores thin-walled, hyaline, cylindric to allantoid, with up to 7 transverse septa, occasionally with both transverse and longitudinal septa and then appearing rnuriform. The genus was validated morphologically and phylogenetically with one species described fron India.

Johncouchia S. Hughes & Cavalc. It is an asexual genus characterized by its colonies pulvinate, scattered or crowded, hairy or velutinous, with sterile ends of conidiophores. Conidiophores macronematous, mononematous, crowded, erect, straight or flexuous, brown to dark brown, paler at the apex, smooth, thick walled, simple or bearing 1 to 4 lateral, solitary or paired branches mostly in the lower part. Conidiogenous cells mono- or diblastic intercalary, and sometimes terminal, cylindrical, determinate, mostly in the lateral branches. Conidia dry, pale brown to brown, irregular in size and contour, globose to broadly ellipsoidal, smooth, solitary or paired, predominantly lateral and arising from the upper part of the conidiogenous cell, often produced in acropetal succession, composed of a protuberant obovoid to pyriform basal cell, closely appressed, straight or curved, 1- or 2(-4)-septate arms which may also be branched. It is a validated genus with one species, but it was not DNA sequences and not has been confirmed.

Septobasidium Pat. is characterized by its basiome resupinate, effused, coriaceous, smooth to rugose surface, hyphae hyaline to brown, cylindrical, clampless, thin walled to somewhat thick-walled. Subiculum white to brown. Probasidia upon the hyphae at or near the hymenial surface, hyaline to brown, globose to cylindrical, thin- or slightly thick-walled. Phragmobasidia auricularioid, remain attached to the hyphae hyaline, obovoid to cylindrical, straight or curved, 4-celled, transversely septate, 3-septate. Basidiospore thin-walled, hyaline, cylindric to allantoid, smooth. *Septobasidium* is the larger genus of the order Sepobasidiales and it is validated with morphological and molecular characters.

Uredinella Couch was described by Couch (1941) to include fungi with minute, circular, flattened, discoid patches 0.2–1.5 mm wide, on the bark of several deciduous trees, easily separable from the substratum, annual, always overgrowing a scale insect. Mature teleutospores (probasidia) uninucleate, cylindrical to pyriform with a distinct germ pore, brownish, thick walled rise to a typical, four-celled, septate phragmobasidia auricularioid, cylindrical, straight or curved, 4-celled, transversely septate, 3-septate. Basidiospores thin-walled, hyaline, cylindric to allantoid, smooth, it originates a secunadry spore over an sterigmata. Growing on scale insects which are parasitized by haustoria of the *Septobasidium* type. *Uredinella* is a validated genus with morphological and molecular characters and include two species.

Plates

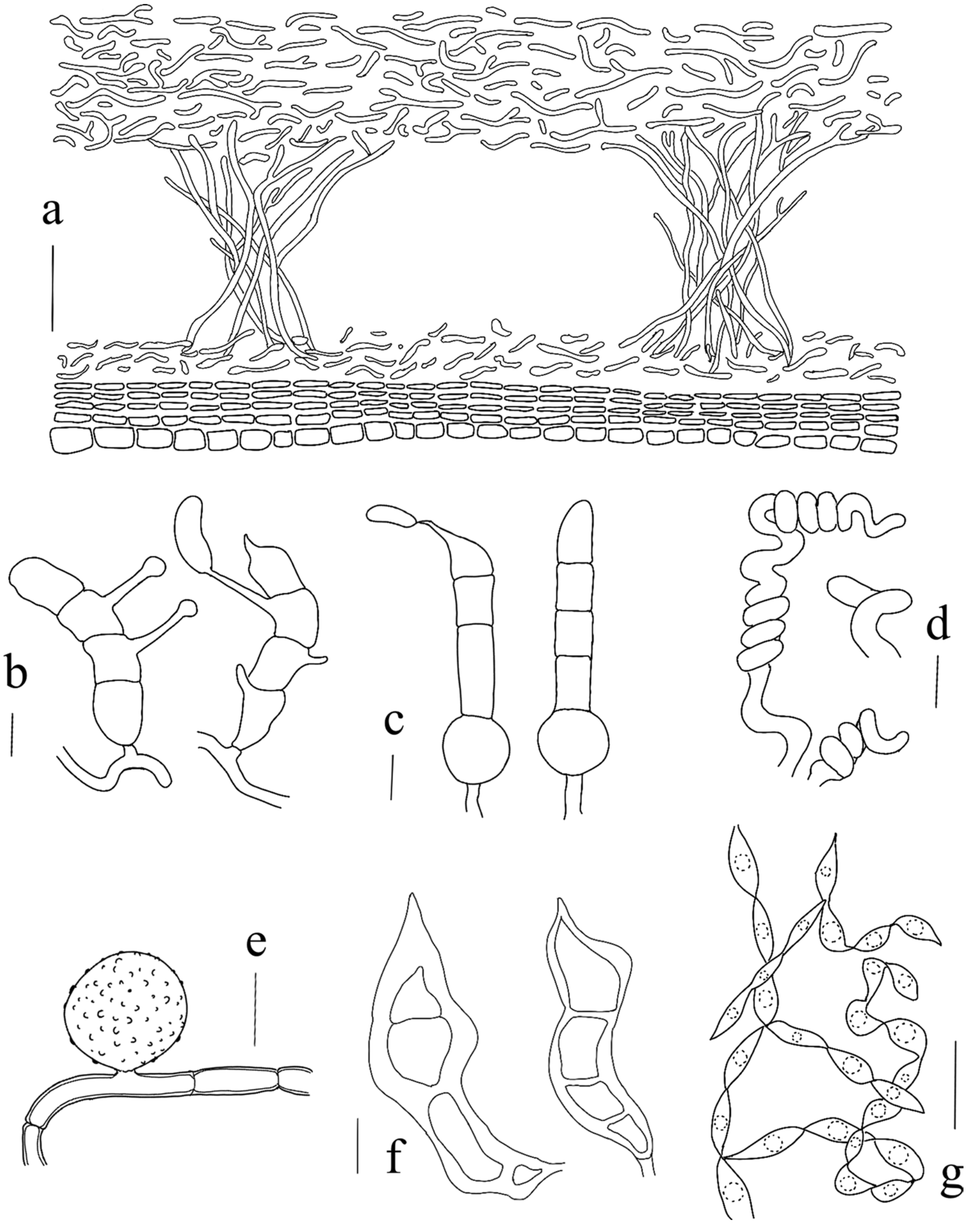


Fig. 52 Septobasidiales. **a**, **c** from *Septobasidium meredithiae*; **b**, **d** from *Septobasidium gomezii*; e,g from *Septobasidium* sp.; **f** from *Septobasidium reevesiae.* **a** cross section of the basidiome showing subiculum with pillars supporting the upper layer; **b**, **c**, **f** basidia; **d**, **g** haustoria; **e** probasidia. Scale bars: a = 50 µm; b–g = 10 µm. Redraw from Henk (2005) and Guo (2015) by Mao-Qiang He. Also see figs. 1–12 in Henk and Vilgalys (2007)

Genera included

Family Septobasidiaceae Racib. 1909
  Aphelariopsis Jülich 1982
  Auriculoscypha D.A. Reid & Manim. 1985
  Coccidiodictyon Oberw. 1989
  Johncouchia S. Hughes & Cavalc. 1983
  Septobasidium Pat. 1892
  = *Ordonia* Racib. 1909
  = *Campylobasidium* Lagerh. ex F. Ludw. 1892
  = *Glenospora* Berk. & Desm. 1849
  = *Mohortia* Racib. 1909
  = *Rudetum* Lloyd 1919
Uredinella Couch 1937

Evolution

Henk and Vilgalys (2007) tentatively conclude that the Septobasidiales is monophyletic and that there is a single origin of scale insect parasitism in the Pucciniomycetes defining a monophyletic Septobasidiaceae, with a sister clade of Pachnocybaceae. Humber (2008) mentioned that random taxonomic distribution of fungi pathogenic or parasitic for insects or other invertebrate hosts that these nutritional habits emerged repeatedly and independently in many different fungal lineages. The only significant basidiomycete-insect associations of Septobasidiales species with coccid scale insects, go far beyond the dependence on a scale's mouthparts to gain access to nutrients from the host plant's phloem. Septobasidiales covers, protects, and allows increases of insect populations while parasitizing a small proportion of apparently living coccid with coiled haustoria that absorb nutrients from the host plant's phloem indirectly through the scale's hemocoel. Kumar et al. (2007) said that traditional and molecular characters place Septobasidiales in a comparatively basal position among the rust fungi. Septobasidiales species are otherwise obligatory phytopathogens; it is difficult to conceive that this unique fungus-scale-plant relationship could have arisen by any means except by the host transference of a phytopathogenic rust fungus onto parasitic scale insects on a shared plant host (Humber 2008).

Justification of order and problems

Septobasidiales is a group of fungi with morphological and molecular evidence and they are validated phylogenetically in the class Pucciniomycetes of the subphylum Pucciniomycotina in the phylum Basidiomycota (Aime et al 2006; Bauer et al. 2006; Henk and Vilgalys 2007; Kumar et al. 2007).

The problematic of the Septobasidiales and Septobasidiaceae are with several genera and species did not have phylogenetic studies with sequences of DNA.

Sistotremastrales L.W. Zhou & S.L. Liu 2022

Contributed by: Li-Wei Zhou, Shi-Liang Liu

Introduction

Sistotremastrales, a group predominantly comprising wood-inhabiting corticioid fungi (with a few species exhibiting a poroid configuration, Dai 2012a), has been segregated from Trechisporales and proposed as a distinct order (Liu et al. 2022a). Most species in this order exhibit a notable microscopic feature, possessing 6–8 sterigmata of basidia, while the basidia in a few species have 4 sterigmata only (Liu et al. 2022a). Presently, the order consists of one family Sistotremastraceae, encompassing two genera: *Sistotremastrum* and *Sertulicium*. The establishment of Sistotremastrales is supported by morphological characteristics, phylogenetic tree analysis and molecular clock analysis (Liu et al. 2022a).

History

During revising the taxonomy of Trechisporales, Liu et al. (2022a) established the order Sistotremastrales with *Sistotremastrum* as the type genus. Larsson (2007) previously proposed differentiating *Sistotremastrum* from other genera in Trechisporales and used the name "*Sistotremastrum* family" for this distinction. Spirin et al. (2021) separated *Sertulicium* from *Sistotremastrum*, and suggested that both genera form a distinct clade within Trechisporales. However, even if the morphological characteristics of *Sertulicium* and *Sistotremastrum* are also distinct, no formal taxonomic changes have been proposed recently, primarily due to insufficient phylogenetic support (Liu et al. 2019a; Spirin et al. 2021). Based on multilocus phylogenetic analysis, Liu et al. (2022a) found that Sistotremastraceae forms a separate lineage distinct from Trechisporales. Complemented with morphological examinations and molecular clock analysis, it is recommended to establish both a new family and an order, namely Sistotremastraceae and Sistotremastrales (Liu et al. 2022a).

Characters that define the taxa in the order

Species of this order have basidiomes resupinate, effused, thin. Hymenophore smooth, grandinioid or odontioid. Hyphal system monomitic, all septa with clamp connections. Cystidia mostly absent. Basidia cylindrical to tubular with four to eight sterigmata. Basidiospores smooth, ellipsoid to cylindrical, inamyloid, acyanophilous. All known species in this order are wood-inhabiting fungi.

Plates

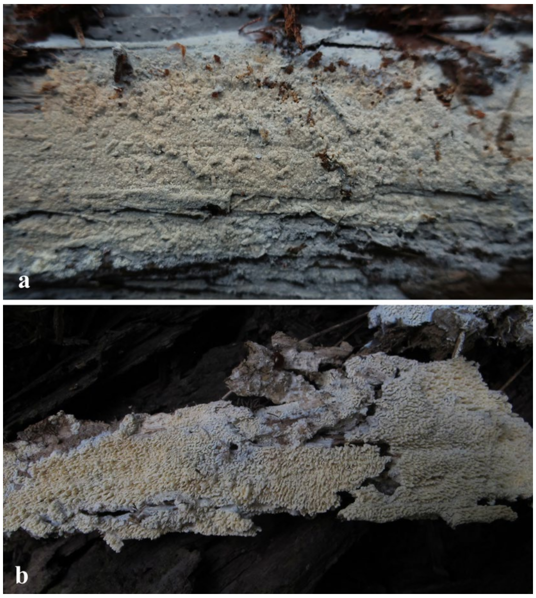


Fig. 53 Typical characteristics of basidiomes in Sistotremastrales. **a** *Sertulicium guttuliferum* (LWZ 20191018-31, Belovezhskaya Pushcha National Park, Republic of Belarus); **b** *Sistotremastrum aculeatum* (LWZ 20180415-15, Selangor, Malaysia)

Genera included

Family Sistotremastraceae L.W. Zhou & S.L. Liu
Sertulicium Spirin, Volobuev & K.H. Larss. 2021
Sistotremastrum J. Erikss. 1958

Evolution

Based on the current phylogenetic analyses of Agaricomycetes, Sistotremastrales and Trechisporales form a sister group. However, this relationship does not compromise the precision of delineating Sistotremastrales from Trechisporales and establishing a distinct order, due to their morphological differences. Moreover, the molecular clock analysis indicates that the divergence between Sistotremastrales and Trechisporales occurred approximately 176 million years ago (Liu et al. 2022a), aligning with the expected divergence time for an order-level classification (He et al. 2019a).

Spiculogloeales R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw. 2006

Contributed by: Nathan Schoutteten, Teun Boekhout

Introduction

As a result of molecular phylogenetic studies integrating both yeast species and dimorphic or filamentous fungi, our understanding of natural groups in Basidiomycota greatly improved. Spiculogloeales is an order that includes both dimorphic fungi known from the filamentous stage and species currently only known from their yeast stage. Filamentous fungi in Spiculogloeales are dimorphic mycoparasites growing intrahymenially in their host. Species only known from yeast stages were mainly isolated from phylloplanes.

History

Spiculogloea was introduced by Roberts (1996) to accommodate *Spiculogloea occulta*, an intrahymenial mycoparasite of *Hyphoderma argillacea*. The genus is defined by transversely three-septate basidia, which are ornamented with fine spicules, and the presence of clamped tremelloid haustoria. Later, several authors described four additional *Spiculogloea* species based on morphological similarities of the basidia (Roberts 1997; Hauerslev 1999; Trichies 2006; Schoutteten et al. 2018). All develop a sexual stage in the hymenium of their fungal host species and interact with their host by means of tremelloid haustoria. Early rDNA-based phylogenetic reconstructions placed clustered *Spiculogloea* and *Mycogloea* isolates on a long branch as sister to Agaricostilbales (Weiss et al. 2004a, b; Bauer et al. 2006; Aime et al. 2006). When Bauer et al. (2006) introduced the class Agaricostilbomycetes, the authors included the Spiculogloeales into it, albeit with the reservation that they may represent a class on their own. In a later work based on multilocus phylogenetic reconstructions, Wang et al. (2015b) found that *Spiculogloea* clusters with asexual yeast species from the subbrunneus group, for which they introduced the genus *Phyllozyma*. Given the large genetic distance with Agaricostilbales, the authors proposed the separate class Spiculogloeomycetes for this clade. Recently, Li et al. (2020b) introduced the genus *Meniscomyces* for two yeast species with a distinct lunate spore morphology, which were isolated from phylloplanes in China.

Characters that define the taxa in the order

Spiculogloeales is mainly defined by its phylogenetic position in which it forms a deep lineage sister to Agaricostilbales (Aime et al. 2006; Bauer et al. 2006) or as a sister group to Mixiomycetes (Wang et al. 2015a). The order comprises species known from filamentous stages only and species for which only the yeast stage is known. However, it is expected that all members of Spiculogloeales are dimorphic and are capable of sexual reproduction in the filamentous stage. Basidia in filamentous *Spiculogloea* species are transversely three-septate, ornamented with fine spicules, and often cyanophilous (Roberts 1996; Bauer et al. 2006). According to Bauer (2004) and Bauer et al. (2006), filamentous members of Spiculogloeales are mycoparasites that have tremelloid haustorial cells which attach to host hyphae. Along the host–parasite interface in the haustorial apex, small nanometer-fusion pores are formed of 14–19 nm diam., which establish cytoplasmic contact between host and parasite.

Plates

Fig. 54 Colony morphology of *Spiculogloea* sp. (culture NS 20-072), also see figures in Bauer et al. (2006), Schoutteten et al. (2018)

Genera included

Family Spiculogloeaceae Denchev 2009
  Meniscomyces Q.M. Wang & F.Y. Bai 2020
  Phyllozyma Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout 2015
  Spiculogloea P. Roberts 1996

Evolution

The presence of both yeast and filamentous stages within a limited number of genera makes it difficult to infer evolutionary trends within the order. The phylogenetic proximity to Mixiomycetes with these two classes having a sister group relation to Agaricostilbomycetes indicates that further phylogenomics investigation including taxa from all these lineages is needed to understand evolutionary trends amongst them. The mycoparasitic ecology enabled by nm-fusion pores is also present in representatives of Agaricostilbomycetes, Classiculomycetes, and Cystobasidiomycetes. Spiculogloeales are estimated to have emerged 266 million years ago (Zhao et al. 2017).

Justification of order and problems

Spiculogloeales forms a distinct lineage within Pucciniomycotina that warrants recognition as a separate order. However, more taxa must be found that belong to this lineage to comprehend the biological diversity observed.

Significance

Ecological and economical roles

The filamentous species are intrahymenial mycoparasites (Bauer et al. 2006), whereas the yeast taxa occur on leaves without a clear ecological strategy.

Chemical diversity

Unknown.

Sporidiobolales Doweld 2001

Contributed by: Teun Boekhout

Introduction

This order within Microbotryomycetes includes the traditional red yeasts, which may or may not form ballistoconidia. When implementing the 'One Fungus = One Name' nomenclature, preference was given to the older names that were initially used for the anamorphic yeasts. Due to this, the generic concepts changed the currently accepted genera and may include asexually and sexually reproducing species (Wang et al. 2015b).

History

Sporidiobolales was proposed by Doweld (2001), but as this order was described in literature not read by yeast taxonomists, it went unnoticed. In 2003, Sampaio and colleagues also described this order, but this name (viz., Sporidiobolales Sampaio, Weiss & Bauer) is superfluous due to priority of Sporidiobolales Doweld.

Characters that define the taxa in the order

Here we follow the description given by Sampaio et al. (2003). The order includes both sexually and asexually reproducing species. Non-phytoparasitic, but probably several members are mycoparasitic. Colonies red, orange, or pink due to the presence of carotenoid pigments. Hyphae without haustorial branches, but in several species colacosomes are present in hyphae. Hyphal septa have 'simple' septal pore complexes. Teliospores are present in sexually reproducing species, germinating with transversely septate basidia from which basidiospores are passively released. Budding yeast cells are present, and ballistoconidia may be present. D-glucuronate and myo-inositol are not utilized.

Plates

See Figs. 127.2–127.10 and 130.2–130.8 in Sampaio (2011a, b).

Genera included

Family Sporidiobolaceae R.T. Moore 1980
  Rhodosporidiobolus Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout 2015
  Rhodotorula F.C. Harrison 1927
  = *Chromotorula* F.C. Harrison 1927
  = *Rhodosporidium* I. Banno 1967
  Sporobolomyces Kluyver & C.B. Niel 1924
  = *Amphiernia* Grüss 1927
  = *Aessosporon* Van der Walt 1970
  = *Blastoderma* B. Fisch. & Breback 1894
  = *Prosporobolomyces* E.K. Novák & Zsolt 1961
  = *Sporidiobolus* Nyland 1950

Evolution

Sporidiobolales was identified in many single gene and multigene based phylogenetic studies (e.g. Fell et al. 2000; Scorzetti et al. 2002; Aime et al. 2006; Bauer et al. 2006; Wang et al. 2015a, b; Zhao et al. 2017). Within Microbotryomycetes, the order appeared to hold a rather basal position (Wang et al. 2015a, b; Zhao et al. 2017), whereas in other studies it clustered more central in this class (e.g. Sampaio et al. 2003; Aime et al. 2006; Bauer et al. 2006). Thus, further in-depth phylogenomics studies are needed to decipher the evolutionary trends within the order, e.g., with respect to evolution of sexual versus asexual reproduction, including the genes involved in mating and meiosis, the presence and absence of ballistoconidia, but also the evolution of genes involved in carotenoid biosynthesis. Sporidiobolales is estimated to have emerged 118 million years ago (Zhao et al. 2017).

Justification of order and problems

Sporidiobolales seems well defined in all phylogenetic studies performed so far (refs see above).

Significance

Ecological and economical roles

The following is taken from The Yeast, a taxonomic Study (Hamamoto et al. 2011; Sampaio 2011a, b, c). Members of Sporidiobolales occur widespread. The more common species are known globally from phyllosphere, marine, estuarine—and brackish waters, but also freshwater, soil, plant detritus, plants and fruits. Some species prefer colder habitats, such as Antarctica. Several species are biotechnologically and agriculturally of interest, e.g., as producers of carotenoid pigments, lipids, as degraders of lignin and aromatic compounds, as biocontrol agents. Some species have biocontrol capabilities, others are involved in russetting of apples, and occasionally, they cause infection of humans.

Chemical diversity

Unknown.

Stereopsidales Sjökvist, E. Larss., B.E. Pfeil & K.H. Larss. 2013

Contributed by: Sergio P. Gorjón

Introduction

Stereopsidales is a small and basal order that represents an early-diverging lineage of Agaricomycetes (Sjökvist et al. 2014). According to He et al. (2019a, b), it contains only one genus, *Stereopsis* D.A. Reid in a single family Stereopsidaceae Sjökvist, E. Larss., B.E. Pfeil & K.H. Larss. and about 15 species. *Clavulicium macounii* (Burt) Parmasto, the type species of *Clavulicium* Boidin, and previously considered a member of Cantharellales, seems to be phylogenetically related to the type species of *Stereopsis, Stereopis radicans* (Berk.) D. A. Reid but there is conflict in the data (Sjökvist et al. 2014).

History

Stereopsidales was circumscribed by Sjökvist et al. (2014), indicating two strongly supported lineages, the stipitate generic type of *Stereopsis, Stereopsis radicans* and the corticioid *Clavulicium globosum* Hjortstam & Ryvarden forming a well supported clade. Therefore, *C. globosum* was combined in *Stereopsis* as *Stereopsis globosa* (Hjortstam & Ryvarden) Sjökvist. *Clavulicium macounii* is included in Stereopsidales when analyzing *rpb2* or LSU and SSu, but not when considering *tef1*.

Characters that define the taxa in the order

Stereopsidales is composed of homobasidiomycetes with effused, stipitate, spathulate or funnel shaped basidiomes with smooth hymenial surface. The basidia are clavate, bearing characteristically two sterigmata. The two sterigmata is an indication of an amphithallic reproductive mode, where two nuclei are sorted to each spore, often omitting outcrossing. Cystidia are usually present. The basidiopores are hyaline, smooth, and upon drying become angular. The highly refractive contents of the spores and the way in which the spores become angular and amber-like upon drying in *Stereopsis radicans*, *S. globosa* and *C. macounii* is a morphological feature which separates them from species in other orders of Agaricomycetes (Sjökvist et al. 2014). Both *Stereopsis* and *Clavulicium* sensu lato display a considerable micromorphological diversity, for example in spore morphology, presence or absence of cystidia, and presence or absence of clamps (Sjökvist et al. 2014).

Stereopsis radicans and *S. globosa* are both found in tropical rainforests and cloud forest. *Clavulicium macounii* is found on strongly decayed wood, mostly in boreal conifer forests, and like *Stereopsis globosa* it forms effused basidiomes with a smooth hymenophore. The micromorpological characters are the same as those in *S. globosa* and *S. radicans*, with the exception of the spore shape, which in *C. macounii* is ellipsoid (Sjökvist et al. 2014).

Plates

Fig. 55 Basidomes of *Stereopsis* sp. on a conifer cone (ZRL20200716, Sichuan province, China)

Genera included

Family Stereopsidaceae Sjökvist, E. Larss., B.E. Pfeil & K.H. Larss. 2014
  Stereopsis D.A. Reid 1965
  Stereopsidales genera *incertae sedis*
  Clavulicium Boidin 1957
  Nothocorticium Gresl. & Rajchenb. 1999

Evolution

The type of *Stereopsis* possesses a typical stipitate basidiome with a smooth hymenophore, but this feature is also present in other lineages of stipitate stereoid fungi such as *Cymatoderma* (Polyporales), *Cotylidia* (Hymenochaetales), *Stereopsis vitellina* (S. Lundell) D.A. Reid (Atheliales), and *Stereopsis humphreyi* (Burt) Redhead & D.A. Reid (Agaricales) (Sjökvist et al. 2012). *Clavulicium macounii* is sister species to the *Stereopsis* clade, and like *Stereopsis globosa* it forms effused basidiomes with a smooth hymenophore. It is likely that the resupinated state may be the ancestral condition, as has been shown in other lineages of Agaricomycetes. This order would be up to 290 Myr, based on a comparison of a dated genome phylogeny (Sjökvist et al. 2014).

Justification of order and problems

According to Sjökvist et al. (2014) placement of *C. macounii* is not equally clear. Samples from this species appear as the sister group to the *S. radicans—C. globosum* clade in analyses of *rpb2*, SSU and LSU, but with bootstrap supports only up to 63% and with low posterior probabilities. *Clavulicium macounii* was not found to be sister to *S. radicans—C. globosum* in analyses of *tef1*. Analyses of rpb2 and SSU reveal a sister relationship between Phallomycetidae and the *S. radicans—C. globosum—C. macounii* clade, whereas the phylogeny of tef1 shows *C. macounii,* and the *S. radicans—C. globosum* clade as a part of a paraphyletic Phallomycetidae. Preliminary ITS and LSU analyses recover *Nothocorticium*, a corticoid genus endemic to Chilean and Argentine Patagonia, closely related to *Clavulicium macounii* (Gorjón, unpublished). Unfortunately, at the moment we do not have genomic data to corroborate these statements.

Thelephorales Corner ex Oberw. 1976

Contributed by: Sten Svantesson, Sergio P. Gorjón

Introduction

Thelephorales is a major order in Agaricomycetes and a well-defined genetic lineage. It currently contains 2 families, 17 genera, and ca. 470 species (Index Fungorum 2023). By contrast the ITS sequence database UNITE hosts more than 15 648 Species Hypotheses at 1.5% minimum distance between sister species (Kõljalg et al. 2013; Nilsson et al. 2018), hence making it the second largest basidiomycete order. This discrepancy is due to a lack of taxonomic studies, especially of its corticioid genera, and problems relating to the description of new species (Svantesson 2020). Species in Thelephorales are distributed globally, except to Antarctica. They are of great importance; the order is predominantly ectomycorrhizal and frequent in occurrence to the extent where its species often co-dominate such communities (e.g. Taylor and Bruns 1999; Ryberg et al. 2009; Botnen et al. 2015). A few species also have culinary value and and many seem to be potentially useful in medicine.

History

The first to treat the approximate assemblage of genera currently placed in Thelephorales as a group was Patouillard (1900), under the name "Série des Phylactéries". Creation of the order was, however, effected much later—it was first discussed by Corner (1968) but validly published by Oberwinkler (1976).

Donk (1964) appears to be the first to delimit Thelephoraceae in the modern sense using the name, i.e. encompassing the genera *Amaurodon, Lenzitopsis, Odontia, Polyozellus, Thelephora, Tomentella* and *Tomentellopsis* (at that time also including *Hydnodon* and *Scytinopogon*). Both his and Patouillard's (1900) circumscription were based on the dark, ornamented spores that are common among both stipitate and corticioid species in the group.

Donk (1961) also described the second family in Thelephorales, Bankeraceae, for the stipitate genera *Phellodon* and *Bankera* (the latter now synonymized with the former). This distinction was made based on the colourless spores of said genera, which he also perceived as more finely ornamented than those of Thelephoraceae. Subsequently, the remaining stipitate genera—*Boletopsis*, *Hydnellum* and *Sarcodon*—were also transferred into Bankeraceae (Jülich 1981; Stalpers 1993).

With the advent of molecular methods Baird et al. (2013) showed that *Bankera* makes *Phellodon* paraphyletic and consequently synonymised *Bankera* with *Phellodon*. Svantesson et al. (2021a) found a similar situation for Polyozellus and *Pseudotomentella*, and thus made the latter a synonym of the former.

A number of mostly monotypic genera, hitherto unstudied by molecular methods, have been added to Thelephorales through the years and it is dubious whether any of them belong to it in its current concept. These are: *Aldrigiella, Bubacia, Gymnoderma, Skepperia and Thelephorella*. As a conservative measure, they are here retained within the order.

Morphological features that define taxa in the order

Species in Thelephorales display a great variability of features in terms of shape of basidiomes. Species in Bankeraceae are typically stipitate and hydnoid (*Hydnellum*, *Phellodon,* and *Sarcodon*) or stipitate and poroid (*Boletopsis*), while most species in Thelephoraceae form corticioid basidiomes with smooth to hydnoid hymenophores (*Amaurodon*, *Odontia*, *Polyozellus*, *Tomentella* and *Tomentellopsis*). Within the latter family there are, however, also species whose basidiomes are finger-like (*Thelephora*), smooth to tuberculate, funnel-shaped (*Amaurodon*, *Thelephora*), cantharelloid (*Polyozellus*) or even sessile, lamellate (*Lenzitopsis*).

In contrast to the considerable macromorphological variation displayed among its members, from a microscopical perspective the order is usually easily recognized by the shape and colour of its basidiospores. Except for two species in *Amaurodon*, whose spores appear smooth under a light microscope, they are warted to echinulate, often angular or lobed, carry prominent aculei and in most cases have darkly pigmented spore walls (Svantesson 2020). Since nearly all species lack cystidia, spore characteristics together with hyphal measurements are the main distinguishing micromorphological features.

Many species are part of species complexes and are very similar in morphology—some to the level where only very slight microscopic differences can be used to separate genera, or where it is necessary to draw on to their mode of nutrition and phylogenetic information in order to do so. One example of this is the sister genera *Hydnellum* and *Sarcodon*, which were until recently considered distinguishable based on the consistency of basidiomes, but where spore size now remains the only morphological difference (Larsson et al. 2019). Another is *Tomentella* and *Odontia*, both groups of resupinate corticioid fungi, where the first contains ectomycorrhizal species and the second harbours only saprotrophic representatives (Tedersoo et al. 2014c; Zhou et al. 2022c).

Plates

Fig. 56 Basidiomes of Thelephorales. **a** *Sarcodon imbricatus* (Jerzy Opioła s.n., Poland); **b** *Boletopsis leucomelaena* (Holger Krisp s.n., Germany); **c** *Polyozellus multiplex* s.l. (Daniel Josefchak s.n., United States of America); **d** *Lenzitopsis oxycedri* (Sergio Pérez Gorjón 3632, Spain); **e** *Thelephora palmata* (Sergio Pérez Gorjón 161, Spain); **f** *Polyozellus griseopergamaceus* (Sten Svantesson 132, Sweden); g, *Odontia ferruginea* (Sten Svantesson 434, Sweden)

Genera included

Family Bankeraceae Donk 1961
= Boletopsidaceae Bondartsev & Singer ex Jülich 1982
= Sarcodontaceae Bondartsev & Singer ex Singer
Boletopsis Fayod 1889
Corneroporus T. Hatt. 2001
Hydnellum P. Karst. 1879
= *Calodon* P. Karst. 1881
= *Phaeodon* J. Schröt. 1888
Phellodon P. Karst. 1881
= *Bankera* Coker & Beers ex Pouzar 1955
Sarcodon Quél. ex P. Karst. 1881
Family Thelephoraceae Chevall. 1826
= Phylacteriaceae Imazeki 1953
= Tomentellaceae Warm. 1890
= Lenzitopsidaceae Jülich 1982
Aldrigiella Rick 1934
Amaurodon J. Schröt. 1888

=*Hypochnopsis* P. Karst. 1889
=*Lazulinospora* Burds. & M.J. Larsen 1974
=*Tomentellago* Hjortstam & Ryvarden 1988
Gymnoderma Humb. 1793
Lenzitopsis Malençon & Bertault 1963
Odontia Pers. 1794
=*Tomentellina* Höhn. & Litsch. 1906
Polyozellus Murrill 1910
=*Phyllocarbon* Lloyd 1920
=*Pseudotomentella* Svrček 1958
Skepperia Berk. 1857
=*Friesula* Speg. 1880
Thelephora Ehrh. ex Willd. 1787
=*Merisma* Pers. 1797
=*Phylacteria* (Pers.) Pat. 1887
=*Scyphopilus* P. Karst. 1881
Tomentella Pers. ex Pat. 1887
=*Acrotamnium* Nees 1816
=*Caldesiella* Sacc. 1877
=*Hypochnus* Fr. 1818
=*Prillieuxia* Sacc. & P. Syd. 1899
=*Tomentellastrum* Svrček 1958
Tomentellopsis Hjortstam 1970
=*Byssocristella* M.P. Christ. & J.E.B. Larsen 1970
genera *incertae sedis*
Bubacia Velen. 1922
Thelephorella P. Karst. 1889

Evolution

According to the present phylogenomic tree, Thelephorales is a sister clade to Polyporales. This relationship was shown in the previous version of this article, based on *LSU*, *SSU*, *rpb1*, *rpb2*, *5.8s* and *tef1* (He et al. 2019a), and has been documented earlier (Hibbett et al. 2007). The deeper nodes within the order, however, remain unknown (e.g. Vizzini et al. 2016).

Among most homobasidiomycete orders, there is a general evolutionary trend from structurally simple, corticioid basidiomes to more complex, stipitate forms, occasionally followed by reversions to simpler basidiomes (Hibbett and Binder 2002; Larsson et al. 2004). In Thelephorales the latter type of transition seems to be evidenced in the large, stipitate genera *Hydnellum* and *Phellodon*, by the presence of the single resupinate species *H. gracilipes* and *P. secretus*. Recently the evolution of simple basidiomes into more complex ones has also been documented, through phylogenetic analysis: in the corticicioid genus *Amaurodon*, a stipitate species has been described as a genetically close sister taxon to one of its previously known members (Svantesson et al. 2021b) and in what is now *Polyozellus* (synonymized with *Pseudotomentella*) the few existing stipitate members have been shown to form but one of many clades among otherwise entirely corticioid species (Svantesson et al. 2021a).

Justification of order and problems

Thelephorales is a well-defined order, both at morphological and molecular levels (Stalpers 1993; Larsson et al. 2004; Hibbett et al. 2007). Among corticioid species several problems are currently hampering the description of new species. The most notable are (1) that nearly all species are part of complexes of morphologically very similar species and (2) that the majority of names are old, with their type specimens often in such a bad condition that they cannot be reliably sequenced. The combined effect, of species complexes riddled with old names, makes taxonomically well-made studies very time-consuming to achieve (Svantesson 2020).

Phylogenetic studies in Thelephorales are relatively scarce to date, and most serve to publish only one or a small number of species (e.g. *Amaurodon*, *Tomentella* and *Polyozellus*; e.g. Miettinen and Kõljalg 2007; Kuhar et al. 2016a; Voitk et al. 2017). In the last few years rapid publication of articles in order to describe new species, mainly from China, has started to change this (e.g. Lu et al. 2018; Mu et al. 2021). Though the pace is commendable, most of these articles do not include type studies of previously described, closely related species with old names, and hence very likely include descriptions of already known species. More comprehensive phylogenies have also been made, at a recently increasing pace, most with the objective of delimiting a genus: *Lenzitopsis* (Zhou and Kõljalg 2013), *Phellodon* vs. *Bankera* (Baird et al. 2013), *Odontia* (Tedersoo et al. 2014c), *Hydnellum* vs. *Sarcodon* (Larsson et al. 2019), *Pseudotomentella* (Svantesson et al. 2019, 2021b), *Amaurodon* (Svantesson et al. 2021c) and *Polyozellus* vs. *Pseudotomentella* (Svantesson et al. 2021a). A small number of articles, based on nuclear, ribosomal DNA, have hinted at the internal structure of the order, but they have thus far not been conclusive (Zhou and Kõljalg 2013; Tedersoo et al. 2014c; Vizzini et al. 2016). The study including the most taxa is probably Vizzini et al. (2016), who pointed to several issues, e.g. that the current delimitation of Bankeraceae and Thelephoraceae might be artificial.

Significance

Ecological and economical roles

Most genera in Thelephorales (*Boletopsis, Hydnellum, Phellodon, Sarcodon, Polyozellus, Thelephora, Tomentella* and *Tomentellopsis*) have been shown to be ectomycorrhizal. Their mycelia are common in ectomycorrhizal communities from the arctic tundra to coastal vegetation in the tropics and is often co-dominating (Taylor and Bruns 1999; Kõljalg et al. 2000; Ryberg et al. 2009; Botnen et al. 2015; Gao et al. 2015). The *Tomentella-Thelephora* lineage has concordantly been found to be one of the most species-rich ectomycorrhizal (ECM) lineages in forest ecosystems (Alvarez-Manjarrez et al. 2016; Tedersoo et al. 2010) and it plays a very important role in pioneering microhabitats of coniferous forests (Ramírez-López et al. 2015; Hilszczanska and Sierota 2006; Iwanski et al. 2006). The ectomycorrhiza of *Thelephora* terrestris may be the most common species found in the soil of tree nurseries worldwide (Smith and Read 2002).

Some species of *Thelephora* are considered gourmet edible mushrooms and are economically important both in this regard and in the capacity of use in traditional medicine. *Thelephora ganbajun* M. Zang is e.g. one of the most popular edible fungi in China (Sha et al. 2008; Xu et al. 2016). Some *Sarcodon* species are also edible, and *Sarcodon imbricatus* (L.) P. Karst. is one of the most commonly consumed wild mushrooms, due to its nutritional value (Li et al. 2022b).

Chemical diversity

A feature common to most species of Thelephorales is the presence of thelephoric acid, a terphenylquinone pigment which is brown in water but turns blue green in KOH in the presence of air. It has been stated as a distinguishing character for the order but is present also in other groups, e.g. Boletales (Bresinsky and Rennschmid 1971). Thelephoric acid has neuroprotective properties (Kwak et al. 1999). It can also be used as a traditional cloth dye to achieve a blue to green colour, thus making e.g. certain *Hydnellum* and *Sarcodon* species sought after in these circumstances.

Many species in Thelephorales seem to produce bioactive substances useful in medicine. These are more or less restricted to certain genera and are mainly p-Terphenyl derivates: boletopsins have anticancer, antibacterial and strong antioxidant properties (e.g. Kaneko et al. 2010; Wossa et al. 2013; Beekman & Barrow 2014); thelephorins, vialinins, ganbajunins, terrestrins, and telephantins from certain species of *Thelephora* have antioxidant, anti-inflammatory, anti-cancer and strong antioxidant activity (Tsukamoto et al. 2002; Norikura et al. 2011; Bailly 2022); atromentin and scabronines in *Hydnellum* possess anticoagulant, anti-inflammory, antibacterial and neurogenerative properties (Khanna et al. 1965; Obara et al. 1999; Hirota et al. 2002; Zheng et al. 2006); certain sarcodonins and sarcoviolins, from *Sarcodon*, have cytotoxic and α-Glucosidase inhibitory activity useful in diabetes treatment (Hirota et al. 2002; Cali et al. 2004; Ma et al. 2014; Meng et al. 2017); phellodonic acid is antibiotic (Stadler et al. 1993) and *Phellodon melaleucus* lectin is anti-carcinogenic (Li et al. 2023b); polyozellin attenuates neuronal cell death, is cytotoxic, a potent cancer chemopreventative and possibly has anti-Alzheimer properties (Hwang et al. 1997; Lee and Nishikawa 2003; Kim et al. 2004; Yang and Song 2015).

Other relevant data and future recommendations

In Europe species in Bankeraceae are to a large part rare and/or restricted to old growth forest. In e.g. Norway and Sweden, a considerable number are nationally Red Listed in accordance with the IUCN guidelines, due to threat of extinction (Artsdatabanken 2021). The situation is presumably similar in other, less well researched countries and perhaps also for the lesser known, corticioid species in Thelephoraceae.

In Europe many Bankeraceae species are used as indicators of forests with high nature values (Nitare and Hallingbäck 2000; Ainsworth 2005; Nitare 2019) and in North America the same is true for the stipitate species in *Polyozellus* (United States Forest Service 1994; Baroni 2017).

Thelephora wakefieldiae (formerly *Tomentella* sublilacina) is dispersed through the action of mites (Lilleskov and Bruns 2005). Its spores can pass through their intestines and also through those of insects that prey on them, such as beetles. Given the high morphological similarity to other corticioid species in Thelephoraceae and their tendency to form very close to or even under the ground, this mode of dispersal may be common within the family.

Pretreatment of wood chips and pulp with *Thelephora* mycelium can be used to reduce chemical usage in paper industries, through the action of the ligninolytic enzymes it produces (Selvam et al. 2011).

Species of *Thelephora* can accumulate heavy metals to high concentrations. *Thelephora penicillata,* in particular, has been shown to hyperaccumulate cadmium and arsenic in extreme amounts (Borovička et al. 2022).

In terms of future recommendations, one need not look further than at the daunting amount of species that remain to be described within Thelephorales—a small order counted by the number of currently named species, but the second largest among basidiomycetes when approximations of undescribed species are included. Most likely, tens of thousands of species still lack names and given currently available data, many probably play important roles in ecosystems around the world as well as contain substances that could be of great benefit to mankind. In addition to continued research in these fields at an increased pace, together with the even more important efforts to protect the probably quite considerable number of species that are threatened by extinction, it is of utmost importance that initiatives to more rapidly provide names for undescribed species are given priority within current research. Without names that by their numbers mirror the abundant diversity of Thelephorales, its significance and prevalence will be hard to communicate and promote. Apart from pure funding of such projects it would be very helpful if herbaria in Europe and North America (where most types are from) could make efforts to sequence type specimens of old Thelephorales names, alternatively create epitypes.

Tilletiales Haeckel 1894

Contributed by: Teodor T. Denchev, Cvetomir M. Denchev, Dominik Begerow, Martin Kemler

Introduction

It is hard to say who first introduced a name of an order for the tilletialean fungi as no rank of taxa was given in numerous old sources, including those related to this name. Haeckel (1894) was probably the first author who used an order-rank name for the holobasidiate smut fungi, although ambiguity of his names with respect to rank.

In the system of Exobasidiomycetes, Tilletiales is characterized by having local interaction zones without interaction apparatus in intercellular hyphae, and a dolipore without pore caps, traversed by two tripartite membranous plates arranged symmetrically (Bauer et al. 1997). They produce small local interaction sites with small electron-opaque deposits of variable shape and size at the host-parasite interface, and only the host response at these sites indicates that they are sites of interaction (Bauer et al. 1997). Intracellular hyphae and haustoria are lacking. The species are plant parasitic on Poaceae (with exception of the *Erratomyces* species, that are parasites on Fabaceae). Sori are formed in the ovaries of the hosts (except a few *Tilletia* species and the *Erratomyces* species producing sori on leaves). Teliospores are darkly pigmented and mostly ornamented. Teliospores germinate with holobasidia, producing an apical whorl of basidiospores. Basidiospores are filiform to fusiform in shape; in some species, the basidiospores conjugate in pairs and give rise to infection hyphae or secondary spores (Castlebury et al. 2005; Vánky 2013; Begerow et al. 2014). The species are united by morphological and ultrastructural characteristics and molecular data (Bauer et al. 1997; Castlebury et al. 2005; Vánky 2013; Begerow et al. 2014). Tilletiales contains two families and seven genera.

Characters that define the taxa in the order

Tilletiales is divided into two families: Tilletiaceae and Erratomycetaceae. Members of both families are morphologically very close, but they were distinguished by specialization on Poaceae and Fabaceae, respectively, and the molecular phylogeny is highly congruent with it.

Tilletiaceae was erected by Schröter (1887). All members of this family are parasites on hosts in various genera of grasses. The largest genus, *Tilletia*, was erected by Tulasne and Tulasne (1847). The infection is mostly systemic, rarely local (in ovaries of some spikelets). Sori are produced in the ovaries, which fill with a semi-agglutinated or powdery mass of spores intermingled with sterile cells. In some species, the sori are formed on leaves and culms, as streaks. Exceptionally, the sori appear as swellings on the culms or cover the surface of the leaves, or form witches' brooms (Vánky 2013; Denchev and Denchev 2018c, d). Peridium and columella are lacking. Spores are single, medium- to large-sized, from pale yellowish brown to dark reddish brown, usually ornamented (reticulate, cerebriform, echinate, verrucose or with cylindrical projections), rarely smooth, often surrounded by a more or less evident hyaline or tinted gelatinous sheath. Spores of some species are with a short, hyaline appendage. In some species, the spore mass has a fetid smell due to the production of trimethylamine. Sterile cells are solitary, variously shaped, smaller or larger than the spores, hyaline or slightly pigmented, smooth or ornamented. Sometimes, subhyaline, intermediate cells with traces of surface ornamentation or with unusual ornamentation are present (Vánky 2013). Spore germination results in a holobasidium, frequently with multiple retraction septa, and an apical whorl of filiform to narrowly falcate primary basidiospores which in some species conjugate in pairs to give rise to infection hyphae, blastospores, and ballistospores (secondary sporidia), while in other species basidiospores are numerous, acicular or filiform, giving rise to infection hyphae without conjugation (Castlebury et al. 2005; Vánky 2013). The number of basidiospores formed per basidium varies considerably among different species. The genus of *Tilletia* is monographically studied by Durán and Fischer (1961) and Vánky (2011). Currently, 189 species are recognized in *Tilletia* (Denchev and Denchev 2018c, d; Denchev et al. 2018).

Neovossia, *Oberwinkleria*, and *Ingoldiomyces* are monotypic genera. Their type species are morphologically too close to the species of *Tilletia*. Nevertheless, these genera have some characters differentiating them from *Tilletia*. *Neovossia moliniae* (Thüm.) Körn. differs from the species of *Tilletia* by a complex of characters that includes (i) presence of elongate, foveolate spores provided with a thin, hyaline sheath and with a long, hyaline appendage (remains of the sporogenous hypha), (ii) lack of sterile cells between the spores, and (iii) a very large number of basidiospores which germinate without conjugation (Vánky 2013).

Oberwinkleria anulata Vánky & C. Vánky is characterized by the presence of spores with a dark ring in the longitudinal spore axis; the absence of an evident basidium—this is reduced to the spore; and the spore germination that results either in 3–6, short basidiospores directly produced on pedicels, or in ramified, aseptate hyphae on which basidiospore-like spores and ballistospores are formed on sterigmata (Vánky and Bauer 1995; Vánky 2013).

Ingoldiomyces hyalosporus (Massee) Vánky differs from the other tilletiaceous species by having peculiarly ridged spores that germinate in aseptate basidia on which apically, on sterigmata, 1–2, curved ballistosporic basidiospores are produced (Ingold 1995; Vanky and Bauer 1996).

Conidiosporomyces consists of three species. They can be easily distinguished from *Tilletia* based on the formation of a sorus composed of a saclike, apically open peridium of host tissue and fungal origin, and a central mass of a mixture of spores, sterile cells, and balls of Y-shaped, hyaline conidia (Vanky and Bauer 1992). The spore germination results in a holobasidium with an apical claster of elongate basidiospores; the germination of basidiospores and conidia results in hyphae on which both blastic conidia and ballistospores are formed (Vanky and Bauer 1992; Vánky 2013).

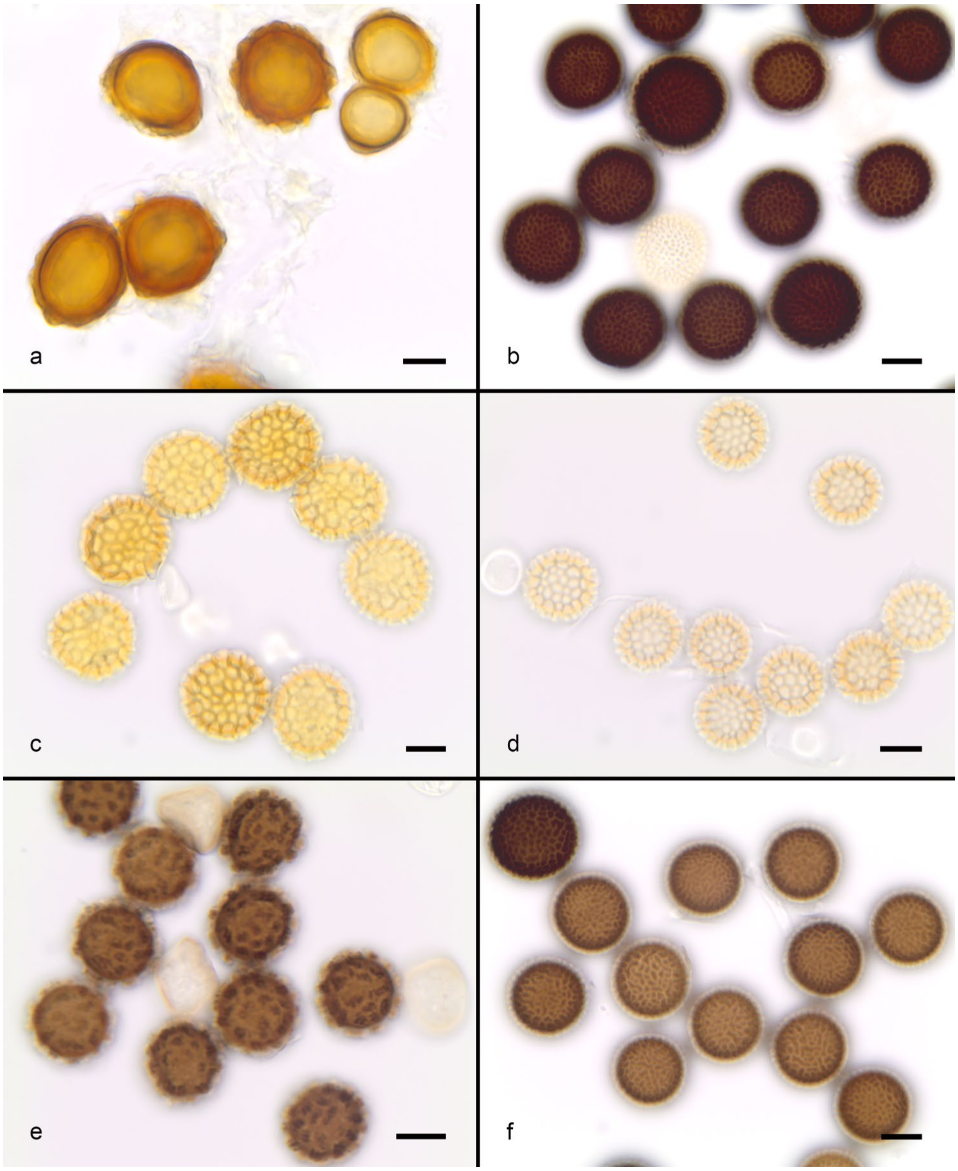
Salmacisia is a monotypic genus, with *S. buchloeana* (Kellerm. & Swingle) D.R. Huff & Amb. Chandra, that is morphologically indistinguishable from the species in *Tilletia*. It was described on the basis of molecular phylogenetic data (Chandra and Huff 2008). Spore germination results in simple or branched multinucleate holobasidia, with an apical whorl of binucleate or mononucleate basidiospores; mononucleate basidiospores conjugate in pairs developing hyphae and secondary sporidia, like those produced by the dikaryotic basidiospores (Durán 1987; Chandra and Huff 2008; Vánky 2013). The infection is systemic.

Erratomycetaceae was erected to accommodate the species of *Erratomyces* (Denchev and Denchev 2013). This genus consists of five species. They are related to *Tilletia* but differ by having spores embedded in the leaf tissue—in *Tilletia*, such localization is an exception (e.g. *T. sterilis* Ule), and by host specialization on *Fabaceae*. Spore germination is of *Tilletia*-type with holobasidia apically bearing needle-shaped basidiospores (Piepenbring and Bauer 1997). Phylogenetic placement of the type species, *Erratomyces patelii* (Pavgi & Thirum.) M. Piepenbr. & R. Bauer, was demonstrated by Castlebury et al. (2005).

Plates

Fig. 57 Tilletiales. **a**–**i** habit. **a** *Conidiosporomyces ayresii* on *Megathyrsus maximus,* Sri Lanka (Vánky Ustil. Exs. 186); **b** *Erratomyces patelii* on *Vigna mungo,* India (Vánky Ustil. Exs. 1052); **c** *Ingoldiomyces hyalosporus* on *Nassella pubiflora,* Bolivia (Vánky Ustil. Exs. 1330); **d** *Neovossia moliniae* on *Phragmites australis,* Italy (Vánky Ustil. Exs. 573); **e** *Tilletia acroceratis* on *Acroceras macrum,* Ethiopia (Vánky Ustil. Exs. 1255); **f** *Tilletia cerebrina* on *Deschampsia cespitosa,* Czech Republic (Vánky Ustil. Exs. 977); **g** *Tilletia fusca* on *Vulpia bromoides,* Ethiopia (Vánky Ustil. Exs. 1269); **h** *Tilletia olida* on *Brachypodium pinnatum*, Hungary (Vánky Ustil. Exs. 358); **i** *Tilletia vittata* on *Oplismenus compositus*, Thailand (Vánky Ustil. Exs. 1297). Arrows in **a**–**i** indicate sori. Scale bars: a–i = 1 cm

Fig. 58 Tilletiales. **a**–**f** spores in LM. **a** *Erratomyces patelii* on *Vigna mungo*, India (Vánky Ustil. Exs. 1052); **b** *Tilletia barclayana* on *Cenchrus alopecuroides,* Korea (SMK 16834); **c** *Tilletia elizabethae* on *Ventenata dubia*, Slovakia (SOMF 29800, holotype); **d** *Tilletia fusca* on *Vulpia ciliata*, Greece (B 70 0015527); **e** *Tilletia oplismeni-cristati* on *Acroceras calcicola*, Madagascar, Denchev 2631; **f** *Tilletia setariae-viridis* on *Setaria viridis,* Korea, Denchev 06-23. Scale bars: a–f = 10 µm



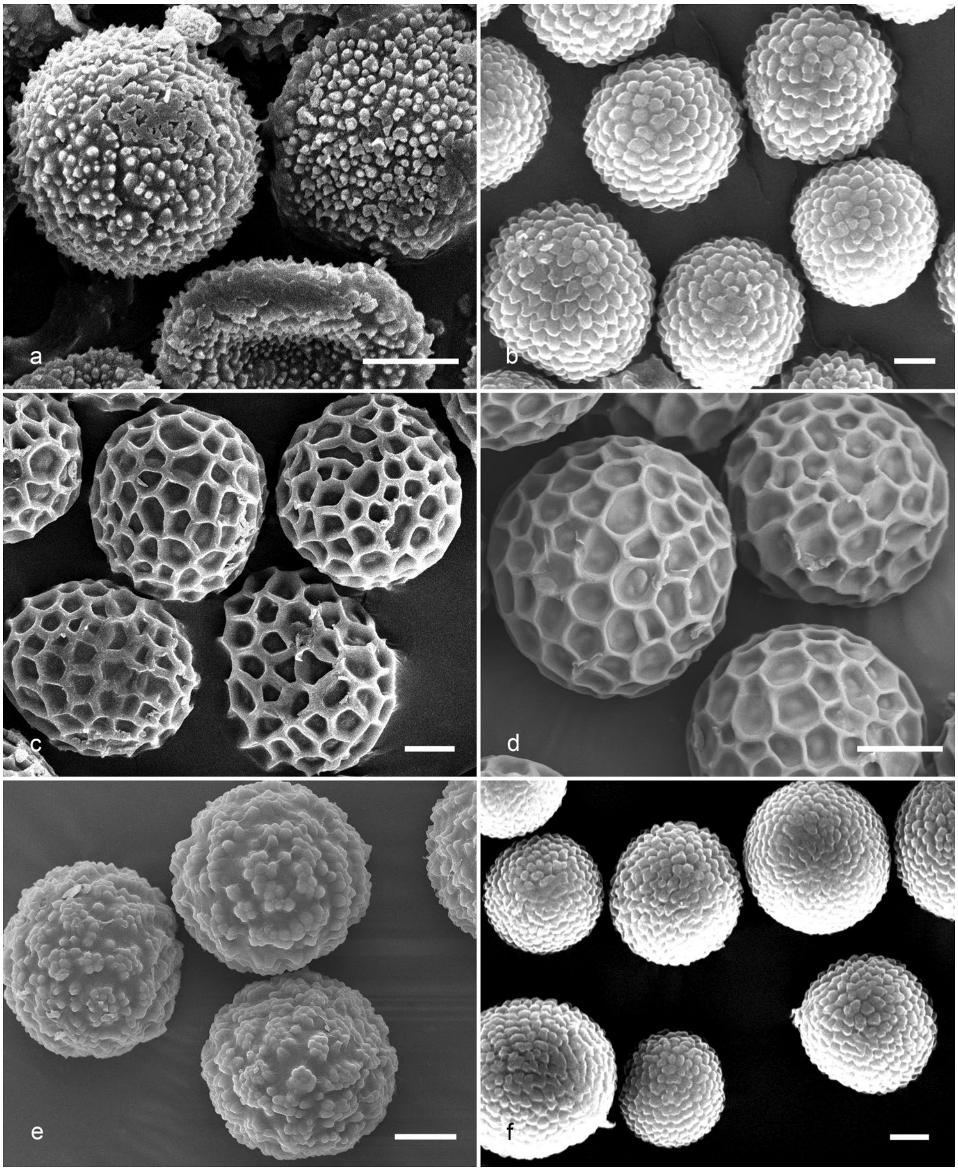


Fig. 59 Tilletiales. **a**–**f** spores in SEM. **a** *Conidiosporomyces ayresii* on *Megathyrsus maximus*, Cameroon, Denchev 3634; **b** *Tilletia barclayana* on *Cenchrus alopecuroides*, Korea (SMK 18300); **c** *Tilletia elizabethae* on *Ventenata dubia*, Slovakia Slovakia (SOMF 29800, holotype); **d** *Tilletia fusca* on *Vulpia ciliata*, Greece (B 70 0015527); **e** *Tilletia oplismeni-cristati* on *Acroceras calcicola*, Madagascar, Denchev 2631; **f** *Tilletia setariae-viridis* on *Setaria viridis*, Korea, Denchev 06-23. Scale bars: a–f = 5 µm

Genera included

Family Tilletiaceae J. Schröt. 1887
- *Conidiosporomyces* Vánky 1992
- *Ingoldiomyces* Vánky 1996
- *Neovossia* Körn. 1879
- = *Vossia* Thüm. 1879 (nom. illeg.)
- *Oberwinkleria* Vánky & R. Bauer 1995
- *Salmacisia* D.R. Huff & A. Chandra 2008
- *Tilletia* Tul. & C. Tul. 1847
- = *Tilletiella* Zambett. 1970 (nom. inval.)

Family Erratomycetaceae Denchev & T. Denchev 2013
- *Erratomyces* M. Piepenbr. & R. Bauer 1997

Evolution and justification of order

Vossia was erected by Thümen (1879) for *Vossia moliniae* Thüm. on *Molinia caerulea* (L.) Moench, but soon afterwards Körnicke (1879) found that this name was illegitimate (a later homonym) and proposed the name *Neovossia*. Brefeld (1895) described and illustrated the spore germination of *N. moliniae*, and described a second species, *N. barclayana* Bref. on *Pennisetum triflorum* Steud. [q.e. *Cenchrus orientalis* (Rich.) Morrone]. Both species are characterized by formation of a very large number of basidiospores which germinate without conjugation. Later 14 additional species have been described as or transferred to *Neovossia* (Carris et al. 2006). Castlebury et al. (2005) and Carris et al. (2006) stated that there is no phylogenetic support for maintaining *Neovossia* as a distinct genus from *Tilletia*, however, Vánky (2011, 2013) considered *Neovossia* as a monotypic genus for *N. moliniae,* with a complex of distinctive characters listed in the text above.

Salmacisia buchloeana on *Bouteloua dactyloides* (Nutt.) Columbus was initially placed in *Tilletia* (as '*T. buchloëana*', Kellerman and Swingle 1889), but based on molecular evidence, it was transferred to a new genus (Chandra and Huff 2008). The host plant is a dioecious grass. *Salmacisia buchloeana* is a remarkable smut fungus for causing induced hermaphroditism. It induces development of ovaries in flowers of otherwise male plants causing host castration where host reproductive organs are sterilized as a consequence of the parasite's own reproduction (Chandra and Huff 2008). Alteration of host reproductive structures evolved at least three times independently within smut fungi, as seen in *Microbotryum*, *Salmacisia,* and *Thecaphora* (Begerow et al. 2014).

The host specificity of some species of *Tilletia* and the correlation between lineages within *Tilletia* with monophyletic host lineages are in need of additional molecular phylogenetic studies.

The monotypic *Tilletiella* was established by Zambettakis (1970) as an asexual genus in order to accommodate conidial forms of some *Tilletia* species (e.g., *Tilletia alopecuri* (Sawada) L. Ling, *Tilletia* on *Bromus,* etc.). *Tilletiella* is an invalidly published name (without a description or diagnosis in Latin, Art. 39.1 Shenzhen Code, and without a type species, Art. 40.1), as is the combination *Tilletiella alopecuri* (Sawada) Zambett. (Art. 35.1). Thus, both names are not names under the Code.

Economic importance

Some species of *Tilletia* cause economically significant diseases of cereal crops. *Tilletia indica* Mitra is the causal agent of Karnal bunt disease of wheat in India, Nepal, Pakistan, Afghanistan, Iran, and Iraq, and as an introduced species, in Mexico, USA, and South Africa. This pathogen is highly regulated and quarantined by many countries (Castlebury 1998; Sing 1998). The infection is local and sori are developed only in some ovaries of the spike. Affected seeds are usually partially bunted and have a characteristic fishlike odor, caused by the production of trimethylamine, which causes a reduction in the quality of the grain (Castlebury 1998). Karnal bunt fungus infects only during specific periods within boot swelling to anthesis stage, unlike *Tilletia caries*, *T. laevis*, and *T. controversa*, and it sporulates on the same generation of the host that it infects, unlike *Ustilago tritici* (Fuentes-Davila 1996; Carris et al. 2006). Thus, *Tilletia indica* differs from other smuts of wheat.

Common bunt caused by *Tilletia caries* (DC.) Tul. & C. Tul. and *T. laevis* J.G. Kühn and dwarf bunt caused by *T. controversa* J.G. Kühn are important seed-borne diseases of wheat (Goates 1996), occurring in most wheat growing regions worldwide. Infection with *T. caries* and *T. laevis* occur below the soil surface, shortly after the seed germinates and prior to emergence. Spores germinate on seed or in the soil, produce infection hyphae, and penetrate the coleoptile. Spores of *T. controversa* germinate at or near the soil surface and infection hyphae infect seedlings (Goates 1996). The common and dwarf bunt fungi are systemically infecting species. Their sori fill the ovaries with a fetid mass of spores and sterile cells. Both *T. caries* and *T. controversa* possess reticulate spores, however, the plants infected with *T. controversa* are dwarfed. Spores of *T. laevis* are smooth. Contaminated grain has reduced quality due to the smell of trimethylamine.

Tilletia horrida Takah. is the causal agent of Rice kernel smut disease that can cause losses in grain production. It is distributed mainly in subtropics and tropics, in most of the rice-cultivating countries (Carris et al. 2006; Vánky 2011). The infection is local.

In India and the Neotropics the angular black spot disease on leaves of beans is caused by *Erratomyces patelii* (Piepenbring and Bauer 1997).

Trechisporales K.H. Larss. 2007

Contributed by: Viktor Papp, Sergio P. Gorjón

Introduction

Trechisporales is a relatively small, angiosperm-associated order that represents an early-diverging lineage of Agaricomycetes (Nagy et al. 2016; He et al. 2019a; Varga et al. 2019). According to He et al. (2019a, b), it contains 16 genera and about 120 species. Recently, Liu et al. (2022a) restricted the order to 12 genera (excluding *Boidinella*, *Litschauerella*, *Sphaerobasidium, Sertulicium*, and *Sistotremastrum*). Phylogenetic studies based on ribosomal DNA regions (ITS and 28S rDNA) showed that the order divides into two well separated, family level clades, the Hydnodontaceae Jülich and a group containing the corticioid genus *Sistotremastrum* J. Erikss., informally called *Sistotremastrum* family (Larsson 2007; Telleria et al. 2013; Gruhn et al. 2018; Liu et al. 2019a). Recently, the *Sistotremastrum* family has been raised to family and order level (Sistotremastraceae, Sistotremastrales) by Liu et al. (2022a) cointaining two genera, *Sertulicium* and *Sistotremastrum*. Except for certain species in the *Trechispora* lineage (e.g. *Hydnodon thelephorus* and *Scytinopogon* spp.), all the taxa in Trechisporales have resupinate basidiomes and most of them have a non-poroid hymenophore (Albee-Scott and Kropp 2011; Hibbett et al. 2014; Desjardin and Perry 2015).

History

Trechisporales was circumscribed by Larsson (2007) indicating two strongly supported clades; Hydnodontaceae and a group with no family level named *Sistotremastrum* family and with no obvious characters to link it with Hydnodontaceae. Hydnodontaceae (= Scytinopogonaceae Jülich, = Subulicystidiaceae Jülich) was introduced by Jülich (1981) to accommodate the monotypic genus *Hydnodon*. However, *Hydnodon* is now considered as a synonym of *Trechispora*, based on morphological similarity (except its stipitate basidioma) and phylogenetic evidence (Ryvarden 2002; Albee-Scott and Kropp 2011; Larsson et al. 2011). In addition to the genus *Trechispora* s. lato, the genera *Brevicellicium*, *Dextrinocystis*, *Fibrodontia*, *Luellia*, *Porpomyces*, *Subulicystidium*, and *Tubulicium* were confirmed to belong in the family Hydnodontaceae by phylogenetic studies (Larsson 2007; Yurchenko and Wu 2012; Birkebak et al. 2013; Telleria et al. 2013; Wu et al. 2015c; Ordynets et al. 2018; Liu et al. 2019a, 2022a; Ushijima et al. 2019). Further genera that morphologically may belong to Hydnodontaceae include *Brevicellopsis*, *Cristelloporia* and *Litschauerella* but they have never been confirmed from a phylogenetic perspective (Oberwinkler 1966; Johansen and Ryvarden 1979; Hjortstam and Ryvarden 2008; Liu et al. 2022a).

Trechispora, the generic type, was established by Karsten (1890) to accommodate the single species, *T. onusta* P. Karst. (= *T. hymenocystis*). Although, the generic type is characterised by a poroid hymenial surface (Larsson 1994), the majority of the species now assigned to *Trechispora* have smooth, poroid, or odontioid to hydnoid hymenophores (eg. Liberta 1973; Larsson 1996; Trichiès and Schultheis 2002; Miettinen and Larsson 2006; Ordynets et al. 2015; Phookamsak et al. 2019; Xu et al. 2019a; Haelewaters et al. 2020). Based on these morphological characteristics, the genus *Trechispora* s. lato comprises *Dextrinodontia*, *Echinotrema*, *Hydnodon* and *Fibriciellum* J. Erikss. & Ryvarden (Larsson 1992, 1994; Ryvarden 2002). Moreover, two further genera, *Cristelloporia* and *Scytinopogon* also show similar micro-morphological characteristics as *Trechispora*, but their systematic position is poorly resolved. From among the six known *Cristelloporia* species (Johansen and Ryvarden 1979; Hattori 2003), only *C. brasiliensis* Corner was transferred to *Trechispora* (Larsson 1992), and the systematic position of the others, including the type (*C. dimitica* I. Johans. & Ryvarden) are not verified by molecular methods. The micromorphological similarity between species of *Trechispora* and *Scytinopogon* was initially observed by Jülich (1981) and Larsson (1992). Subsequent studies by Larsson et al. (2011), Birkebak et al. (2013), Desjardin and Perry (2015), and Liu et al. (2019a), based on phylogenetic data, revealed that *Scytinopogon* species are nested within the *Trechispora* clade. Currently, *Scytinopogon* is formally recognized as a synonym of *Trechispora* (Meiras-Ottoni et al. 2021).

Characters that define the taxa in the order

Trechisporales is a highly diverse order with stipitate, clavarioid, or resupinate basidiomes. The hymenial configuration varies from smooth, grandinioid, odontioid, hydnoid or poroid. Basidia are usually short, bearing two to four sterigmata. The basidiospores are smooth or variously ornamented. All species of Trechisporales bear a mono- or dimitic hyphal system with clamp connections in a fragile context, variably presence of cords, and in most species is usual to find ampullaceous septa (in cords and subiculum), short-celled, and richly branching subhymenial hyphae. In most species is also normal to find rich accumulations of calcium oxalate crystals in the hyphae. Most known species of Trechisporales may be saprotrophs on wood, while some species are considered to be ectomycorrhizal fungi or at least have a plant biotrophic lifestyle (Vanegas-León et al. 2019).

Plates

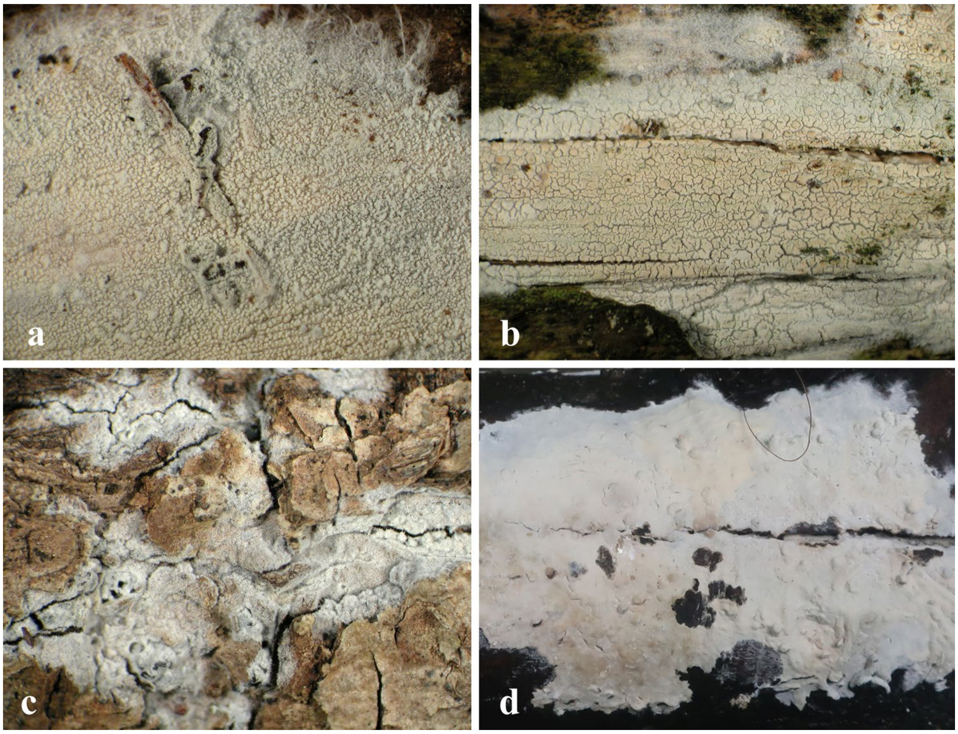


Fig. 60 Diversity of basidiome types in Trechisporales. **a** *Trechispora farinacea* (SPG 1095, Spain); **b** *Trechispora cohaerens* (SPG 656, Spain); **c** *Subulicystidium longisporum* (SPG 551, Spain); **d** *Fibrodontia alba* (LWZ 20180923-4, Yunnan province, China)

Genera included

- Family Hydnodontaceae Jülich 1982
    - *Allotrechispora* L.W. Zhou & S.L. Liu 2022
    - *Brevicellicium* K.H. Larss. & Hjortstam 1978
    - *Dextrinocystis* Gilb. & M. Blackw. 1988
    - = *Oxyflavus* Ryvarden 1973
    - *Fibrodontia* Parmasto 1968
    - *Luellia* K.H. Larss. & Hjortstam 1974
    - *Porpomyces* Jülich 1982
    - *Pteridomyces* Jülich 1979
    - *Subulicystidium* Parmasto 1968
    - = *Aegeritina* Jülich 1984
    - *Suillosporium* Pouzar 1958
    - *Trechispora* P. Karst. 1890
    - = *Cristelloporia* I. Johans. & Ryvarden 1979
    - = *Dextrinodontia* Hjortstam & Ryvarden 1980
    - = *Echinotrema* Park.-Rhodes 1955
    - = *Fibriciellum* J. Erikss. & Ryvarden 1975
    - = *Fibuloporia* Bondartsev & Singer 1941
    - = *Fibuloporia* Bondartsev & Singer 1944
    - = *Hydnodon* Banker 1913
    - = *Osteomorpha* G. Arnaud ex Watling & W.B. Kendr. 1979
    - = *Pseudohydnum* Rick 1904
    - = *Murrilloporus* Ryvarden 1985
    - = *Scytinopogon* Singer 1945
    - = *Tomentella* P. Karst. 1889
    - *Tubulicium* Oberw. 1965
    - = *Tubulixenasma* Parmasto 1965
- Trechisporales genera *incertae sedis*
    - *Boidinella* Nakasone 2011
    - *Brevicellopsis* Hjortstam & Ryvarden 2008

Evolution

According to the present phylogenomic tree, Trechisporales is a sister clade to Phallomycetidae, composed by Gomphales, Geastrales, Phallales, Hysterangiales. This position is still inconclusive and does not agree with the position of the order according to the analysis of the combined dataset of ITS, nrLSU, *tef1-α* and *rpb2* regions proposed by Liu et al. (2022a) where Trechisporales and Sistotremastrales form a basal lineage separate from Phallomycetidae. These inconsistencies will be solved in the future once more genomes of the group are incorporated into the analyses.

Justification of order and problems

Trechisporales is a taxon-poor order compared with most other orders within Agaricomycetes, Basidiomycota (Wijayawardene et al. 2022b). *Sertulicium* and *Sistotremastrum* (*Sistotremastrum* family or Sistotremastraceae) have recently been segregated in the order Sistotremastrales by Liu et al. (2022a). Sistotremastrales is characterized by corticioid basidiomes on wood, basidia with four to eight sterigmata, and smooth basidiospores. Comparing with the circumscription of Trechisporales sensu He et al. (2019a, b) and Spirin et al. (2021), some species in the reduced concept of Trechisporales also have smooth basidiospores, and thus are similar to species bearing basidia with four sterigmata in Sistotremastrales; however, species of Trechisporales differ in soft basidiomes, subicular hyphae with ampullate septa and presence of cystidia with various shapes (Spirin et al. 2021; Liu et al. 2022a; 2022e). In the work of Liu et al. (2022a) the order Sistotremastrales is segregated based on multilocus phylogenetic analyses. The present phylogenomic analyses only have in consideration two genomes, vid. *Sertulicium niveocremeum* and *Sistotremastrum suecicum*, both the type species of *Sertulicium* and *Sistotremastrum*, respectively. According to the fungal genomics tree in JGI (https://mycocosm.jgi.doe.gov/mycocosm/species-tree/tree;4fUe21?organism=agaricomycetes), these two species were separated from *Porpomyces mucidus*, the only representative of Trechisporales. In the future, more genomes from Trechisporales and Sistotremastrales will help to further clarify the taxonomic independence of these two orders.

Luo and Zhao (2022) included sequences of *Litschauerella gladiola* and *Sphaerobasidium minutum* in the phylogenetic tree of Trechisporales. However, the available sequences of Sphaerobasidium minutum suggest *Sphaerobasidium* has a closer affinity to Hymenochaetales rather than Trechisporales (Liu et al. 2022a). Similarly, *Litschauerella* was excluded from Trechisporales (Liu et al. 2022a).

Currently, *Trechispora*, the genus with the most species in the order, contains 87 legitimate names (Liu et al. 2022a). However, a large number of DNA sequences of unidentified *Trechispora* spp. from different regions of the world are deposited in the UNITE database. These sequences (including environmental DNA data) predict many hitherto formally undescribed *Trechispora* spp., especially from tropical regions.

Significance

Ecological and economical roles

Trechispora is an important genus of wood-inhabiting fungi that have the ability to decompose rotten wood in the forest ecosystem, but some sequences amplified by Vanegas-León et al. (2019) from apparently ectomycorrhizal roots belong to *Trechispora* and suggested a root-associated ecology, at least biotrophic and possibly ectomycorrhizal. Future investigations in subtropical regions are needed to determine whether such a mode of nutrition is widespread among *Trechispora* and other Trechisporales and its importance in the forest ecosystems.

Tremellales Fr. 1821

Contributed by: Xin-zhan Liu

Introduction

Tremellales is the largest order in the class Tremellomycetes that includes yeasts and dimorphic fungi forming macroscopic gelatinous basidiomes such as *Tremella*, *Pseudotremella*, *Phaeotremella*, and *Sirobasidium* (Weiss et al. 2014; Liu et al. 2015a). Several species are only known in the yeast stage. Most of the yeast species have only an asexual stage as presently known, whereas some species in *Papiliotrema, Rhynchogastrema,* and *Bullera* have both asexual and sexual stages, but without conspicuous basidiomes (Metzler et al. 1989; Sampaio et al. 2002, 2004). Besides, there are several groups of lichen-inhabiting taxa distributed in Tremellales, such as Tremella clade I, II and III (Millanes et al. 2011; Diederich et al. 2022b). Tremellales is an order with various life styles and nutrition modes, comprising saprotrophs, mycoparasites, human parasites, and fungicolous species.

History

Tremellales was proposed by Fries in 1821 for fungi with gelatinous basidiomes. Its concept has been redefined several times from using features of basidial morphology to ultrastructure, the nature of haploid states and trophic modes (Weiss et al. 2014). Tremellales was recognized by the classical fungal barcode markers of the ITS regions and D1/D2 LSU domains of the rDNA (Fell et al. 2000; Scorzetti et al. 2002). The Assembling the Fungal Tree of Life project provided a chance to better understand the phylogenetic relationship of Tremellales. (Matheny et al. 2006). There was some debate as to whether to include Trichosporonales into Tremellales (Hibbett et al. 2007). However, a multigene-based phylogenetic analysis indicated that these two orders are separate (Liu et al. 2015b). Upon the coming of the genomics era, phylogenomic studies using genome-scale datasets will advance our understanding of fungal tree of life and the relationships between the orders in Tremellomycetes. The monophyletic nature of Tremellales was challenged as Phaeotremellaceae including *Phaeotremella fagi*, and *Phaeotremella skinneri* appeared to belong to a clade separate from the other species of Tremellales (Li et al. 2021c).

Characters that define the taxa in the order

Basidial morphology in Tremellales mainly comprises longitudinally septate basidia, although some other types of septation have been reported as well. The basidiome texture in Tremellales is usually gelatinous, and the size of the basidiomes differs among species and genera. Some species produce only minute basidiomes, or completely live inbetween the hymenium of other fungi (especially the so-called intrahymenial mycoparasites). Gelatinous basidiomes are the most typical characteristic, and they are usually called jelly fungi (Bandoni 1995; Weiss et al. 2014). Some species of genera such as *Trimorphomyces*, *Papiliotrema*, and Rhynchogastrema, form minute basidiomes, but the sexual state of *Bullera alba* was only observed in pure culture (Boekhout et al. 1991). To recognize asexual yeast species of Tremellales, molecular phylogenetic analysis is the main strategy for species recognition, because no distinct morphological characteristics are available. Millanes et al. (2011) showed that these morphological characters are plesiomorphic and do not correlate with phylogeny. Different types of basidial septation and fruitbody morphology evolved multiple times in this group.

Plates

Fig. 61 Basidiome of *Tremella fuciformis* in the field from China. Also See Figs. 1 and 2 in Millanes et al. (2011). See Figs. 100.9–100.16, 126.2 (*Papiliotrema*), 129.2 (*Sirobasidium*) 132.1, 132-3-11 (*Tremella*), and 133.1 (*Trimorphomyces*) in Boekhout et al. (2011), Sampaio (2011e), Bandoni et al. (2011b), and Bandoni and Boekhout (2011b)

Genera included

Family Bulleraceae Xin Zhan Liu, F.Y. Bai, M. Groenew. & Boekhout 2015
  Bullera Derx 1930
  = *Bulleromyces* Boekhout & Á. Fonseca 1991
  Fonsecazyma Xin Zhan Liu, F.Y. Bai, M. Groenew. & Boekhout 2015
  Genolevuria Xin Zhan Liu, F.Y. Bai, M. Groenew. & Boekhout 2015
  Pseudotremella Xin Zhan Liu, F.Y. Bai, A.M. Yurkov, M. Groenew. & Boekhout 2015
Family Bulleribasidiaceae Xin Zhan Liu, F.Y. Bai, M. Groenew. & Boekhout 2015
  Bulleribasidium J.P. Samp., M. Weiss & R. Bauer 2002
  = *Mingxiaea* F.Y. Bai, Q.M. Wang, Boekhout & Nakase 2011
  Derxomyces F.Y. Bai & Q.M. Wang 2008
  Dioszegia Zsolt 1957
  Hannaella F.Y. Bai & Q.M. Wang 2008
  Nielozyma Xin Zhan Liu, F.Y. Bai, M. Groenew. & Boekhout 2020
  = *Nielozyma* Xin Zhan Liu, F.Y. Bai, M. Groenew. & Boekhout 2015
  Vishniacozyma Xin Zhan Liu, F.Y. Bai, M. Groenew. & Boekhout 2015
Family Carcinomycetaceae Oberw. & Bandoni 1982
  Carcinomyces Oberw. & Bandoni 1982
Family Cryptococcaceae Kütz. ex Castell. & Chalm. 1919
  Cryptococcus Vuill. 1901
  = *Atelosaccharomyces* Beurm. & Gougerot 1909
  = *Cryptococcus* Kütz. 1833
  = *Filobasidiella* Kwon-Chung 1976
  = *Tsuchiyaea* Y. Yamada, H. Kawas., Itoh, I. Banno & Nakase 1988
  Kwoniella Statzell & Fell 2008
  Teunia Q.M. Wang & F.Y. Bai 2020
Family Cuniculitremaceae J.P. Samp., R. Kirschner & M. Weiss 2001
  Fellomyces Y. Yamada & I. Banno 1984
  Kockovaella Nakase, I. Banno & Y. Yamada 1991
  Sterigmatosporidium G. Kraep. & U. Schulze 1983
  = *Cuniculitrema* J.P. Samp. & R. Kirschner 2001
Family Naemateliaceae Xin Zhan Liu, F.Y. Bai, M. Groenew. & Boekhout 2015
  Dimennazyma Xin Zhan Liu, F.Y. Bai, M. Groenew. & Boekhout 2015
  Naematelia Fr. 1818
Family Phragmoxenidiaceae Oberw. & R. Bauer 1990
  Phragmoxenidium Oberw. 1990
Family Rhynchogastremaceae Oberw. & B. Metzler 1989

Papiliotrema J.P. Samp., M. Weiss & R. Bauer 2002
Rhynchogastrema B. Metzler & Oberw. 1989
= *Bandoniozyma* Boekhout, P. Valente, Pagnocca, C.A. Rosa, C.F. Lee, S.O. Suh, M. Blackw., G. Péter & Fell 2012
Family Sirobasidiaceae Lindau 1897
Sirobasidium Lagerh. & Pat. 1892
Fibulobasidium Bandoni 1979
Family Tremellaceae Fr. 1821
Hormomyces Bonord. 1851
Mycocryptococcus Pollacci & Nann. 1927
Tremella Pers. 1794
= *Dermatangium* Velen. 1926
= *Encephalium* Link 1816
= *Epidochium* Fr. 1849
= *Gelatina* Raf. 1808
= *Gyraria* Nees 1816
= *Hepataria* Raf. 1808
= *Lindauopsis* Zahlbr. 1906
= *Nakaiomyces* Kobayasi 1939
= *Tremella* Dill. ex L. 1753
Family Trimorphomycetaceae Xin Zhan Liu, F.Y. Bai, M. Groenew. & Boekhout 2015
Carlosrosaea A.M. Yurkov, Xin Zhan Liu, F.Y. Bai, M. Groenew. & Boekhout 2015
Saitozyma Xin Zhan Liu, F.Y. Bai, M. Groenew. & Boekhout 2015
Sugitazyma A.M. Yurkov, X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout 2015
Trimorphomyces Bandoni & Oberw. 1983
Tremellales genera *incertae sedis*
Biatoropsis Räsänen 1934
Dictyotremella Kobayasi 1971
Neotremella Lowy 1979
Sigmogloea Bandoni & J.C. Krug 2000
Sirotrema Bandoni 1986
Tremellina Bandoni 1986
Xenolachne D.P. Rogers 1947

Evolution

Tremellales is closely related to Trichosporonales. Based on the evidence of molecular data, the order contains families Bulleraceae, Bulleribasidiaceae, Carcinomycetaceae, Cryptococcaceae, Cuniculitremaceae, Phaeotremellaceae, Sirobasidiaceae, Naemateliaceae, Rhynchogastremaceae, Tremellaceae, Trimorphmycetaceae (Liu et al. 2015b). The mean time of origin of the order is estimated to be about 153 million years ago (Zhao et al. 2017). The lifestyle and nutrition mode vary in different clades. The sexual reproduction strategy shows a transition from tetrapolar in *Tremella* species to bipolar in *Cryptococcus* species (Metin et al. 2010).

Justification of order and problems

The circumscription of Tremellales is well justified, using both morphology (basidiomes and basidium morphology) but importantly molecular phylogenetic studies (Fell et al. 2000; Scorzetti et al. 2002; Liu et al. 2015a, b; He et al. 2019a; Li et al. 2020b) The ambiguous taxonomy of Phaeotremellaceae has been raised in some studies, especially in genome-based research (Li et al. 2020b, 2021c).

Significance

Ecological and economical roles

Many yeast species of Tremellales are plant-related or soil-inhabitant species, such as *Bullera, Derxomyces, Dioszegia, Hannaella, Kockovaella* and *Papiliotrema* (Boekhout et al. 2022). These species constitute the biome of plant surface or soil that promote the plant growth or soil health. Several species in yeast genera *Bullera*, *Dioszegia*, *Hannaella*, *Mrakia*, and *Papiliotrema* are found to inhabitant extreme environments (Buzzini et al. 2018). The yeast species of *Papiliotrema* is identified to be a member of microbial community in the International Space Station (Bijlani et al. 2020). Mycoparasitic fungi such as *Tremella* species have long been used as food or traditional medicine in Asian countries. The industrial cultivation of *Tremella fuciformis* has been practiced for more than 30 years, and some new cultivars have been domesticated (Zhang et al. 2022a). Several species of the genus *Cryptococcus* are well-known human opportunistic pathogens, e.g. *C. neoformans, C. gattii,* and *C. deuterogattii,* but they also occur in the environment, e.g. pigeon droppings, trees etc. (Lin and Heitman 2006; Hagen et al. 2015; Bahn et al. 2020).

Chemical diversity

Within the order variation exists in the number of isoprenologues of the co-enzyme Q system. Most species have CoQ10 while CoQ9 also occurs (Fonseca et al. 2011).

Other relevant data and future recommendations

Elaborate genome investigations have been performed in the *Cr.* neoformans/*Cr. gattii* complex due to its clinical importance. More genome studies should be launched for other members of the order to better understanding the evolution at the ordinal level.

Tremellodendropsidales Vizzini 2014

Contributed by: Alfredo Vizzini

Introduction

Tremellodendropsidales was established by Vizzini (2014) based on morphology and unpublished molecular data. Later, Berbee et al. (2016) molecularly confirmed the status of the taxon as independent order. It contains the only family Tremellodendropsidaceae with the single genus *Tremellodendropsis* typified with *T. tuberosa* (Grev.) D.A. Crawford. Eight species are recognized worldwide within the genus by Agerer (2018).

History

The type species was published by Greville (1825) as *Merisma tuberosa*, presumably from Scottish material. Corner (1950) described the genus *Aphelaria* for those clavarioid fungi with a monomitic system and flattened branching. Later, he erected the subgenus *Tremellodendropsis* of *Aphelaria* for these species with clamped thin-walled hyphae and subtremellaceous basidia (with partial, cruciate apical septation), and designated *Aphelaria tuberosa* (Grev.) Corner as the type species (Corner 1953). He distinguished *Aphelaria* subgenus *Tremellodendropsis* from *Tremellodendron* G.F. Atk. by clavate basidia (versus globose basidia) and not truly tremellaceous, and the thin-walled hyphae with clamp-connections (versus thick-walled hyphae without clamp-connections). Crawford (1954), in a study on New Zealand clavarioid fungi, raised *Tremellodendropsis* to generic rank, separating it from *Aphelaria* s. stricto in having clamped hyphae and partially or completely cruciately septate apices of the basidia. Additionally, Crawford described in the same paper the new *Tremellodendropsis* subgenus *Transeptia* (typified with *T. transpusio* D.A. Crawford) for those species in which the apices of the basidia are completely cruciately septate. Reid (1956) established the genus *Pseudotremellodendron* for encompassing *T. transpusio* and allied species. Corner (1970) recognized *Tremellodendropsis* as an independent genus from *Aphelaria*, with the two subgenera *Transeptia* (subgelatinous basidiomes, basidia with a transverse septum before spore-formation) and *Tremellodendropsis* (coriaceous basidiomes, basidia with the septum formed after spore development). He reduced *Pseudotremellodendron* as a later synonym of *Tremellodendropsis* and considered the genus as a clavorioid link between homobasidiomycetes and heterobasidiomycetes. Wojewoda (1981) included *Tremellodendropsis* within the Tremellales. Jülich (1981) established the new family Tremellodendropsidaceae for accommodating the species within the Tremellales with richly branched basidiomes, and basidia which are partially (incompletely) septate at the apex. Bandoni (1984) excluded Tremellodendropsidaceae from both Auriculariales and Tremellales and considered them as most closely related to Tulasnellaceae and Ceratobasidiaceae within the Tulasnellales. Wells (1994) recognized Tremellodendropsidaceae as a family in the Auriculariales.

The first phylogenetic analysis including a member of the genus was that by Weiss and Oberwinkler (2001) where, based only on nrLSU sequences, a clade (bootstrap 98%, NJ) containing *Protomerulius brasiliensis*, *P. africanus*, an unidentified species of *Tremellodendropsis* (USJ 54427) from Costa Rica, *Heterochaetella dubia*, and *Protodontia piceicola* was highlighted within the Auriculariales.

In the phylogeny of the Auriculariales inferred from nrLSU sequence data by Zhou and Dai (2013), a well supported (100% MLB, 1 BPP) clade (named as the "Protomerulius family'' clade) consisting of *Tremellodendropsis* sp. (the same collection as in Weiss and Oberwinkler 2001), *Protomerulius africanus*, *P. brasiliensis*, *P. substuppeus* and two unidentified isolates of *Protomerulius* (O 19171 and Zhou 60), was recognized.

Berbee et al. (2016), based on ribosomal markers, indicated that *Tremellodendropsis tuberosa* cannot be included within the Auriculariales or Sebacinales and is an early diverging member of Agaricomycetes, without providing unequivocal support for its sister group relationships within the class. They supported the erection of the order Tremellodendropsidales previously made by Vizzini (2014).

Finally, Agerer (2018) included Tremellodendropsidales within Agaricomycotina, Tremellomycetes, Tremellomycetidae.

Order circumscription and characters that define the taxa in the order

Tremellodendropsis species are characterized by a combination of features such as basidiome annual, erect, clavarioid, usually multi-branched, branches terete to flattened, dichotomous to polychotomous, smooth to rugose, light coloured, consistency subcoriaceus to tough; context homogeneous; hymenium amphigeneous and usually thickening; hyphal system monomitic; hyphae hyaline, smooth, not or slightly inflated, thin- to slightly thick-walled, rarely secondarily septate, and clamped; spores hyaline, smooth, inamyloid, subglobose, ellipsoid, fusiform to amygdaliform, with small apiculus, thin- to slightly thick-walled, with homogeneous content or minutely multi-guttulat; basidia clavate to suburniform, 1–4 spored, hyaline, thin-walled, longitudinally septate only at apex, usually with a basal clamp; cystidia absent; entire septal pore cap (parenthesome imperforate); growth on soil. (Crawford 1954; Corner 1970; Jülich 1981; Wells 1994; Vizzini 2014; Berbee et al. 2016; Agerer 2018).

Taxon definition is mainly based on basidiome shape (unbranched versus branched), basidiome colour, presence/absence of gelatinous tissues, shape and size of the spores, and different timing in basidia septation (transverse septum formed before or after spore-formation) (Corner 1950, 1953, 1966b, 1970; Crawford 1954; Schild 1971; Petersen 1985, 1987; Nitare 2014; Berbee et al. 2016).

Plates

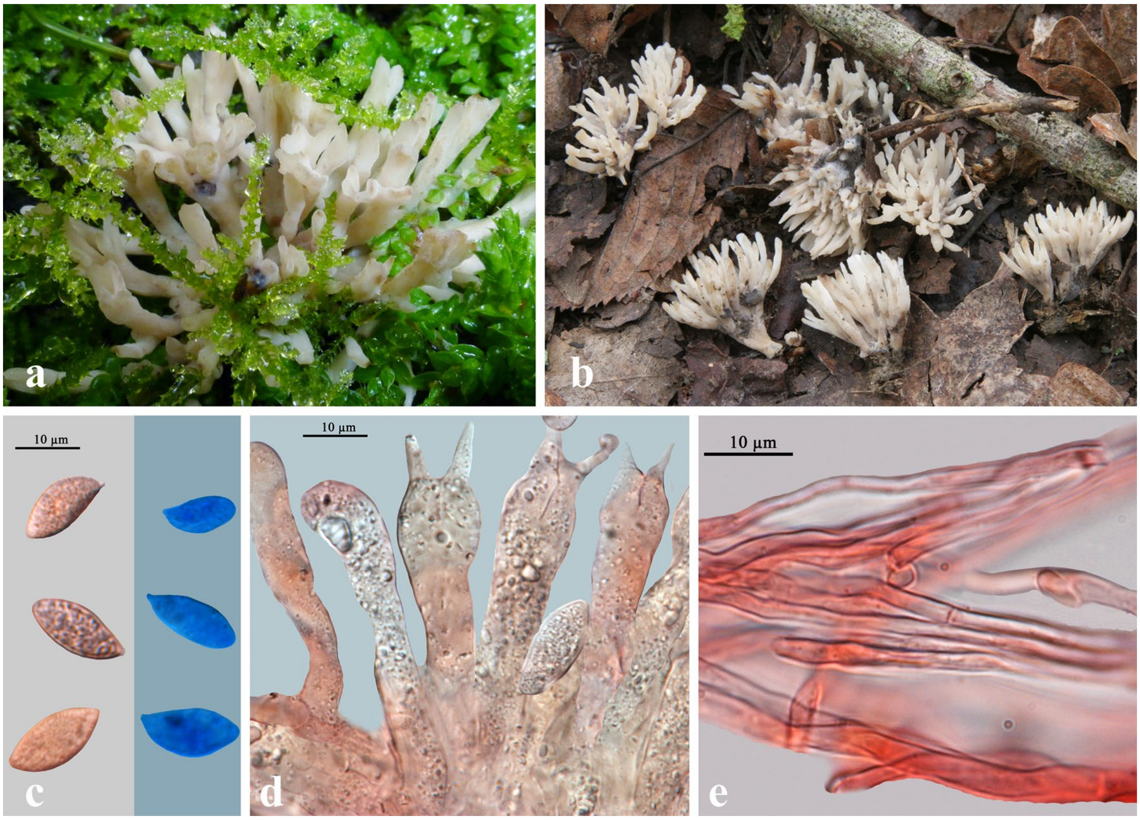


Fig. 62 Morphological characters of Tremellodendropsidales. **a**, **b** *Tremellodendropsis tuberosa* (M&F161115-07, GDOR3123 from Tuscany and Liguria, Italy); **c** basidiospores in Congo red and cotton blue; **d** basidia with longitudinal septa at apex; **e** context hyphae with clamp connections (credit: Paolo Franchi, Fabrizio Boccardo, Mauro Marchetti)

Genera included

Family Tremellodendropsidaceae Jülich 1982
Tremellodendropsis (Corner) D.A. Crawford 1954
= *Polyozus* P. Karst. 1881
= *Pseudotremellodendron* D.A. Reid 1957

Justification of order and problems

Placement of Tremellodendropsidales within Agaricomycetes is not resolved and not obvious. Since only ribosomal markers for these taxa are available up to now, a genome sequencing project or at least the use of extraribosomal markers are desirable in the near future for further resolving its phylogenetic position.

Significance

Ecological and economical roles

Ribosomal DNA phylogenies by Truong et al. (2017) suggested that Tremellodendropsidales encompasses diverse ectomycorrhizal fungi that associate with a wide range of angiosperms (including *Fagus*, *Eucalyptus*, *Lithocarpus*, and *Nothofagus*) worldwide.

Trichosporonales Boekhout & Fell 2000

Contributed by: Teun Boekhout, Nathan Schoutteten, Andrey Yurkov

Introduction

Yeasts that form hyphae and reproduce with arthroconidia occur in Saccharomycotina (Ascomycota) and Agaricomycotina (Basidiomycota). Within the latter group, species of Trichosporonales, a basal lineage within Tremellomycetes and phylogenetically closely related to the jelly fungi (Tremellales), predominantly reproduce by such arthroconidia. The order was already recognized in early studies using sequence analysis of the D1-D2 domains of the LSU rDNA (Fell et al. 2000). Hitherto, a sexual stage has not been observed, with the exception of the sexually characterized and basidiome forming species *Tetragoniomyces uliginosus* (Millanes et al. 2011; Liu et al. 2015b). Several species are important because they cause infections in humans and animals, and often trigger allergic reactions. In contrast, several species are also interesting from an applied point of view.

History

Before, arthroconidia-forming yeasts belonging to both Ascomycota and Basidiomycota were classified in a single genus *Trichosporon*. However, using a variety of biochemical tests, early molecular observations such as molar percentage guanine and cytosine, and ultrastructural features allowed a distinction between ascomycetous and basidiomycetous arthroconidial yeasts. Consequently, arthroconidial yeasts of those two major fungal lineages were reclassified and the asexually basidiomycetous yeasts were classified in the genus *Trichosporon*. Molecular phylogenetic studies revealed considerable heterogeneity within the genus, and five clades were recognized (viz. cutaneum, ovoides, brassicae, gracile, porosum clades) (Sugita 2011). Interestingly, these molecular phylogenies demonstrated that some non-arthroconidia-forming budding yeasts of the genera *Asterotremella*, *Bullera*, *Cryptococcus*, and *Vanrija*, clustered among species of *Trichosporon.* A multigene-based phylogeny resulted in a reclassification of the genus *Trichosporon* (Liu et al. 2015a, b) and the following genera were recognized *Apiotrichum*, *Cryptotrichosporon*, *Cutaneotrichosporon, Effuseotrichsporon*, *Haglerozyma*, *Takashimella*, *Trichosporon*, and *Vanrija* (Liu et al. 2015b). Somewhat later, Takashima et al. (2019) using comparative genomics added the genus *Pascua* with *P. guehoae*, a species that was classified in *Cutaneotrichosporon* by Liu et al. (2015b). *Aegeritella catenulata*, an ant pathogen clustered sister to *P. guehoae* (Wrzosek et al. 2016) and if true this genus name might have taxonomic priority over *Pascua*. Takashima et al. (2019) described *Prillengera* to accommodate *P. fragicola*, a species placed in *Vanrija* by Liu et al. (2015b). The species formerly known as *T. pullulans* belongs to *Cystofilobasidiales* and was reclassified as *Guehomyces pullulans* (Fell and Scorzetti 2004) and more recently as *Tausonia pullulans* (Liu et al. 2015b). Three species, *Cutaneotrichosporon mucoides*, *Trichosporon coremiiforme and Trichosporon ovoides* were found to be hybrids (Sriswasdi et al. 2019).

Characters that define the taxa in the order

Trichosporonales is mainly phylogenetically recognized, but most species produce hyphae that disarticulate into arthroconida, but budding yeasts also occur. As far as known hyphal septa have dolipores with tubular or vesiculate parenthesomes (i.e., septal pore caps), cell walls contain xylose, and they have coenzyme Q9 or Q10 (Fell et al. 2000). Trichosporonales is sister to Tremellales, followed by Holtermanniales, Filobasidiales and Cystofilobasidiales (Liu et al. 2015a, b). *Tetragoniomyces uliginosus* is a peculial mycoparasite belonging to Trichonosporales and is so far the only known species in this group to produce basidiomes. This species produces a small mucoid layer on sclerotia of its basidiomycetous host. *Tetragoniomyces uliginosus* interacts with its host by means of basally clamped tremelloid haustoria growing on hyphae, which produce nm-fusion pores at the host-parasite interface (Bauer and Oberwinkler 1990b). Hyphae are clamped and produce basidiophores which terminally produce basidia. Basidia are four-celled, longitudinally septated, cell walls and septa are thick-walled. Basidia germinate directly by dikaryotic hyphae or germination tubes that conjugate and initiate a dikaryon outside the basidium. Outgrowing sterigmata and basidiospore production have not been observed (Koske 1972; Oberwinkler and Bandoni 1981). As such, it can be questioned whether the structures interpreted as basidia are truly meiosporangiophores, and wheather true sexual reproduction, including genetic recombination, takes place in this species. Consequently, the presence of sexual reproduction in Trichonosporales should be interpreted with some reservations.

Plates

See Figs. 161.2–161.82 in Sugita (2011)

Genera included

Family Tetragoniomycetaceae Oberw. & Bandoni 1981
  Bandonia Yurkov, Xin Zhan Liu, F.Y. Bai, M. Groenew. & Boekhout 2015
  Cryptotrichosporon Okoli & Boekhout 2007
  Takashimella Q.M. Wang 2015
  Tetragoniomyces Oberw. & Bandoni 1981
Family Trichosporonaceae Nann. 1934
  Apiotrichum Stautz 1931
  = *Hyalodendron* Diddens 1934
  Cutaneotrichosporon Xin Zhan Liu, F.Y. Bai, M. Groenew. & Boekhout 2015
  Effuseotrichosporon Yurkov, Xin Zhan Liu, F.Y. Bai, M. Groenew. & Boekhout 2015
  Haglerozyma Xin Zhan Liu, F.Y. Bai, M. Groenew. & Boekhout 2015
  Pascua Takashima, Manabe, Nishimura, Sriswasdi, Ohkuma, Iwasaki & Sugita 2019
  Prillingera Takashima, Manabe, Nishimura, Sriswasdi, Ohkuma, Iwasaki & Sugita 2019
  Trichosporon Behrend 1890
  = *Berkhoutia* Verona & Cif. 1939
  Vanrija R.T. Moore 1980
  = *Asterotremella* Prillinger, Lopandić & Sugita 2007

Evolution

Trichosporonales contains two main lineages that are recognized as families, namely Trichosporonaceae and Tetragoniomycetaceae. The latter family contains the only known sexually defined species in the order, hence mating experiments are required to find this for the other species. Biologically interesting is the notion that several species seem to have originated from a hybridization event (Sriswasdi et al. 2019). The mean time of origin of the order is estimated at 153 million years ago (Zhao et al. 2017).

Justification of order and problems

Trichosporonales seems to be well circumscribed by molecular phylogenetic reconstructions, either by using (partial) rDNA sequences or whole genome data, and to some extent also morphologically by the general presence of arthroconidia. Despite the fact that the number of genera was largely increased recently, it may well be that future studies will demonstrate the relative heterogeneity of some of the currently recognized genera, e.g., *Trichosporon* and *Apiotrichum*. It would be interesting to see if sexual stages could be demonstrated for some of the species of these various genera within the order.

Pontes et al. (2017) noticed that the association of *Tetragoniomyces* with *Cryptotrichosporon* and Trichosporonales was based on short sequences from herbarium material (Millanes et al. 2011) and questioned the reliability of earlier phylogenetic analyses. Newly sequences obtained from the only available living culture of *Tetragoniomyces uliginosus* PYCC 6958 showed similarity to genera *Papiliotrema* in Tremellales. Thus, it is possible that the genus *Tetragoniomyces* and the respective family Tetragoniomycetaceae do not belong to the order Trichosporonales. Additional samples and sequences of *Tetragoniomyces uliginosus* are needed to clarify the position of *Tetragoniomyces*.

While Trichosporonales has been resolved as a monophyletic lineage, its relationship with the sister clade Tremellales requires additional clarification with respect to the position of the genera *Gelidatrema* and *Phaeotremella* (Liu et al. 2015a; Li et al. 2020b).

Significance

Ecological and economical roles

Several species of Trichosporonales are clinically relevant as they cause deep seated infections, superficial infections such as white piedra on hair, or can contaminate indwelling devices, such as catheters. *Trichosporon asahii* is clinically mostly encountered. Most clinically relevant species of *Trichosporon* are still classified in the genus *Trichosporon,* but other clinically relevant species belong to *Cutaneotrichosporon* and *Apiotrichum* (Arastehfar et al. 2021; Sugita 2011).

Some Trichosporonales are also interesting from a biotechnological perspective, including production of lipase, esterase, cytochrome P450, cocoa butter equivalents, organic volatile compounds, enantioselective degradation of (RS)-ibuprofen, use as biosensors, e.g. to detect volatiles, degradation of phenol, degradation of xenobiotics, degradation of phenol at low temperatures, transformation of lignin, hydrolysis of lactose in dairy products, degradation of mycotoxins, etc. (Arastehfar et al. 2021; Sugita 2011). Several species were explored as cell factory for custom tailored microbial oils and oleaginous yeasts.

Chemical diversity

Chemical diversity is known for the co-enzyme Q system with CoQ9 and CoQ10 being present. Also, several serotypes have been identified and to a large extent both CoQ and serotypes coincide with the clades as previously recognized and that now are recognized as genera (Sugita 2011; Liu et al. 2015b).

Other relevant data and future recommendations

Most species of the order can be successfully identified based on the combination of ribosomal ITS and LSU nucleotide sequences. In Trichosporonales, nucleotide sequences of the D1/D2 domains of the LSU rRNA gene are often more variable than those of ribosomal ITS (Scorzetti et al. 2002).

Tritirachiales Aime & Schell 2011

Contributed by: Teun Boekhout, Nathan Schoutteten

Introduction

Tritirachiales was until recently classified in Pezizomycotina, Ascomycota. However, molecular phylogenetic analysis has changed this view drastically. Following the work of Schell et al. (2011), these fungi were found to belong to Pucciniomycotina, in which they hold an order on themselves.

History

Limber (1940) described the genus *Tritirachium* and included three species. These fungi were classified in Ascomycota in the obsolete class Hyphomycetes. A multigene-based phylogeny, however, clearly demonstrated that *Tritirachium* belonged to Pucciniomycotina and holds an isolated phylogenetic position. Consequently, the class Tritirachiomycetes, order Tritirachiales, family Tritirachimycetaceae were introduced (Schell et al. 2011; Cao et al. 2021b).

Characters that define the taxa in the order

The fungi that belong to Tritirachiales have a unique morphology with long erect conidiophores with verticils of conidiogenous cells, on which conidia are formed in a sympodial rachis, strongly resembling a bunch of grapes. Hyphal septal pore complexes have a 'simple' organisation (Schell et al. 2011). Schell et al. (2011) used a multigene approach and a phylogenetic species concept to circumscribe several species. Morphological boundaries were not fully coinciding with the phylogenetic data. A sexual state was described for *Paratritirachium curvibasidium*, including curved, pale brown basidia that originate directly on the binucleate hyphae with unfused clamp connections. The oval uninucleate basidiospores are formed on short sterigmata and are probably sessile (Nguyen et al. 2014).

Plates

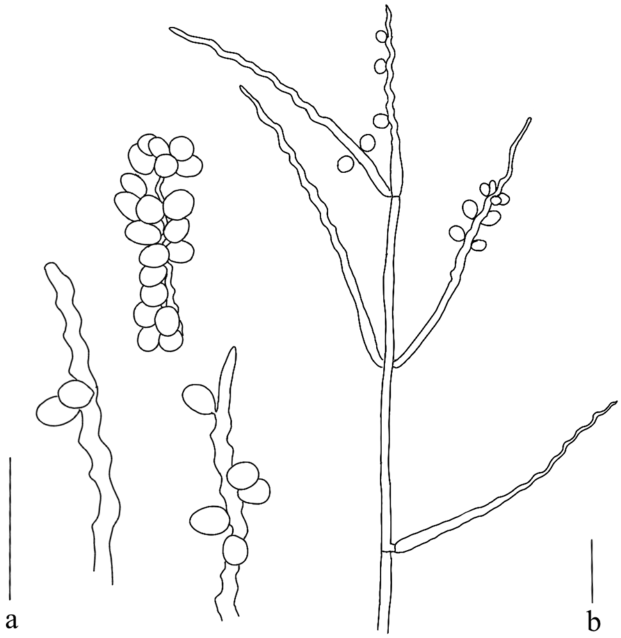


Fig. 63 Conidiophores, conidiogenous cells and conidia of *Tritirachium*. Scale bars: a = 5 µm; b = 10 µm. Redraw from Schell et al. (2011) and Manohar et al. (2014) by Mao-Qiang He

Genera included

Family Tritirachiaceae Aime & Schell 2011
Tritirachium Limber 1940
= *Spirotrichum* Saito ex J.F.H. Beyma 1940
Paratritirachium Beguin, Pyck & Detandt 2012

Evolution

In a multigene-based phylogeny, Tritirachiales occurs as sister group to Agaricostilbomycetes/Mixiomycetes (Schell et al. 2011; Wang et al. 2015a). The unique morphology of the conidial stage does not agree with those known from other members of Basidiomycota. The estimated time of origin is estimated 356 million years ago (Zhao et al. 2017).

Justification of order and problems

The order seems well circumscribed and species belonging here are also morphologically well characterized. The morphology of the basidia, whether unicellular or septated, needs further investigation.

Significance

Ecological and economical roles

Most species originate from plant material, but also clinical samples, and marine ones, including sponges (Manohar et al. 2014; Cao et al. 2021b). *Paratritirachium curvibasidium* is thermoresistant (Nguyen et al. 2014). As stated by Cao et al. (2021a, b), the order is likely undersampled, and species may also occur in indoor environments and might pose a risk for human health. The ecological strategy of these species is unclear, and experimental approaches are needed to gain insights in this. Sampling in habitats with extreme conditions, e.g., high temperature, low water activity is recommended.

Chemical diversity

Unknown.

Uleiellales Garnica, K. Riess, M. Schön, H. Butin, M. Lutz, Oberw. & R. Bauer 2016

Contributed by: Teodor T. Denchev, Cvetomir M. Denchev, Dominik Begerow, Martin Kemler

Introduction

Uleiellales consists of a single family, Uleiellaceae, that was erected to accommodate the species of *Uleiella* (Vánky 2001; Riess et al. 2016). *Uleiella* is a unique genus among the smut fungi being the only genus known to occur on gymnosperms (*Araucaria* spp.). Furthermore, the species of *Uleiella* are among the very few smut fungi that parasitize woody plants.

In Ustilaginomycetes, Uleiellales is characterized by having enlarged interaction zones in intracellular hyphae, and mature septa in soral hyphae and in cultural hyphae without pore. Presence of enlarged interaction zones supports the placement in Ustilaginomycetes. Haustoria are present; they are not constricted at the penetration point and extended only a short distance into the host cell (Riess et al. 2016).

Characters that define the taxa in the order

Uleiella is distinguished from the other smut fungi by specialization on *Araucaria* (Araucariaceae). This genus includes two species: *U. paradoxa* J. Schröt. forming sori on the surface of the basal part of the scales of male and female cones, and in the ovules of *Araucaria angustifolia* (Bertol.) Kuntze and *A. imbricata* Pav. in Brazil, and *U. chilensis* Dietel & Neger producing sori on the scales of female cones, and in the ovules of *A. araucana* (Molina) K. Koch and *A. imbricata* in Chile and Argentina (Vánky 2011; Riess et al. 2016).

Species of *Uleiella* form quite specific propagule—a rounded and pigmented structure, covered by a thick reticulate cover and with one to usually many units inside (treated by Vánky 2001, 2013, as 'spores'), embedded in a hyaline mass. Vánky (2001, 2013) called this structure 'spore-complex' with spores inside. These propagules, however, were considered by Riess et al. (2016) as teliospores that during sporogenesis became multi-celled by septation, forming segments in the mature teliospore. Segments germinate into germination tubes through the spore wall and the spore germination results in sterigma-like hyphae that produce terminally sporidia (Riess et al. 2016).

Plates

For illustrations, see Vánky (2013), Riess et al. (2016).

Genera included

Family Uleiellaceae Vánky 2001
Uleiella J. Schröt. 1894
= *Ulea* J. Schröt. 1892 (nom. inval.)

Evolution and justification of order

Uleiellales was recently introduced based on molecular phylogenetic results as sister taxon to Violaceomycetales (Riess et al. 2016). It is the only known lineage within the Ustilaginomycotina that infects gymnosperms and could be the result of a host jump (Riess et al. 2016; Begerow and McTaggart 2018).

For the first time, a smut fungus on *Araucaria* was reported by Schröter, as *Ulea paradoxa* J. Schröt., at a meeting of the Society of the Silesian Culture in 1892 (Schröter 1892). In 1894, this species was published under a different generic name, as *Uleiella paradoxa* J. Schröt. (Schröter 1894). From a footnote to the second publication (Schröter 1894) it is clear that the name *Ulea* was published by Schröter as a preliminary report, making this name invalidly published (Art. 36.1(a) Shenzhen Code).

Economic importance

None is known about the significance of the infection on *Araucaria*.

Urocystidales R. Bauer & Oberw. 1997

Contributed by: Teodor T. Denchev, Cvetomir M. Denchev, Dominik Begerow, Martin Kemler

Introduction

In Ustilaginomycetidae, Urocystidales was erected to accommodate species having enlarged interaction zones and septa with simple pores (with the exception of *Glomosporium* which soral hyphae are without septal pores) (Bauer et al. 1997). The teleomorphic members are plant parasites, but several species are known as yeasts only and their taxonomy is based on phylogenetic analyses (Begerow and McTaggart 2018). Saprotrophic yeast-like growth of secondary sporidia is known for some *Thecaphora* and *Urocystis* species (Vánky et al. 2008a; Begerow et al. 2014).

Urocystidales is divided into six families: Doassansiopsidaceae, Fereydouniaceae, Floromycetaceae, Glomosporiaceae, Mycosyringaceae, and Urocystidaceae.

Characters that define the taxa in the order

Species of Urocystidaceae are characterized by the following complex of characters: formation of spore balls (with sterile cells outside), pigmented teliospores, presence of a simple septal pore with two outer membrane caps and two inner, non-membranous plates closing the pore, and host-parasite interaction by haustoria (Bauer et al. 1997; Vánky 2013; Begerow et al. 2014). In some genera, spore-ball formation is secondarily reduced to single spores.

Urocystis with about 180 species is the largest genus of the family and in the order as well. Species of this genus sporulate mostly in leaves and stems, sometimes in flowers (e.g., *U. kmetiana* Magnus) or seeds (e.g., *U. primulae* (Rostr.) Vánky), less often on the base of stems (e.g., *U. leimbachii* Oertel), in leaf veins (e.g., *U. rodgersiae* (S. Ito) Denchev & Kakish.) or roots (*U. coralloides* Rostr.). Host spectrum is diverse and includes members of the monocots (Alstroemeriaceae, Amaryllidaceae, Asparagaceae, Colchicaceae, Cyperaceae, Dioscoreaceae, Hypoxidaceae, Iridaceae, Ixioliriaceae, Juncaceae, Liliaceae, Melanthiaceae, and Poaceae), basal eudicots (Circaeasteraceae and Ranunculaceae), superrosids (Saxifragaceae), rosids (Brassicaceae, Oxalidaceae, Rosaceae, and Violaceae), and asterids (Apiaceae, Boraginaceae s. lat., Ericaceae, Orobanchaceae, Polemoniaceae, Primulaceae, and Solanaceae). The infection is mostly systemic. Sori form dark brown or blackish brown streaks, spots, swellings or galls, containing a powdery mass of spore balls. Spore balls are persistent, composed of one to several, pigmented teliospores, surrounded by paler and smaller sterile cells (Vánky 2013). Spore germination is holobasidiate. An anamorph (*Paepalopsis*) is present in some species (Vánky 2013).

Flamingomyces includes one species, *F. ruppiae* (Feldmann) R. Bauer et al., on *Ruppia maritima* (Ruppiaceae). Sori are developed in basal part of leaves and rhizomes. Spores are embedded in the host tissue, pigmented, produced singly, not forming balls; sterile cells are absent. Spore germination results in hyphae (Bauer et al. 2007). *Melanoxa* consists of two species with sori on vegetative parts of *Oxalis* (Oxalidaceae). Spores are pigmented, produced singly, not forming balls; sterile cells are absent. Spore wall in TEM is multilayered (Lutz et al. 2012). *Melanustilospora* includes two species that have sori in leaves of hosts in Araceae. Spores are darkly pigmented, single, thick-waled, embedded in the host tissue; sterile cells are absent (Denchev 2003). *Vankya* consists of three species, producing sori in leaves of hosts in Liliaceae and Asparagaceae. Spores are single but sterile cells are present between the spores. Spore germination is phragmobasidiate (Vánky 2013). *Ustacystis* is a monotypic genus. *Ustacystis waldsteiniae* (Peck) Zundel forms sori in the veins of leaves of plants in Rosaceae. Spores are single, in pairs, or in indefinite, loose balls. Sterile cells are absent. Spore germination results in two-celled basidia (Vánky 2013). *Mundkurella* includes five parasitic species on Araliaceae (*Aralia, Heptapleurum, Kalopanax*, and *Schefflera*). They are among the very few smut fungi that parasitize woody plants. The mature spores are of two kinds: (i) one-celled, subhyaline to pale-colored, sterile and usually collapsed spores, and (ii) one to several-celled, pigmented, fertile spores with rich cell contents. Spore germination results in 1–4-celled basidia, often in several basidia from the same spore, producing laterally and apically sessile basidiospores (Denchev and Kakishima 2007).

Floromycetaceae (*Antherospora* and *Floromyces*) sporulate in the flowers of monocots. Their spores are pigmented, single or in balls, sterile cells are absent. The host-parasite interaction is by haustoria; septal pore is simple, with two membrane caps and two inner plates closing the pore (Bauer et al. 2008; Vánky et al. 2008b; Vánky 2013). Members of *Antherospora* (12 spp.) produce their sori in the flowers (mostly in anthers) of plants in the Hyacinthaceae. The infection is systemic, and all flowers of an inflorescence are affected. Spores are single. Spore germination is phragmobasidiate (Vánky 2013). *Floromyces* is a monotypic genus. *Floromyces anemarrhenae* (C.H. Chow & Chi C. Chang) Vánky et al. is a parasite in flowers of *Anemarrhena asphodeloides* Bunge (Asparagaceae). The infection is systemic. Permanent spore balls, composed of spores only, are present. Spore germination results in both septate and non-septate basidia, but also in ramifying hyphae (Vánky et al. 2008b; Vánky 2013).

Mycosyringaceae is represented by a single genus, *Mycosyrinx*, with four species. Their sori form witches' brooms on plants in *Cissus* (Vitaceae). Spores are in pairs, darkly pigmented, hemispherical, connected on their flattened sides, initially embedded in the host, later powdery (Vánky 2013). Spore germination, known from *M. cissi* (DC.) Beck, results directly in basidiospores with a sigmoid shape, i.e., the basidium is reduced to the teliospore (Begerow et al. 2014). Intracellular hypha or haustoria, and septal pores are lacking. The host-parasite interaction is by enlarged interaction zones in intercellular hyphae (Bauer et al. 1997).

Fereydouniaceae is represented by a single genus and species. It is known as yeast-like anamorph only, isolated from undetermined plant remnants. Sexual structures and teliospores are absent (Nasr et al. 2014a).

Doassansiopsidaceae consists of one genus, *Doassansiopsis*, and 14 species. The hosts are aquatic or paludal plants in the monocots (Alismataceae, Potamogetonaceae), basal angiosperms (Nymphaeaceae), and asterids (Potamogetonaceae). Sori are formed in leaves, petioles, stems or ovaries, as spots or swellings. Spore balls are present, embedded in the host tissue, persistent, composed of a central mass of sterile fungal cells surrounded by the firmly adhering, colorless or pale pigmented spores, and an external cortex of sterile cells (Vánky 2011, 2013). Species of *Doassansiopsis* share with Urocystidaceae and Floromycetaceae an identical septal pore apparatus, composed of a simple septal pore with two outer membrane caps and two inner, non-membranous plates closing the pore. The host-parasite interaction is by haustoria (Bauer et al. 1997; Begerow et al. 2014). Spore germination is holobasidiate. Anamorphs are present.

Glomosporiaceae includes a single genus, *Thecaphora*. The host spectrum is diverse and includes 16 families of the eudicots. Sori are in various parts of the infected plants, filled with masses of spore balls, rarely the spores are single, yellowish- to dark reddish brown. Spore balls are composed of few to many, loosely or firmly agglutinated spores; no sterile cells (Vánky 2011, 2013). Some species are with single spores, not in balls (e.g., *T. thlaspeos* (Beck) Vánky). Spore germination is variable, ranging from holobasidiate to development of aseptate or septate hyphae (Bauer et al. 1997). The host-parasite interaction is by intracellular hyphae. The mature septa are poreless (Bauer et al. 1997). Some species (e.g., *T. seminis-convolvuli* (Duby) Liro, *T. thlaspeos*) with anamorphs.

Plates

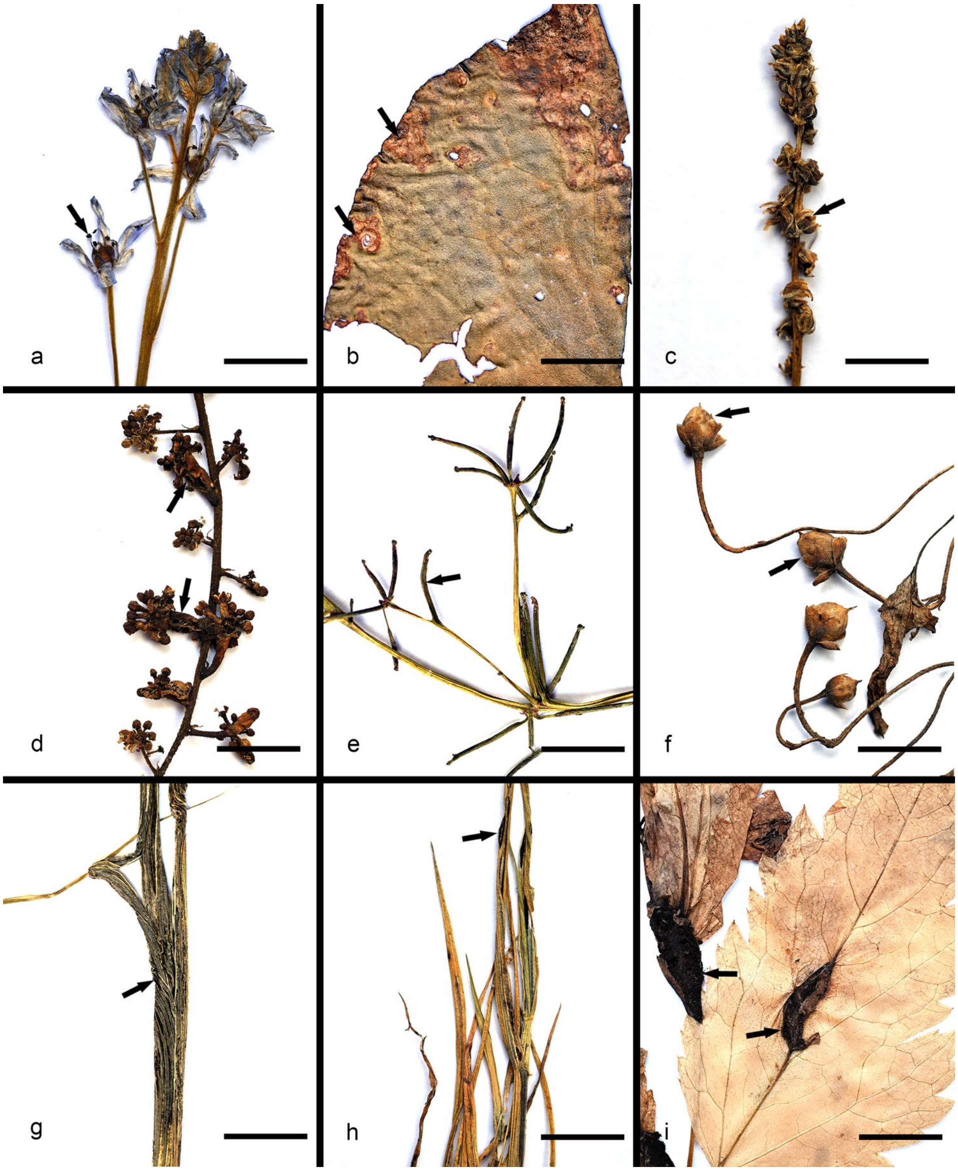


Fig. 64 Urocystidales. **a**–**i** habit. **a** *Antherospora scillae* on *Scilla bifolia*, Bulgaria (SOMF 2859); **b** *Doassansiopsis tomasii* on *Nymphaea nouchali,* Ethiopia (Vánky Ustil. Exs. 1259); **c** *Floromyces anemarrhenae* on *Anemarrhena asphodeloides,* China (Vánky Ustil. Exs. 1303); **d** *Mundkurella schefflerae* on *Schefflera digitata,* New Zealand (Vánky Ustil. Exs. 1014, isotype); **e** *Mycosyrinx cissi* on *Cissus verticillata,* Costa Rica (Vánky Ustil. Exs. 835); **f** *Thecaphora seminis-convolvuli* on *Convolvulus arvensis,* Germany (Vánky Ustil. Exs. 290); **g** *Urocystis achnatheri* on *Achnatherum sibiricum,* China (Vánky Ustil. Exs. 1271, isotype); **h** *Urocystis bolivari* on *Lolium rigidum,* Australia (Vánky Ustil. Exs. 1148); **i** *Urocystis carcinodes* on *Actaea spicata,* Sweden (Vánky Ustil. Exs. 532). Arrows indicate sori. Scale bars: a–i = 1 cm

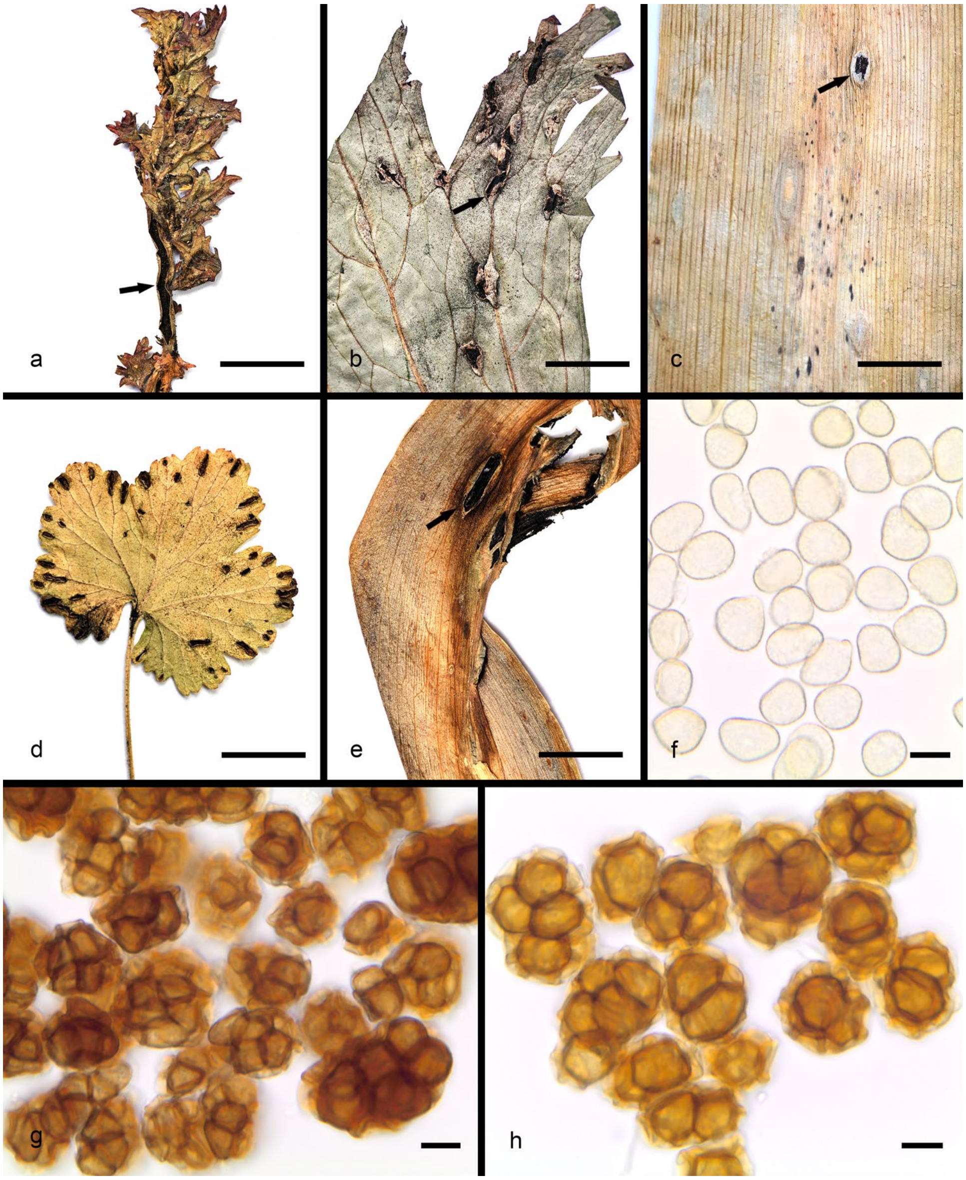


Fig. 65 Urocystidales. **a**–**e** habit. **a** *Urocystis filipendulae* on *Filipendula vulgaris*, Sweden (Vánky Ustil. Exs. 866); **b** *Urocystis irregularis* on *Aconitum septentrionale*, Norway (Vánky Ustil. Exs. 237); **c** *Urocystis magica* on *Allium nigrum*, Italy (Vánky Ustil. Exs. 1308); **d** *Ustacystis waldsteiniae* on *Waldsteinia geoides*, Hungary (Vánky Ustil. Exs. 629); **e** *Vankya heufleri* on *Tulipa urumoffii,* Bulgaria (SOMF 18886); **f**–**h** spores in LM. **f** *Thecaphora thlaspeos* on *Arabis serpillifolia,* Spain (MA 331875); **g** *Urocystis sorosporioides* on *Thalictrum alpinum*, Greenland (C-F-111318); **h** *Urocystis triseti* on *Trisetum spicatum,* Greenland (O, s.n.). Arrows in **a**–**c**, **e** indicate sori. Scale bars: a–e = 1 cm, f–h = 10 µm

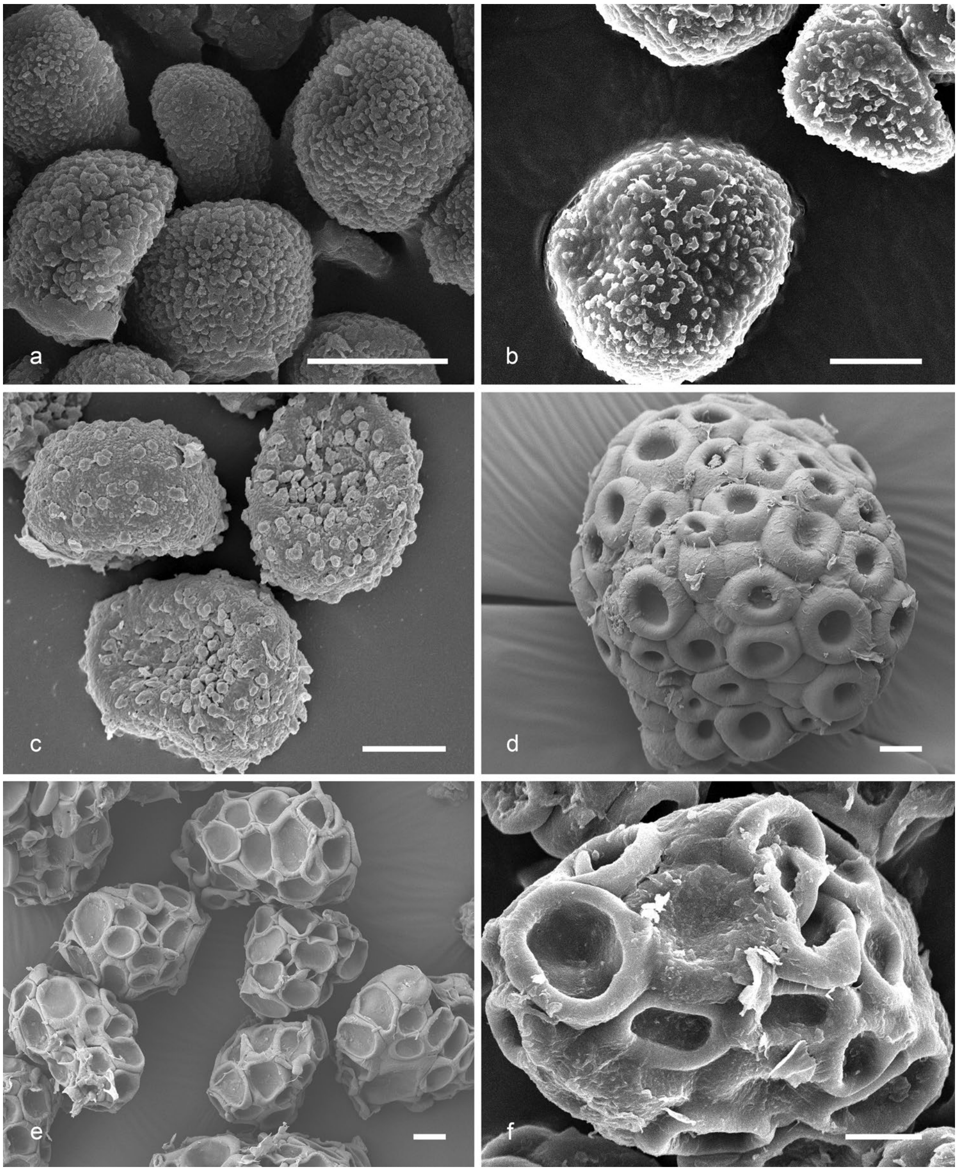


Fig. 66 Urocystidales. **a**–**f** spores in SEM. **a** *Antherospora hortensis* on *Muscari armeniacum*, Greece (W 1964-16348); **b** *Mundkurella japonica* on *Kalopanax pictus*, Japan (KPM-NC0015229); **c** *Thecaphora thlaspeos* on *Arabis pubescens*, Algeria (MA 48394); **d** *Urocystis corsica* on *Stipa capensis*, Greece (B, s.n.); **e** *Urocystis johansonii* on *Juncus bufonius,* Greece (B, s.n.); **f** *Urocystis sorosporioides* on *Thalictrum alpinum*, Greenland (C-Greenland herb., s.n.). Scale bars: a–f = 5 µm

Genera included

Family Doassansiopsidaceae Begerow, R. Bauer & Oberw. 1898
  Doassansiopsis (Setch.) Dietel 1897
  = *Doassansiella* Zambett. 1970 (nom. inval.)
Family Fereydouniaceae S. Nasr, Soudi, H.D.T. Nguyen, M. Lutz & Piątek 2014
  Fereydounia S. Nasr, Soudi, H.D.T. Nguyen, M. Lutz & Piątek 2014
Family Floromycetaceae M. Lutz, R. Bauer & Vánky 2008
  Antherospora R. Bauer, M. Lutz, Begerow, Piątek & Vánky 2008
  Floromyces Vánky, M. Lutz & R. Bauer 2008
Family *Glomosporiaceae* Cif. 1963
  Thecaphora Fingerh. 1836 (nom. cons.)
  = *Sorosporium* F. Rudolphi 1829 (nom. rejic.)
  = *Poikilosporium* Dietel 1897
  = *Glomosporium* Kochman 1939
  = *Rhombiella* Liro 1939
  = *Angiosorus* Thirum. & M.J. O'Brien 1974
  = *Thecaphorella* H. Scholz & I. Scholz 1988
  = *Tothiella* Vánky 1999
  = *Kochmania* Piątek 2005
Family Mycosyringaceae R. Bauer & Oberw. 1997
  Mycosyrinx Beck 1894
Family Urocystidaceae Begerow, R. Bauer & Oberw. 1998
  Flamingomyces R. Bauer, M. Lutz, Piątek, Vánky & Oberw. 2007
Melanoxa M. Lutz, Vánky & R. Bauer 2012
Melanustilospora Denchev 2003

Mundkurella Thirum. 1944
Urocystis Rabenh. ex Fuckel 1870 (nom. cons.)
= *Granularia* Sowerby 1815 (nom. illeg.)
= *Tuburcinia* Fr. 1832 (nom. rejic.)
= *Polycystis* Lév.1846 (nom. rejic.)
= *Urocystis* Rabenh. 1857 (nom. inval.)
= *Paepalopsis* J.G. Kühn 1882
= *Polysaccopsis* Henn. 1898
= *Ginanniella* Cif. 1938
= *Tuburciniella* Zambett. 1970 (nom. inval.)
Ustacystis Zundel 1945
= *Whetzelia* Zundel 1945 (nom. illeg.)
Vankya Ershad 2000

Evolution and justification of order

Genera in Urocystidales are extremely diverse in their morphology and spore germination. In the current system, families in this order are defined based on ultrastructural data and phylogenetic analyses.

Species of *Doassansiopsis*, similar to that in Doassansiales, are ecologically well characterized by their occurrence on paludal or aquatic plants and complex spore balls (with numerous teleospores and sterile cells), as adaptation to this specific ecological niche. Thus, *Doassansiopsis* and Doassansiales are examples of the independent, convergent evolution of similar structures under the same environmental condition (Begerow et al. 2014).

The generic name *Urocystis* 1870 is conserved against the teleomorph-typified names *Tuburcinia* 1832 and *Polycystis* 1846. An anamorph-typified generic name, *Paepalopsis* 1882, was proposed for conidial stages of *Urocystis*: *P. irmischiae* J.G. Kühn (q.e. *Urocystis primulae*) and *P. trientalis* (Berk.) Cif. (q.e. *U. trientalis* (Berk. & Broome) B. Lindeb.) (Kühn 1882; Ciferri 1959), but *Urocystis* has priority over *Paepalopsis*. The generic name *Tuburciniella*, proposed for the conidial stages of *Tuburcinia*, is an invalidly published (without a description or diagnosis in Latin, Art. 39.1, and without indication of a type, Art. 40.1) and illegitimate name (Art. 52.1, being a superfluous name for *Paepalopsis*, cited as a synonym, when published by Zambettakis (1970).

Another generic name, *Doassansiella*, was erected by Zambettakis (1970) for accommodation of the conidial stages of *Doassansiopsis*. In fact, only the type species was assigned to this genus—*Doassansiella aquatilis* (Peck) Zambett., based on *Ramularia aquatilis* Peck (q.e. *Doassansiopsis hydrophila* (A. Dietr.) Lavrov) (Zambettakis 1970). *Doassansiella aquatilis* is an illegitimate name (Art. 52.1), being a superfluous name for *Savulescuella aquatilis* (Peck) Cif., but prior to that, the name *Doassansiella* is invalidly published (Art. 39.1) making the combination *D. aquatilis* (Peck) Zambett. also invalid (Art. 35.1).

Rhombiella and *Thecaphorella* are anamorph-typified generic names reduced to synonyms of *Thecaphora*.

Economic importance

Urocystis species cause economically significant diseases of wheat (*U. tritici* Körn.), rye (*U. occulta* (Wallr.) Rabenh.), and onion (*U. magica* Pass.), as well as of some ornamental plants. *Thecaphora solani* (Thirum. & M.J. O'Brien) Mordue causes an economically important disease of potatoes. *Thecaphora frezzii* Carranza & J.C. Lindq. affects production of peanut causing yield losses (Arias et al. 2021).

Ustilaginales G. Winter 1880

Contributed by: Teodor T. Denchev, Martin Kemler, Dominik Begerow, Cvetomir M. Denchev

Introduction

In Ustilaginomycetes, Ustilaginales is characterized by the presence of a mature septum without pores, and host-parasite interaction by intracellular hyphae (with the exception of the Melanotaeniaceae that have a septum with a simple pore, and haustoria) (Bauer et al. 1997; Begerow and McTaggart 2018). Ustilaginales is the largest order in subphylum Ustilaginomycotina, containing over 930 species.

Ustilaginales is divided into seven families: Anthracoideaceae, Clintamraceae, Geminaginaceae, Ustilaginaceae, Melanotaeniaceae, Pericladiaceae, and Websdaneaceae.

Characters that define the taxa in the order

Species of Anthracoideaceae are characterized by poreless septa and host-parasite interaction by intracellular hyphae. Spore germination is with transversely septate basidia or with ramified hyphae. Species are parasites on Cyperaceae and Juncaceae.

Anthracoidea is the largest genus of the family. Their sori form globose to broadly ellipsoidal or ovoid, black, hard bodies around aborted nuts of cyperaceous plants, mainly on *Carex*. Spores are formed singly. Spore germination results in a two-celled aerial basidium forming one or more basidiospores on each cell. The basidiospores may infect flowers. Infection is local and confined to individual flowers (Kukkonen 1963; Hendrichs et al. 2005; Vánky 2011; Denchev et al. 2013, 2020b). *Planetella* is a monotypic genus closely related to *Anthracoidea. Planetella lironis* Savile infects *Carex maritima* Gunnerus and *C. sabulosa* Kunth. Its spores have a thick-walled equatorial band and two, thin-walled polar areas (Denchev and Denchev 2018a). Species of *Farysia, Moreaua, Schizonella,* and *Orphanomyces* are parasites on species of *Carex*. Sori of *Farysia* are localized in single flowers, when young they are covered by a fungal peridium. Spores are single. Spore mass is traversed by numerous, capillitium-like fascicles of sterile hyphae functioning as elaters (Vánky 2013). Some anamorphic species of *Farysizima* (nom. inval.) were transferred into *Farysia*, based on molecular data (Wang et al. 2015d). Sori of *Moreaua* are naked on the surface of inner floral organs. Spores are firmly adhered in spore balls. Sori of *Schizonella* are in leaves as black, pustulate streaks. Infection is systemic. Spores are originally in pairs, arising by internal division of a mother cell, later often are separated, rarely spore pairs agglutinated into balls (*S. cocconii* (Morini) Liro) (Vánky 2013). Sori of *Orphanomyces* are external on the leaf surface, as black crusts. Infection is systemic. Infected plants do not flower. Spores are single or in balls (Savile 1974). Species of *Dermatosorus* infect cyperaceous plants.Sori are in ovaries, covered by a peridium, filled with spore balls, with a central columella. Spore balls composed of a cortex of sterile cells and a central mass of fertile cells (Vánky 2013).

The heterogeneous *Cintractia* s. lat. was split into several genera (Piepenbring et al. 1999; Piepenbring 2000; Vánky 2004). Species of *Cintractia* s. str. cause local infection of cyperaceous plants. Sori covered by a peridium, surround mostly bases of peduncles; mycelial stroma is present. Spores are single (Piepenbring 2000; Vánky 2013). Species of *Leucocintractia* cause systemic infection of *Rhynchospora.* Sori surround all the pedunculi of an inflorescence or the upper internodes of the stem; peridium and sterile stroma are present. Spores are single (Piepenbring 2000; Vánky 2013). Species of *Ustanciosporium* infect cyperaceous plants. Their sori are in all spikelets of an infected inflorescence or in groups of spikelets, surrounding the tip of the axis of sterile spikelets and filling them with a spore mass. Sterile fungal stroma and peridium absent. Spores are single or in loose balls; often with a hyaline appendage (Piepenbring 2000; Vánky 2013). Species of *Stegocintractia* have hosts in the Juncaceae. Infection is systemic. Their sori are in all spikelets or around pedunculi of an infected inflorescence. Young sori are covered by a fungal peridium, sterile stroma is lacking. Spores are single, without an appendage (Piepenbring 2000; Vánky 2013). *Pilocintractia* infect *Fimbristylis*. Their sori are in some flowers of a spikelet, forming black, hard bodies around the nuts, with sterile filaments between the spores. Peridium and stroma may be present. Spores are agglutinated, produced in radially arranged, cup-shaped pockets (Vánky 2004). Sori of *Trichocintractia* are in scattered spikelets of *Rhynchospora,* forming swollen, sac-like bodies, covered by a peridium and opened on its distal part. The spores are powdery, mixed with long, sterile cells (Vánky 2013).

Clintamraceae is a monotypic family, with a monotypic genus. *Clintamra nolinae* (G.P. Clinton) Cordas & Durán on *Nolina* spp. (Asparagaceae) has poreless septa and host-parasite interaction by intracellular hyphae. Sori are external on the surface of young leaves and inflorescences, forming blackish brown powdery spore mass. Spores are single, in pairs or small groups. Spore germination results in a bifurcate basidium bearing 2 apical, multiseptate basidiospores (Vánky 2013).

Species of Ustilaginaceae are characterized by poreless septa and host-parasite interaction by intracellular hyphae. Spore germination is with transversely septate basidia (with exception of *Bambusiomyces*). Members of this family are parasites on hosts mostly in the Poaceae or are known as anamorphic yeasts isolated from plant material only.

In Ustilaginaceae, the most recognizable genus is *Ustilago*, with the type species *U. hordei* (Pers.) Lagerh.—the causal agent of barley smut. Species of this genus are parasites on hosts in various genera of grasses or anamorphic species, isolated as yeasts from plant surfaces. Sori of the parasitic species are formed in various vegetative or generative organs of the infected plant, at maturity bursting and exposing usually powdery, sometimes agglutinated, blackish or olive-brown spore mass. Sterile cells are absent. Spores are single, pigmented, usually ornamented (punctate, verruculose, echinulate, echinate, tuberculate), rarely smooth. Spore germination results in phragmobasidia bearing lateral and apical basidiospores or hyphae (Vánky 2013). The *Ustilago–Sporisorium–Macalpinomyces* complex was divided by McTaggart et al. (2012c) into *Anthracocystis*, *Langdonia*, *Macalpinomyces*, *Sporisorium* s. str., *Stollia*, *Triodiomyces*, and *Ustilago*. Species of *Sporisorium* are parasites on grasses or anamorphic species isolated as yeasts from plant surfaces. Sori are in flowers or inflorescence of the infected plant, covered by a peridium formed of fungal elements and host tissue. A stout, cylindrical or woody, branched or unbranched columella is present, composed of host tissue and sporogenous hyphae. Spores at first are somewhat agglutinated, later are single, pulverulent, pigmented. Sterile cells are present, intermixed with the spores (McTaggart et al. 2012c; Vánky 2013). Species of *Anthracocystis* are parasites on grasses. Sori replace inflorescence or all of the racemes, or are localized in spikelets of an inflrescence; covered by a peridium formed of hyphal cells surrounded by host cells. A filiform, flattened or flexuous columella is present, often separated into several columellae. TSpores are in compact spore balls. Sterile cells are usually absent (McTaggart et al. 2012c; Vánky 2013). Species of *Macalpinomyces* are parasites on grasses. Sori are in ovaries or culms, usually producing hypertrophy, covered by a peridium of host tissue permeated by hyphae. A true columella is absent. Spores are pigmented and tightly packed, filling the sori. Hyaline or pale colored sterile cells are present in the spore mass (Vánky 2013). *Langdonia* are parasites on *Aristida* and *Stipagrostis*. Sori are in some or all ovaries of the infected plant. Columella and sterile cells absent. Spores are usually compacted into spore balls. *Stollia* are parasites on hosts in the Andropogonae. Sori are in ovaries, covered by a thick peridium derived from host tissue. Columella is absent. Spores are single. Sterile cells are in loose irregular groups, hyaline. *Triodiomyces* are parasites on *Triodia* or anamorphic species isolated as yeasts from plant surfaces. Sori of the parasitic species are in culms or inflorescence. Spores are single. Peridium, columella, spore balls, and sterile cells are absent (McTaggart et al. 2012c; Vánky 2013). *Mycosarcoma* are parasites on grasses, but anamorphic stages were isolated as yeasts from plant surfaces. Type species of this genus is *M. maydis* (DC.) Bref.—the causal agent of corn smut on maize. Sori are usually in some ovaries of an inflorescence, derived from hypertrophied host tissue, often tubular, splitting longitudinally to expose the spore mass; rarely in stems, leaves and mail inflorescences (e.g., *M. maydis*). Columellae are absent. Spores single (McTaggart et al. 2016; Begerow and McTaggart 2018). *Tranzscheliella* are parasites on grasses. Their sori are on stems or aborted inflorescence branches, superficial, naked or with ephemeral peridium. Infection is systemic. Spores are single (Vánky 2013). Species of *Moesziomyces* are parasites on grasses but anamorphic stages were isolated as yeasts from plant surfaces. Sori of the parasitic species are in ovaries, covered by green later brown peridium of host tissue. Spores in many-spored balls, firmly agglutinated and mixed with sterile cells (Begerow and McTaggart 2018). The only species of *Bambusiomyces*, *B. shiraianus* (Henn.) Vánky, develops sori on stems of bamboo (Poaceae). Spores are single. Spore germination results in a short holobasidium, producing apically basidiospores (Vánky 2013).

Eriocaulago and *Eriosporium* are parasites in ovaries of hosts in Eriocaulaceae. Spores of *Eriocaulago* are single, while that of *Eriosporium* are in spore balls (composed of spores only). In both genera, peridium, columella, and sterile cells are absent (Vánky 2005). The only species of Parvulago, *P. marina* (Durieu) R. Bauer et al., develops sori as swellings at the base of culms of *Eleocharis* (Cyperaceae). Spores are single (Bauer et al. 2007). *Melanopsichium* are parasites on Polygonaceae. Sori are as conspicuous galls in various parts of the plant, composed of hypertrophied host tissue and hyphae, with numerous chambers filled with spores embedded in a gelatinous matrix (Vánky 2013).

Kalmanozyma and *Pseudozyma* are known as anamorphic yeasts isolated from plant surfaces. Sexual reproduction is unknown (Wang et al. 2015d; Begerow and McTaggart 2018).

Species of the Websdaneaceae are parasites on hosts in the Restionaceae (Poales). They have poreless septa and host-parasite interaction by intracellular hyphae. Sori of *Restiosporium* are in fruits, replacing the seeds with a black, granular powdery mass of spore balls. Spore balls are composed of spores only. The sori of *Websdanea* are as bullate, dark reddish-brown striae on the distal internodes of the culms, filled with a black, granular mass of spore balls, initially covered by the epidermis which ruptures at maturity. Spore balls are composed of spores only. Infection is systemic, the smutted culms are sterile (Vánky 2013). In both genera, spore germination is with transversely septate basidia.

Geminaginaceae is monotypic with the sole genus *Geminago*. The single described species *G. nonveilleri* (Zambett. & Foko) Vánky & R. Bauer is a parasite on *Triplochiton scleroxylon* K. Schum. (rosids, Malvaceae). *Geminago nonveilleri* is one of the very few smut fungi that parasitize woody plants. The mature septa are poreless. The host-parasite interaction is by intracellular hyphae, coated by an electron-opaque matrix (Vánky 1996). Sori are in hypertrophied flowers. Spores are in pairs, later they may separate partially or completely. Spore mass is embedded in the hypertrophied host tissue, in lysigenous cavities. Spore germination results in septate, ramified basidia bearing basidiospores in chains (Vánky 1996).

Pericladiaceae is a monotypic family represented by *Pericladium*, with three species, all of them on hosts in *Grewia* (rosids, Malvaceae). Species of *Pericladium*, similarly to *Geminago nonveilleri*, are among the very few smut fungi that parasitize woody plants. The mature septa are poreless. The host-parasite interaction is by intracellular hyphae, coated by an electron-opaque matrix (Vánky 2013). Sori of *Pericladium* are as pustules or galls on twigs of the infected plant, formed by a coriaceous peridium of hypertrophied host tissue and hyphae, enclosing dark spore mass of single spores. Spore germination results in multinucleate holobasidia, giving rise to septate, ramified hyphae on which secondary sporidia are developed, or from the spores directly septate, ramified hyphae arise (Vánky 2013).

Melanotaeniaceae species are characterized by host-parasite interaction with haustoria and the presence of simple septal pores with two membrane caps, but without inner plates (Bauer et al. 1997). The family includes three genera.

Exoteliospora is a monotypic genus. *Exoteliospora osmundae* (Peck) R. Bauer et al. forms external sori on hypertrophied, deformed leaves of *Osmunda* (ferns, Osmundaceae). Spores are produced in chains on the infected leaves. The host-parasite interaction is by coralloid haustoria penetrating into the epidermal cells (Bauer et al. 1999b). *Melanotaenium* are parasites on hosts in core eudicots (Gunneraceae), rosids (Euphorbiaceae), and asterids (Rubiaceae, Plantaginaceae, Lamiaceae, Campanulaceae, and Adoxaceae). Sori are formed in leaves, stems or roots as black or dark colored spots or swellings. Spores are embedded in host tissue, single, often aggregated, dark-colored, thick walled. Spore germination is holobasidiate (Vánky 2013). Members of *Yelsemia* are parasites on hosts in monocots (Asparagaceae), superasterids (Droseraceae), and asterids (Byblidaceae, Campanulaceae). Sori are formed in various organs of the infected plants; swollen, bursting at maturity and exposing a black, powdery spore mass. Spores are single, darkly pigmented, with two oppositely situated, light-colored polar caps. Spore germination is holobasidiate (Walker 2001; Vánky 2013).

Plates

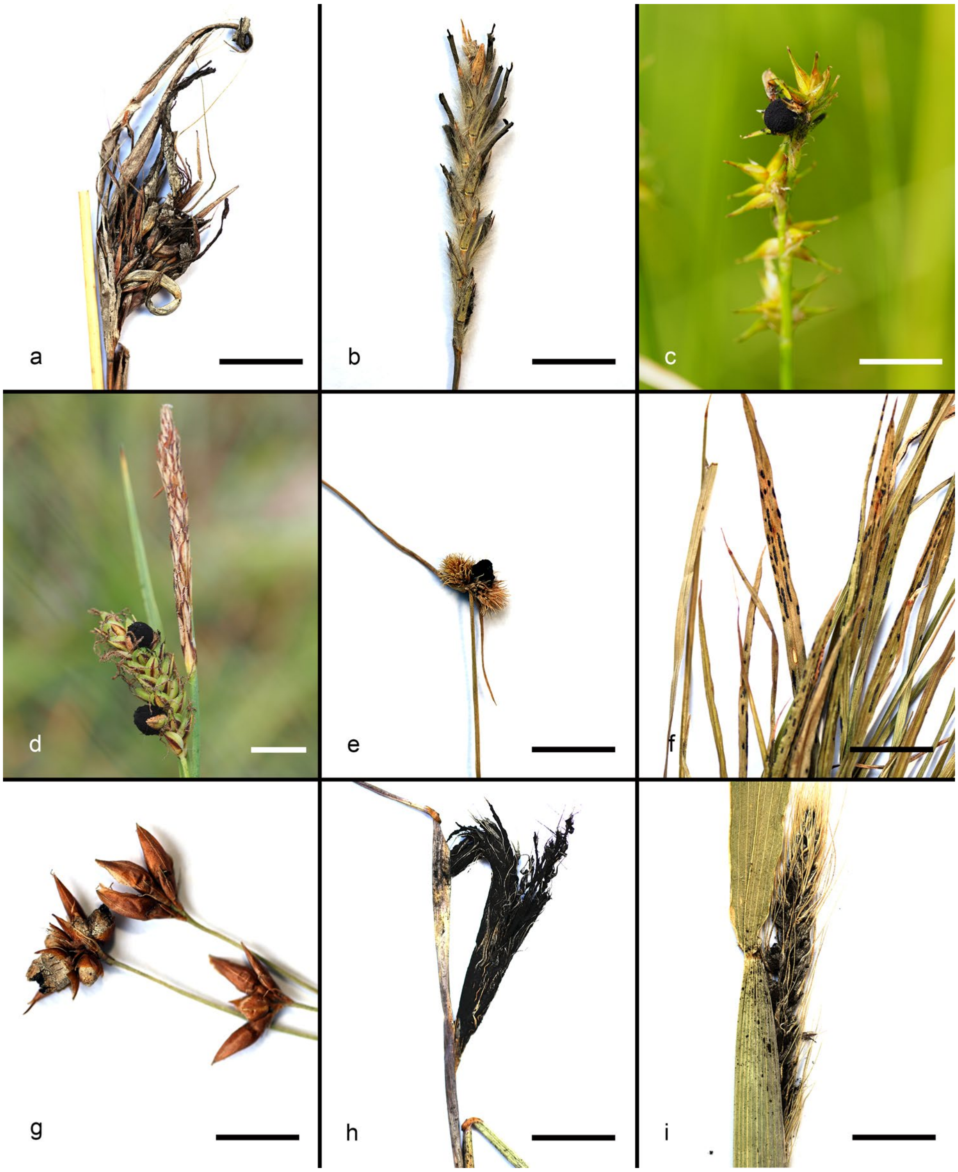


Fig. 67 Ustilaginales. **a**–**i** habit. **a** *Anthracocystis congensis* on *Hyparrhenia diplandra*, Uganda (Vánky Ustil. Exs. 1179); **b** *Anthracocystis elionuri* on *Elionurus muticus*, South Africa (Vánky Ustil. Exs. 1019); **c** *Anthracoidea karii* on *Carex echinata*, Bulgaria, Denchev 1662; **d** *Anthracoidea pratensis* on *Carex flacca*, Bulgaria, Denchev 1911; **e** *Cintractia lipocarphae* on *Lipocarpha microcephala*, Australia (Vánky Ustil. Exs. 1086); **f** *Schizonella melanogramma* on *Carex digitata*, Austria (Dupla Graecensia Fung. 318); **g** *Trichocintractia utriculicola* on *Rhynchospora corymbosa*, Argentina (Vánky Ustil. Exs. 1068); **h** *Ustilago dregeana* on *Pentaschistis curvifolia*, South Africa (Vánky Ustil. Exs. 1047); **i** *Ustilago nuda* on *Hordeum leporinum*, Greece (Vánky Ustil. Exs. 997). Scale bars: a–i = 1 cm

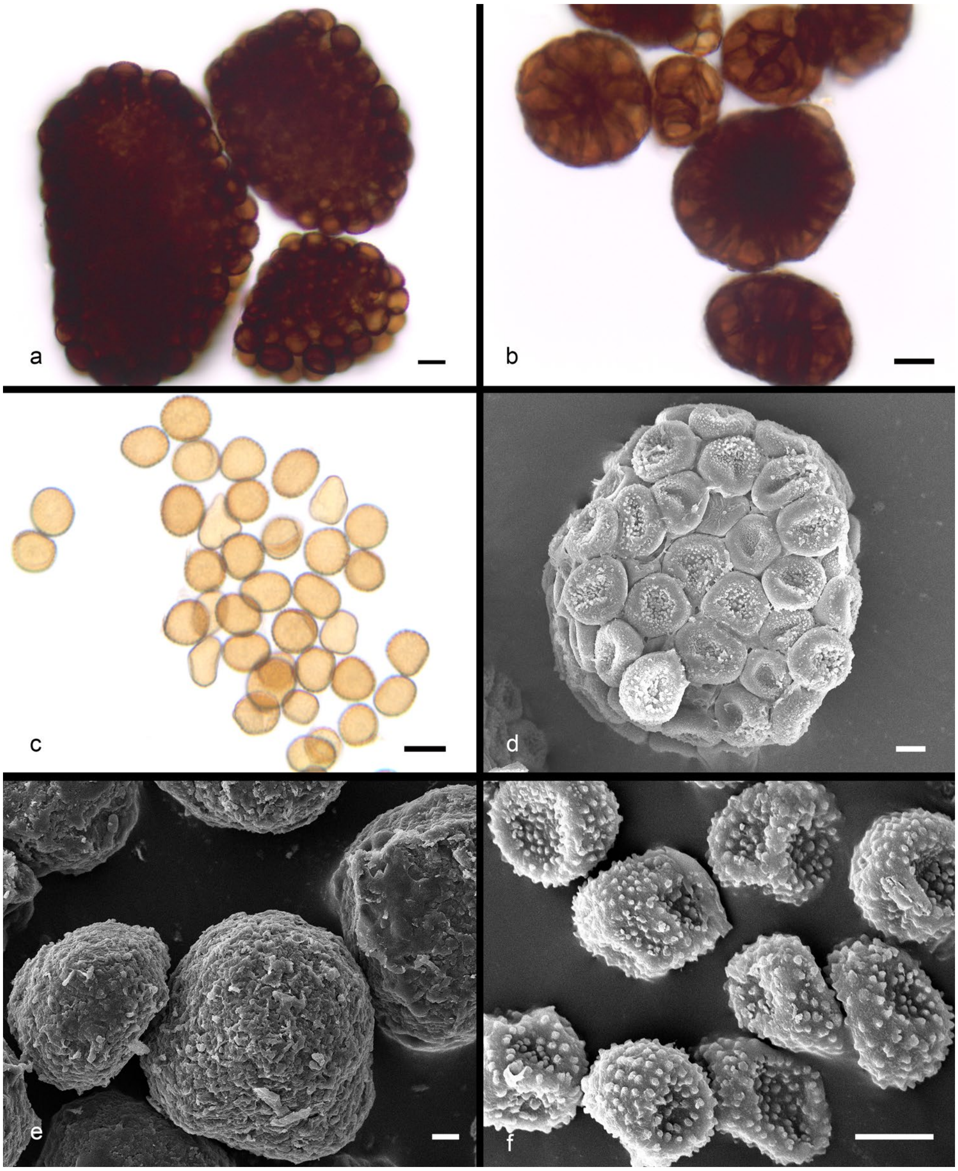


Fig. 68 Ustilaginales. **a**–**c** spores in LM. **a** *Anthracocystis compacta* on *Cymbopogon giganteus*, Senegal (B 10 0506797, isotype); **b** *Moreaua kochiana* on *Schoenus nigricans*, Austria (W 2001-0009591); **c** *Ustilago constantineanui* on *Sporobolus schoenoides*, Algeria (P02655721); **d**–**f** Spores in SEM, **d** *Anthracocystis compacta* on *Cymbopogon giganteus*, Mali (P02236427); **e** *Moreaua kochiana* on *Schoenus nigricans*, Austria (W 2001-0009591); **f** *Ustilago constantineanui* on *Sporobolus schoenoides*, Algeria (P02655721). Scale bars: a–c = 10 μm, d–f = 5 μm

Genera included

Family Anthracoideaceae Denchev 1997
    Anthracoidea Bref. 1895
    = *Crotalia* Liro 1939
    = *Cintractiomyxa* Golovin 1952
    Cintractia Cornu 1883
    Dermatosorus Sawada ex L. Ling 1949
    = *Zundelula* Thirum. & Naras. 1952
    Farysia Racib. 1909
    = *Elateromyces* Bubák 1912
    Farysporium Vánky 1999
    Heterotolyposporium Vánky 1997
    Kuntzeomyces Henn. ex Sacc. & P. Syd. 1899
    = *Didymochlamys* Henn. 1897 (nom. illeg.)
    = *Perichlamys* Clem. & Shear 1931
    Leucocintractia M. Piepenbr., Begerow & Oberw. 1999
    Moreaua Liou & H.C. Cheng 1949
    Orphanomyces Savile 1974
    Pilocintractia Vánky 2004
    Planetella Savile 1951
    Portalia V. González, Vánky & Platas 2007
    Schizonella J. Schröt. 1877
    Stegocintractia M. Piepenbr., Begerow & Oberw. 1999
    Testicularia Klotzsch 1832
    Tolyposporium Woronin ex J. Schröt. 1887
    Trichocintractia M. Piepenbr. 1995
    Ustanciosporium Vánky 1999
    = *Gymnocintractia* M. Piepenbr., Begerow & Oberw. 1999
Family Clintamraceae Vánky 2001

Clintamra Cordas & Durán 1977
Family Geminaginaceae Vánky 2001
Geminago Vánky & R. Bauer 1996
Family Melanotaeniaceae Begerow, R. Bauer & Oberw. 1998
Exoteliospora R. Bauer, Oberw. & Vánky 1999
Melanotaenium de Bary 1874
Yelsemia J. Walker 2001
Family Pericladiaceae Vánky 2011
Pericladium Pass. 1875
=*Xylosorium* Zundel 1939
Family Ustilaginaceae Tul. & C. Tul. 1847
Ahmadiago Vánky 2004
Aizoago Vánky 2013
Anomalomyces Vánky, M. Lutz & R.G. Shivas 2006
Anthracocystis Bref. 1912
Bambusiomyces Vánky 2011
Centrolepidosporium R.G. Shivas & Vánky 2007
Dirkmeia F.Y. Bai, Q.M. Wang, Begerow & Boekhout 2015
Eriocaulago Vánky 2005
Eriosporium Vánky 2005
Franzpetrakia Thirum. & Pavgi 1957
Kalmanozyma Q.M. Wang, F.Y. Bai, Begerow & Boekhout 2015
Langdonia McTaggart & R.G. Shivas 2012
Macalpinomyces Langdon & Full. 1977
=*Endosporisorium* Vánky 1995
Melanopsichium Beck 1894
Moesziomyces Vánky 1977
=*Tolyposporidium* Thirum. & Neerg. 1978
=*Eriomoeszia* Vánky 2005
Mycosarcoma Bref. 1912
Parvulago R. Bauer, M. Lutz, Piątek, Vánky & Oberw. 2007
Pattersoniomyces Piątek, M. Lutz & C.A. Rosa 2017
Pseudozyma Bandoni 1985
Shivasia Vánky, M. Lutz & Piątek 2012
Sporisorium Ehrenb. ex Link 1825
=*Endothlaspis* Sorokīn 1884
=*Lundquistia* Vánky 2001
Stollia McTaggart & R.G. Shivas 2012
Tranzscheliella Lavrov 1936
Triodiomyces McTaggart & R.G. Shivas 2012
Ustilago (Pers.) Roussel 1806
=*Farinaria* Sowerby 1803
=*Pericoelium* Bonord. 1851
=*Ustilagidium* Herzberg 1895
=*Crozalsiella* Maire 1917
=*Yenia* Liou 1949
=*Juliohirschhornia* Hirschh. 1986
=*Tubisorus* Vánky & M. Lutz 2011
Yunchangia L. Guo & B. Xu 2013
Family Websdaneaceae Vánky 2001
Restiosporium Vánky 2000
Websdanea Vánky 1997

Evolution and justification of order

Genera in the Ustilaginales are extremely diverse in their morphology and spore germination. Evolution of these smut fungi on their hosts is discussed by Begerow et al. (2004, 2014), Hendrichs et al. (2005), and McTaggart et al. (2012a, b).

Economic importance

A number of species are important cereal pathogens, including *Ustilago avenae* (Pers.) Rostr. on oats, *U. hordei* (Pers.) Lagerh. on barley, *Ustilago tritici* (Bjerk.) Rostr. on wheat, *Sporisorium cruentum* (J.G. Kühn) Vánky, *S. sorghi* Ehrenb. ex Link, and *S. reilianum* (J.G. Kühn) Langdon & Full. on sorghum, *Mycosarcoma maydis* (DC.) Bref. (*Ustilago maydis* (DC.) Corda) and *Sporisorium reilianum* on maize, *Moesziomyces bullatus* (J. Schröt.) Vánky (*Tolyposporium penicillariae* Bref.) and *Anthracocystis ehrenbergii* (J.G. Kühn) McTaggart & R.G. Shivas (*Sporisorium ehrenbergii* (J.G. Kühn) Vánky) on pearl millet, *Sporisorium destruens* (Schltdl.) Vánky on common millet (proso millet), *Sporisorium scitamineum* (Syd.) M. Piepenbr. et al. on sugarcane.

Mycosarcoma maydis (*Ustilago maydis*) produces large galls on maize that are prized as food in Mexico. Culms of *Zizania latifolia* (Griseb.) F. Muell. infected with *Ustilago esculenta* Henn. are used as a vegetable in China.

Violaceomycetales Albu, Toome & Aime 2015

Contributed by: Martin Kemler, Cvetomir M. Denchev, Dominik Begerow, Teodor T. Denchev

Introduction

Violaceomycetales was erected to accommodate the species *Violaceomyces palustris* Albu et al. (Albu et al. 2015). It was erected purely on phylogenetic evidence only contains the family Violaceomycetaceae with the genus *Violaceomyces*.

The single described species *V. palustris* has been recovered mainly from specimens of the aquatic fern species *Salvinia molesta* and *S. minima* (Salviniaceae), but also occurred on several other aquatic plants (Albu et al. 2015).

Currently, one family, one genus, and one species are included in this order.

Characters that define the taxa in the order

Violaceomyces palustris is only known in its yeast and pseudohyphal stage and is characterized by grayish-violet pigmented yeast colonies (Albu et al. 2015). Two yeast forms are known. During initial growth on artificial media, elongated yeasts are produced that proliferate via budding, balistoconida formation or germination as pseudohyphae. These yeasts are characterized by containing numerous vacuoles and lipid bodies in the cytoplasm (Albu et al. 2015). The second type of yeast has only been observed after several days of growth on artificial media. It is bulbous and often centrally septated, and also proliferates via budding and balistoconidia (Albu et al. 2015). Sexual reproduction is unknown. Although *V. palustris* grows on a wide range of carbon sources, it only does so in the presence of oxygen and fermentation is not known (Albu et al. 2015).

Plates

For illustrations, see Albu et al. (2015).

Genera included

Family Violaceomycetaceae Albu et al. 2015

Violaceomyces Albu et al. 2015

Evolution and justification of order

Violaceomycetales is only phylogenetically characterized. Together with Uleiellales they form the sister group to the rest of the Ustilaginomycetes (Riess et al. 2016; McTaggart et al. 2020).

Economic importance

The association of *Violaceomyces palustris* with *Salvinia* species indicates that it might be adapted to aquatic habitats (Albu et al. 2015), but nothing is known about its economic importance in these environments.

Wallemiales Zalar, de Hoog & Schroers 2005

Contributed by: Teun Boekhout

Introduction

Wallemiales is a monotypic order with one family Wallemiaceae and one genus *Wallemia* (Zalar et al. 2005). *Wallemia* is xerophilic and includes species that are important as food spoilage organisms, but that also occur in indoor air (Zalar et al. 2005).

History

The taxonomic position of *Wallemia* remained enigmatic for a long time until electron microscopic analyses of the septa revealed a dolipore and, hence, it was concluded that *Wallemia* represents a basidiomycete (Moore 1996). Later Zalar and coworkers made a phylogenetic analysis using small subunit rDNA and confirmed the basidiomycetous affinity, but also that *Wallemia* holds a basal position in Basidiomycota. Hence, these authors postulated the family Wallemiomycetaceae and order Wallemiales (Zalar et al. 2005). It has also been suggested that two cryptic genera may be present, based on the extensive nucleotide variation between the known *Wallemia* species (Zalar et al. 2005).

Characters that define the taxa in the order

Xerophilic members of Basidiomycota. Asexually reproducing with unbranched or sympodially, smooth, branched conidiophores on which chains of (sub)globose verrucose conidia are formed basauxically. Arthroconidia-like conidia present. Hyphal septal pore complexes with a dolipore.

Plates

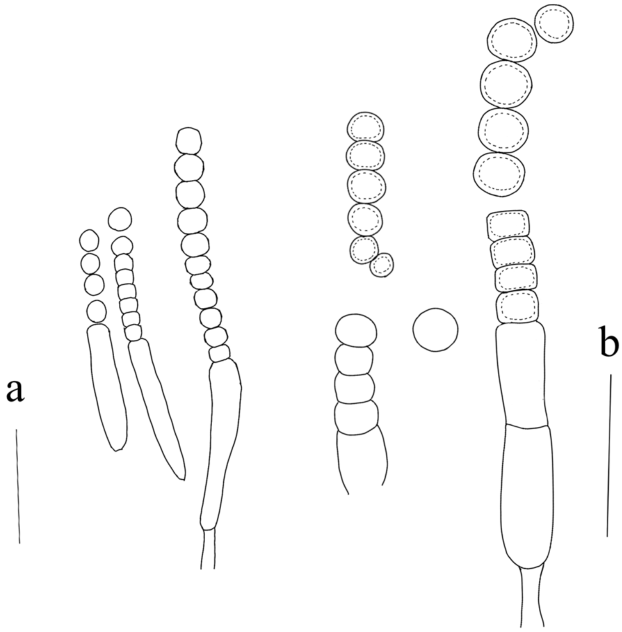


Fig. 69 Micromorphology of *Wallemia*. a,b, conidiogenous cell producing conidia. Redraw from Zalar et al. (2005) by Mao-Qiang He

Genera included

Family Wallemiaceae R.T. Moore 1996
Wallemia Johan-Olsen 1887
=*Bargellinia* Borzí 1888
=*Hemispora* Vuill. 1906

Evolution

Wallemiales is the currently known most basal lineage of Agaricomycotina (Zalar et al. 2005; Methany et al. 2006; Zajc et al. 2013; Jančič et al. 2015) and it has been estimated that the ancestor of Wallemiomycetes separated from that of Agaricomycotina 250 million years ago (Zajc et al. 2013). Zhao et al. (2017) reported a time of divergence of Wallemiomycetes of 487 million years ago. *Wallemia ichtyophaga* is the most halophilic fungus known and has a compact genome of 9.6 Mb with 4884 protein coding genes, and has lost the capability for meiosis, contrary to the close relative *Wallemia sebi* (Zajc et al. 2013). Currently the order comprises only one genus, *Wallemia*, but it has been suggested that this in fact might represent two cryptic genera (Zalar et al. 2005).

Justification of order and problems

Wallemiales is well supported by molecular phylogenetic, morphological, and physiological characteristics. The extent of sequence diversity observed has suggested that *Wallemia* as presently interpreted might represent two cryptic genera (Zalar et al. 2005), but this needs further in-depth studies.

Significance

Ecological and economical roles

Wallemia species occur in sea salt, hypersaline waters, salty food products, high sugar food products, indoor environments, hay, air, dust, seeds, soil, and plants. They grow at low water activity and cause food spoilage. Species can be xerotolerant and halophilic. Also known from a clinical specimen (Zalar et al. 2005; Jančič et al. 2015).

Chemical diversity

Considerable diversity is present in LSU rDNA and ITS sequences of *W. sebi* and *W. ichtyophaga* (Zalar et al. 2005). Species may differ in the activities of β-glucosidase, esterase, and urease. Enzyme activities were also found to be dependent on salinity (Jančič et al. 2015). At least 25 secondary metabolites have been reported from *Wallemia* species and its production is species dependent, but also depending of the physiological conditions, especially differences in salinity (Jančič et al. 2015, 2016).

Xenasmatellales L.W. Zhou & S.L. Liu 2023

Contributed by: Li-Wei Zhou, Shi-Liang Liu

Introduction

Xenasmatellales was established with the single genus *Xenasmatella* Oberw. A phylogenetic analysis utilizing seven loci provided evidence that *Xenasmatella* represents a distinct lineage within the Agaricomycetes. Based on its phylogenetic position in Agaricomycetes and morphological characteristics, Xenasmatellales and Xenasmatellaceae were proposed. Further molecular clock analysis also supports ranking this clade as an order. Species of Xenasmatellales are distinguished from other orders within the Agaricomycetes by a combination of corticioid hymenophores, pleural basidia, aculeate basidiospores and growth on wood (Liu et al. 2023c).

History

Xenasmatella, typified by *X. subflavidogrisea* (Litsch.) Oberw., was erected by Oberwinkler (1966). After its initial publication, *Xenasmatella* was forgotten and subsequently replaced by the later established genus *Phlebiella*. Some species of *Xenasmatella* were placed in *Phlebiella* (Hjortstam and Larsson 1987; Boidin and Gilles 1989, 2000; Telleria et al. 1997; Larsson 2007; Bernicchia and Gorjón 2010; Huang et al. 2019; Zong and Zhao 2021). Piątek (2005) proposed that *Xenasmatella* should be the earliest valid name of this fungal group, as *Phlebiella* lacks a generic description when it was erected (Karsten 1890). The placement of this genus is also debated. It was placed in Xenasmatales (Jülich 1981), Polyporales (Kirk et al. 2008), and Russulales (He et al. 2019a), but no widely accepted evidence can be found to support these taxonomic placements. Liu et al. (2023c) further clarified the monophyly of *Xenasmatella* and proposed the order based on multilocus phylogenetic analyses, morphological characteristics and divergence time.

Characters that define the taxa in the order

Species of this order have resupinate, effused, thin, soft membranous to ceraceous basidiomes. Hymenophore smooth to grandinioid; margin fibrillose with hyphal strands. Hyphal system monomitic. Septa with clamp connections. Cystidia absent. Basidia usually pleural, cylindrical or broadly clavate, and four-spored. Basidiospores aculeate, thin- to slightly thick-walled, subglobose to ellipsoid, inamyloid, indextrinoid, acyanophilous.

Plates

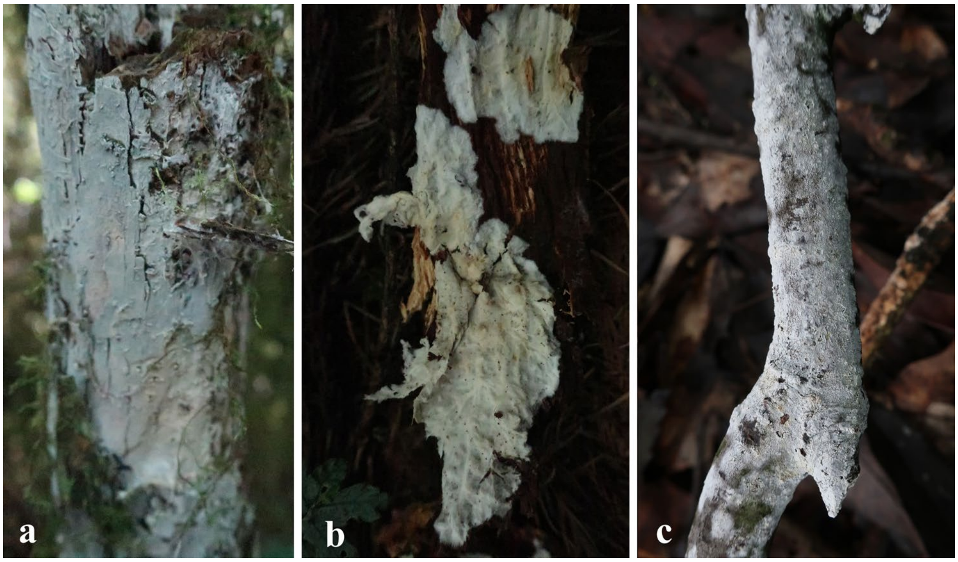


Fig. 70 Typical characteristics of basidiomes in Xenasmatellales. **a** *Xenasmatella ailaoshanensis* (LWZ 20190811–37a, Sichuan province of China); **b** *Xenasmatella gossypina* (LWZ 20190819–18b, Sichuan province of China); **c** *Xenasmatella* sp. (LWZ 20200819–9b, Sichuan province of China)

Genera included

Family Xenasmatellaceae L.W. Zhou & S.L. Liu
  Xenasmatella Oberw. 1965
  =*Phlebiella* P. Karst. 1890

Evolution

The sister relationship of Xenasmatellales with Sistotremastrales and Trechisporales clade lacks statistical support in the Maximum Likelihood analysis. However, in the maximum-clade-credibility tree it is fully supported. The stem age of Xenasmatellales is estimated to be 163 Myr.

Outline of genera *incertae sedis* on supra-ordinal rank

Agaricomycetes genera *incertae sedis*
  Aldridgea Massee 1892
  Amnocutis K.H. Larss. 2020
  Aphelaria Corner
  Arthrodochium R.F. Castañeda & W.B. Kendr. 1990
  Arualis Katz 1980
  Cenangiomyces Dyko & B. Sutton 1979
  Ceraceopsis Hjortstam & Ryvarden 2007
  Cilicia Fr. 1825
  Corallofungus Kobayasi 1983
  Corticomyces A.I. Romero & S.E. López 1989
  Cruciger R. Kirschner & Oberw. 1999
  Dendrosporomyces Nawawi, J. Webster & R.A. Davey 1977
  Ellula Nag Raj 1980
  Fibulocoela Nag Raj 1978
  Fibulotaeniella Marvanová & Bärl. 1988
  Gloeomucro R.H. Petersen 1980
  Gloeosynnema Seifert & G. Okada 1988
  Glomerulomyces A.I. Romero & S.E. López 1989
  Glutinoagger Sivan. & Watling 1980
  Hallenbergia Dhingra & Priyanka 2011
  Heteroacanthella Oberw. 1990
  Intextomyces J. Erikss. & Ryvarden 1976
  Korupella Hjortstam & P. Roberts 2000
  Minostroscyta Hjortstam & Ryvarden 2001
  Mylittopsis Pat. 1895
  Myriococcum Fr. 1823
  Oliveonia Donk 1958
  Odontiochaete Rick 1940
  Pagidospora Drechsler 1960
  Parastereopsis Corner 1976
  Paullicorticium J. Erikss. 1958
  Phaeoaphelaria Corner
  Phlyctibasidium Jülich 1974
  Purpureocorticium S.H. Wu 2017
  Pycnovellomyces R.F. Castañeda 1987
  Radulochaete Rick 1940
  Repetobasidiellum J. Erikss. & Hjortstam 1981
  Riessia Fresen. 1852
  Riessiella Jülich 1985
  Taiwanoporia T.T. Chang & W.N. Chou 2003
  Titaeella G. Arnaud ex K. Ando & Tubaki 1985
  Trechinothus E.C. Martini & Trichiès 2004
  Trimitiella Dhingra 2008
  =*Trimitiella* Dhingra 2006
  Tubulicrinopsis Hjortstam & Kotir. 2007
  Tumidapexus D.A. Crawford
  Xerotus Fr. 1828
  =*Xerotinus* Rchb. 1828

Cystobasidiomycetes families *incertae sedis*
Family Microsporomycetaceae Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout 2015
  Microsporomyces Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout 2015
Family Symmetrosporaceae Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout 2015
  Symmetrospora Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout 2015

Cystobasidiomycetes genera *incertae sedis*
Queiroziella C.R. Félix, J.D.P. Bezerra, R.P. Neves & Landell 2018

Microbotryomycetes families *incertae sedis*
Family Chrysozymaceae Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout 2015
  Bannozyma Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout 2015
  Chrysozyma Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout 2015
  Fellozyma Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout 2015
  Hamamotoa Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout 2015
Family Colacogloeaceae Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout 2015
  Colacogloea Oberw. & Bandoni 1991

Microbotryomycetes genera *incertae sedis*
  Atractocolax R. Kirschner, R. Bauer & Oberw. 1999
  Curvibasidium Samp. & Golubev 2004
  Libkindia Mašínová, A. Pontes, J.P. Samp. & Baldrian 2017

Oberwinklerozyma Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout 2015
Pseudohyphozyma Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout 2015
Pseudoleucosporidium V. de Garcia, M.A. Coelho, T. Maia, L.H. Rosa, A.B.M. Vaz, C.A. Rosa, J.P. Samp., P. Gonç., M.R. Van Broock & Libkind 2015
Sampaiozyma Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout 2015
Slooffia Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout 2015
Spencerozyma Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout 2015
Trigonosporomyces Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout 2015
Udeniozyma Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout 2015
Vonarxula Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout 2015
Yunzhangia Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout 2015
Yurkovia Mašínová, A. Pontes, J.P. Samp. & Baldrian 2016

Tremellomycetes family *incertae sedis*
Family Phaeotremellaceae Yurkov & Boekhout 2015
Gelidatrema A.M. Yurkov, Xin Zhan Liu, F.Y. Bai, M. Groenew. & Boekhout 2015
Phaeotremella Rea 1912

Tremellomycetes genera *incertae sedis*
Heteromycophaga P. Roberts 1997
Phyllopta (Fr.) Fr. 1825

Ustilaginomycetes genera *incertae sedis*
Capitulocladosporium L.Y. Sun, X. Sun & L.D. Guo 2017
Eriocortex Vánky & R.G. Shivas 2013

Wallemiomycetes genus *incertae sedis*
Chernovia A.M. Yurkov & Begerow 2016

Pucciniomycotina genera *incertae sedis*
Kryptastrina Oberw. 1990
Paraphelaria Corner 1966
Zygogloea P. Roberts 1994

Basidiomycota genera *incertae sedis*
Anastomyces W.P. Wu, B. Sutton & Gange 1997
Anguillomyces Marvanová & Bärl. 2000
Arcispora Marvanová & Bärl. 1998
Arrasia Bernicchia, Gorjón & Nakasone 2011
Celatogloea P. Roberts 2005
Cystogloea P. Roberts 2006
Microstella K. Ando & Tubaki 1984
Neotyphula Wakef. 1934
Radulodontia Hjortstam & Ryvarden 2008
Restilago Vánky 2008

Discussion

Phylogenomic relationships within Basidiomycota

Phylogenomic relationships within the deep nodes (above order) revealed in this study agree well with the previous studies (Zhao et al. 2017; Li et al. 2021c). However, the phylogenetic positions of some orders and clades still needs further clarification. For example, Amycocorticiales could be sister to Atheliales or Agaricales, but both relationships lack full support in previous phylogenomics and in this study (Zhao et al. 2017; Li et al. 2021c). Nodes with statistical support lower than 90 (see Fig. 2, nodes marked with stars) indicate that further studies focusing on the taxa of these nodes are needed to elucidate their phylogenetic relationships.

Agaricales and Polyporales are the top two orders of Basidiomycota with 51 and 31 families, respectively. To examine their current taxonomic system, we provided a relatively well-populated sampling in Agaricales and Polyporales. Nine suborders of Agaricales are well resolved. All families (34 out of 51) are well-accommodated in each suborder except Mycenaceae, which clustered in Marasmiineae in Dentinger et al. (2016), but, formed a sister clade to Schizophyllineae in this study. Based on the phylogenomic relationship and the divergence time of Mycenaceae, we proposed it as a new suborder in Agaricales. Polyporales is another diverse order with abundant families, and 15 out of 31 families were included in the phylogenomic analysis for this study. All of the families are well supported and accepted in the outline. of note, the placement of Ganodermataceae is controversial. Several studies have accepted it as a distinct family separate from Polyporaceae (Cui et al. 2019; Costa-Rezende et al. 2020). However, in this study, we accept it as a synonym of Polyporaceae to avoid producing a polyphyletic Polyporaceae. For a detailed discussion please see the Polyporales note. Based on the findings of this study, we suggest a suborder rank for Polyporales, like Agaricales, to clarify the relationship of this diverse family-level group.

Our study further indicated several problems remain unresolved in the current taxonomic system of Basidiomycota. In Agaricales, Strophariaceae and Hymenogastraceae are highly polyphyletic. Therefore, the current taxonomic system for these two families requires further revision. Phaeotremellaceae has been proposed to be grouped within Tremellales (Liu et al. 2015b), but our phylogenomic tree analysis indicated that it formed a clade out of Tremellales. More genomic data from this family will be needed to clarify the position and rank of this clade. Exobasidiomycetes, the only polyphyletic class in Basidiomycota, is particularly large and diverse (Begerow et al. 2006, Wang et al. 2015a; He et al. 2019a, in this study). We suggest re-classifying Exobasidiomycetes to better conform to the current taxonomic system. The clade with Exobasidiales should be remained as Exobasidiomycetes, and the ranks of related lineages should be reconsidered to be in Ustilaginomycotina.

Updates of the outline

The outline of Basidiomycota is updated with two more classes accepted: Bartheletiomycetes in Agaricomycotina and Peribolosporomycetes in Ustilaginomycotina. Nine new orders are accepted, namely Bartheletiales, Chionasterales, Sistotremastrales, and Xenasmatellales in Agaricomycotina; Heitmaniales and Rosettozymales in Pucciniomycotina; Cintractiellales, Franziozymales, and Peribolosporales in Ustilaginomycotina. Additionally, 56 families and 206 genera have been added in the current outline. Four subphyla, 20 classes, 77 orders, 297 families, and 2134 genera are accepted in the current outline of Basidiomycota.

Many updates on the ordinal and supra-ordinal ranks have been proposed based on the previously known taxa. For example, *Heitmania*, which was placed as genus *incertae sedis* in Microbotryomycetes, now has been re-classified as Heitmaniales based on a more comprehensive sampling and phylogenetic analysis. A similar reclassification has occurred to *Bartheletia* and *Chionaster* which were previously known as *incertae sedis* in Wallemiomycetes and Tremellomycetes, now have been raised as Bartheletiales and Chionasterales, respectively. Two orders in Agaricomycetes, Sistotremastrales and Xenasmatellales are proposed to accommodate the known corticoid fungi segregated from Trechisporales and Russuales. Only three new orders have been proposed based on the discovery of new species. These new orders are Franziozymales, Rosettozymales, and Peribolosporales, which are all yeast-like basidiomycetes isolated from different environments. We believe that the ordinal ranks for macrofungi (mainly in Agaricomycetes) is nearly complete. In the last ten years, new orders of macrofungi were proposed mainly from systematic reconstruction research requiring an update to nomenclature based on convention. However, in the case of micro basidiomycetes (mainly in Tremellomycetes, Pucciniomycotina, and Ustilaginomycotina) the situation is different. In the systematic reconstruction, not only have new orders been proposed based on nomenclature, but new species have been discovered in various habitats, for example, Peribolosporales (Witfeld et al. 2023). It can be speculated that discoveries and reclassifications regarding Basidiomycota ordinal diversity will continue, mainly coming from microfungi research.

Future perspectives to the systematics of Basidiomycota

New techniques that emerged in the past years were critical to solving problematic taxa. For example, with shallow whole-genome sequencing data, targeted capture sequencing was used for the first time in fungal taxonomy in basidiomycetes by Liimatainen et al. (2022). This approach helped to establish a new generic classification in the family Cortinariaceae, an important ectomycorrhizal family with more than 5000 species and worldwide distribution, which represented the first family revision in Agaricales based on genomics data. Later, similar approaches were applied to rebuild the taxonomic system of genus *Tricholoma* of which the taxonomic system has long been unsettled (Ding et al. 2022). Targeted capture sequencing provides a cost-efficient way to produce -omics data in species-rich groups and has also successfully been used in lichen-forming *Ascomycota* (Widhelm et al. 2019, 2021; Grewe et al. 2020). The -omics data in Liimatainen et al. (2022), as well as e.g., in Dentinger et al. (2016), has been produced from dried fungarium specimens, demonstrating the value of museum specimens in the study of the fungal tree of life.

Divergence times and ranking in Basidiomycota

Systematic studies of Basidiomycota at different ranks have used divergence times as an additional criterion to classify taxa in recent years (Hussain et al. 2022; Liu et al. 2023b, c). In this study, we estimated the divergence times of Basidiomycota based on genomic data. The results showed that subphyla diverged in a time range of 443–490 Myr, classes in a time range of orders 312–412 Myr, and orders in a range of 102–361 Myr. Families diverged in a time range of 50–289 Myr, 76–224 Myr, and 62–156 Myr in Agaricomycotina, Pucciniomycotina, and Ustilaginomycotina, respectively. Compared with previous studies, the time ranges proposed in this study are relatively older (Zhao et al. 2017; He et al. 2019a; Varga et al. 2019). This discrepancy may be due to limited taxon sampling available as many clades lack genomic data. For example, in Pucciniomycetes, genomic data is only available for one of five orders.

The following criteria are suggested to rank taxa and/or build taxonomic system in Basidiomycota: (i) the taxa must be monophyletic and statistically well-supported in multi-gene analyses; (ii) their respective stem ages should be roughly equivalent, and higher taxon stem ages must be older than lower level taxa stem ages; and (iii) the taxa should be identifiable phenotypically, whenever possible (Zhao et al. 2016a; He et al. 2019a). Toward building a robust taxonomy of Basidiomycota in the genomic era, generating molecular phylogenetic data becomes easier, finding phenotypical characteristics, especially those that can be applied for identification and classification, is becoming a more complex and challenging task.

In memory of Philippe Callac

In this work, we commemorate Philippe Callac (28 February 1954–25 August 2023), a much-loved superior mycologist at the Institut national de la recherche agronomique in France (INRA, that became INRAE, the National Research Institute for Agriculture, Food and Environment in January 2020). He devoted all his passion to mushroom research throughout his life. Not only was he an outstanding scientist, he was also a remarkable teacher and friend to numerous foreign younger mycologists. He always inspired, motivated, guided and supported his younger friends to go far in mycology. We commemorate his passion for mushroom research, the dissemination of mycological knowledge, and his great contribution to mycology.

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Declarations

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References

Accioly T, Sousa JO, Moreau PA, Lécuru C, Silva BDB, Roy M, Gardes M, Baseia IG, Martín MP (2019) Hidden fungal diversity from the Neotropics: *Geastrum hirsutu*m,*G. schweinitzii* (Basidiomycota, Geastrales) and their allies. PLoS ONE 14:e0211388. https://doi.org/10.1371/journal.pone.0211388

Acero D, Khan FS, Medina-Ortiz AJ, Rivero-Cruz I, Raja HA, Flores-Bocanegra L, Fajardo-Hernández CA, Wan B, Franzblau SG, Hematian S, Figueroa M (2022) New terpenoids from the corticioid fungus *Punctularia atropurpurascens* and their antimycobacterial evaluation. Planta Med 88:729–734

Adams GC, Kropp BR (1996) *Athelia arachnoidea*, the sexual state of *Rhizoctonia carotae*, a pathogen of carrot in cold storage. Mycologia 88(3):459–472

Agerer R (1999) *Gyroporus cyanescens* (Bull.: Fr.) Quél. +*Pinus sylvestris* L. Descr Ectomyc 4:43–47

Agerer R, Beenken L (1998) *Geastrum fimbriatum* Fr. +*Fagus sylvatica* L. Descr Ectomyc 3:13–18

Agerer R et al (2018) Tremellodendropsidales. In: Begerow D (ed) Syllabus of plant families—A. Engler's syllabus der Pflanzenfamilien, Part 1/3: Basidiomycota and Entorrhizomycota. Schweizerbart Science Publishers, Stuttgart, p 141

Aime MC, McTaggart AR (2021) A higher-rank classification for rust fungi, with notes on genera. Fungal Syst Evol 7:21–47

Aime MC, Matheny PB, Henk DA, Frieders EM, Nilsson RH, Piepenbring M, McLaughlin DJ, Szabo LJ, Begerow D, Sampaio JP, Bauer R, Weiss M, Oberwinkler F, Hibbett D (2006) An overview of the higher level classification of Pucciniomycotina based on combined analyses of nuclear large and small subunit rDNA sequences. Mycologia 98:896–905

Aime MC, Toome M, Mclaughlin DJ (2014) Pucciniomycota. In: McLaughlin D, Spatafora J (eds) Systematics and evolution. The Mycota (A comprehensive treatise on fungi as experimental systems for basic and applied research), vol 7A. Springer, Berlin, pp 271–294

Aime MC, McTaggart AR, Mondo SJ et al (2017) Phylogenetics and of rust fungi. Adv Genet 100:267–307

Aime MC, Bell CD, Wilson AW (2018a) Deconstructing the evolutionary complexity between rust fungi (Pucciniales) and their plant hosts. Stud Mycol 89:143–152

Aime MC, Castlebury LA, Abbasi M et al (2018b) Competing sexual and asexual generic names in Pucciniomycotina and Ustilaginomycotina (Basidiomycota) and recommendations for use. IMA Fungus 9:75–89

Aime MC, Kijpornyongpan T, Abbasi M, Wood KR, Flynn T (2018c) A new species of *Cintractiella* (Ustilaginales) from the volcanic island of Kosrae, Caroline Islands, Micronesia. MycoKeys 42:1–6

Aime MC, Urbina H, Liber JA, Bonito G, Oono R (2018d) Two new endophytic Atractiellomycetes,*Atractidochium hillariae* and *Proceropycnis hameedii*. Mycologia 110(1):136–146

Ainsworth GC (1971) Ainsworth and Bisby's dictionary of the fungi. Commonwealth Mycological Institute, Kew

Ainsworth AM (2005) BAP fungi handbook. English Nature, Peterborough

Akar ST, Gorgulu A, Kaynak Z, Anilan B, Akar T (2009) Biosorption of reactive blue 49 dye under batch and continuous mode using a mixed biosorbent of macro-fungus *Agaricus bisporus* and *Thuja orientalis* cones. Chem Eng J 148:26–34

Akulov OY, Fomenko MI, Khudych AS, Borisenko TO (2022) The first find of *Naohidea sebacea* (Naohideales, Basidiomycota) in Ukraine. Ukrainian Bot J 79:308–313

Aladoasura SO (1963) Fruiting in Sphaerobolus with special reference to light. Ann Bot 27:123–145

Albee-Scott S, Kropp BR (2011) A phylogenetic study of Trechispora thelephora. Mycotaxon 114:395–399

Albu S (2012) A survey of ballistosporic phylloplane yeasts in Baton Rouge, Louisiana. Dissertation, Louisiana State University

Albu S, Toome M, Aime MC (2015) *Violaceomyces palustris* gen. et sp. nov. and a new monotypic lineage, Violaceomycetales ord. nov. in Ustilaginomycetes. Mycologia 107:1193–1204

Alexopoulos CJ, Mims CW, Blackwell M (1996) Introductory mycology. Wiley and Sons Inc, New York

Alvarado P, Moreno G, Vizzini A, Consiglio G, Manjón JL, Setti L (2015) *Atractosporocybe*, *Leucocybe* and *Rhizocybe*: three new clitocyboid genera in the Tricholomatoid clade (Agaricales) with notes on *Clitocybe* and *Lepista*. Mycologia 107(1):123–136

Alvarado P, Moreau PA, Dima B, Vizzini A, Consiglio G, Moreno G, Setti L, Kekki T, Huhtinen S, Liimatainen K, Niskanen T (2018a) Pseudoclitocybaceae fam. nov. (Agaricales, Tricholomatineae), a new arrangement at family, genus and species level. Fungal Divers 90:109–133

Alvarado P, Moreau PA, Sesli E, Khodja LY, Contu M, Vizzini A (2018b) Phylogenetic studies on *Bonomyces* (Tricholomatineae, Agaricales) and two new combinations from*Clitocybe*. Cryptogam Mycol 39(2):149–168

Alvarenga RLM, Spirin V, Malysheva V, Gibertoni T, Larsson K (2019) Two new genera and six other novelties in *Heterochaete* sensu lato (Auriculariales, Basidiomycota). Botany 97:439–451. https://doi.org/10.1139/cjb-2019-0046

Alvarenga RLM, Gibertoni TB (2021) *Crystallodon* Alvarenga gen. nov., a new genus of the Auriculariales from the Neotropics. Cryptogam Mycol 42(2):17–24

Alvarez-Manjarrez J, Villegas-Ríos M, Garibay-Orijel R, Contreras-Pacheco M, Kõljalg U (2016)*Tomentella brunneoincrustata*, the first described species of the Pisonieae-associated Neotropical *Tomentella* clade, and phylogenetic analysis of the genus in Mexico. Mycol Prog 15:1–11. https://doi.org/10.1007/s11557-015-1152-x

Amend A (2014) From dandruff to deep-sea vents: *Malassezia*-like fungi are ecologically hyper-diverse. PLoS Pathog 10(8):e1004277. https://doi.org/10.1371/journal.ppat.1004277

Amend A, Burgaud G et al (2019) Fungi in the marine environment: open questions and unsolved problems. mBio 10(2):e01189-18. https://doi.org/10.1128/mBio.01189-18

Andersen TF, Stalpers JA (1994) A checklist of Rhizoctonia epithets. Mycotaxon 51:437–457

Andrew C, Büntgen U, Egli S et al (2019) Open-source data reveal how collections-based fungal diversity is sensitive to global change. Appl Plant Sci 7(3):e01227

Angelini C, Contu M, Vizzini A (2014) *Tricholosporum caraibicum* (Basidiomycota, Tricholomataceae), a new species from the Dominican Republic. Mycosphere 5(3):430–439

Antignac E, Nohynek GJ, Re T, Clouzeau J, Toutain H (2011) Safety of botanical ingredients in personal care products/cosmetics. Food Chem Toxicol 49:324–341

Antonelli A, Smith RJ, Fry C et al (2020) State of the World's Plants and Fungi. Royal Botanic Gardens, Kew

Antonín V, Hosaka K, Kolařík M (2022) Taxonomy and phylogeny of *Paramarasmius* gen. nov. and *Paramarasmius mesosporus*, a worldwide distributed fungus with a strict ecological niche. Plant Biosyst 157(2):286–293

Antunes F, Marçal S, Taofiq O, Morais AMMB, Freitas AC, Ferreira ICFR, Pintado M (2020) Valorization of mushroom by-products as a source of value-added compounds and potential applications. Molecules 25:2672

Arastehfar A, de Almeida Júnior JN, Perlin DS, Ilkit M, Boekhout T, Colombo AL (2021) Multidrug-resistant Trichosporon species: underestimated fungal pathogens posing imminent threats in clinical settings. Crit Rev Microbiol 47(6):679–698

Argüelles-Moyao A, Garibay-Orijel R, Márquez-Valdelamar LM, Arellano-Torres E (2017) Clavulina-Membranomyces is the most important lineage within the highly diverse ectomycorrhizal fungal community of *Abies religiosa*. Mycorrhiza 27:53–65

Arias SL, Mary VS, Velez PA, Rodriguez MG, Otaiza-González SN, Theumer MG (2021) Where does the peanut smut pathogen, *Thecaphora frezii*, fit in the spectrum of smut diseases? Pl Diseases 105:2268–2280

Ariyawansa HA, Hyde KD, Jayasiri SC, Buyck B et al (2015) Fungal diversity notes 111–252 taxonomic and phylogenetic contributions to fungal taxa. Fungal Divers 75:1–248

Artsdatabanken (2021) Norsk rødliste for arter 2021. https://www.artsdatabanken.no/lister/rodlisteforarter/2021/

Asad F, Anwar H, Yassine HM, Ullah MI, Kamran Z, Sohail MU (2020) White button mushroom,*Agaricus bisporus* (Agaricomycetes), and a probiotics mixture supplementtion correct dyslipidemia without influencing the colon microbiome profile in hypercholesterolemic rats. Int J Med Mushrooms 22:235–244

Aučina A, Rudawska M, Wilgan R, Janowski D, Skridaila A, Dapkūnienė S, Leski T (2019) Functional diversity of ectomycorrhizal fungal communities along a peatland–forest gradient. Pedobiologia 74:15–23

Aulinger K, Besl H, Spiteller P, Spiteller M, Steglich W (2001) Melanocrocin, a polyene pigment from *Melanogaster broomeianus* (Basidiomycetes). Z Naturforsch C J Biosci 56:495–498

Aykut B, Pushalkar S, Chen R, Li Q, Abengozar R, Kim JI, Shadaloey SA, Wu D, Preiss P, Verma N, Guo Y (2019) The fungal mycobiome promotes pancreatic oncogenesis via activation of MBL. Nature 574(7777):264–267

Bâ A, Duponnois R, Diabaté, Dreyfus B (2011) Les champignons ectomycorhiziens des arbres forestiers en Afrique de l'Ouest. Institut de recherche pour le développement, Marseille

Baetsen-Young AM, Kaminski JE, Kasson MT, Davis DD (2015) Insights into the biology of*Sphaerobolus stellatus* as a causal agent of thatch collapse in golf turfs. Crop Sci 55:2342–2351

Baetsen-Young AM, Kaminski JE, Tien M (2017) Lignocellulose degrading capabilities of *Sphaerobolus stellatus* in creeping bentgrass. Int Turfgrass Soc Res J 13:145–152

Bahn YS, Sun S, Heitman J, Lin X (2020) Microbe profile: *Cryptococcus neoformans* species complex. Microbiology 166(9):797

Bailly C (2022) Anti-inflammatory and anticancer p-terphenyl derivatives from fungi of the genus *Thelephora*. Bioorg Med Chem 70:116935. https://doi.org/10.1016/j.bmc.2022.116935

Baird R, Wallace LE, Baker G, Scruggs M (2013) Stipitate hydnoid fungi of the temperate southeastern United States. Fungal Divers 62:41–114. https://doi.org/10.1007/s13225-013-0261-6

Baker GE (1936) A study of the genus Helicogloea. Ann Mo Bot Gard 23:69–129

Bakshi BK, Reddy MAR, Puri YN, Singh S (1972) Forest disease survey final technical report 1967-72. Dehra Dun, India

Baldrian P, Bell-Dereske L, Lepinay C et al (2022) Fungal communities in soil sunder global change. Stud Mycol 103:1–24

Bandala VM, Montoya L, Villegas R, Cabrera TG, Gutiérrez M, Acero T (2014) "Nangañaña" (Tremelloscypha gelatinosa, Sebacinaceae), hongo silvestre comestible del bosque tropical deciduo en la depresión central de Chiapas, México. Acta Botanica Mexicana 106:149–159

Bandoni RJ (1956) A preliminary survey of the genus *Platygloea*. Mycologia 48:821–840. https://doi.org/10.1080/00275514.1956.12024597

Bandoni RJ (1973) Epistolae mycologicae II. Species of Platygloea from British Columbia. Syesis 6:229–232

Bandoni RJ (1984) The Tremellales and Auriculariales: an alternative classification. Trans Mycol Soc Jpn 25:489–530

Bandoni RJ (1995) Dimorphic heterobasidiomycetes, taxonomy and parasitism. Stud Mycol 38:13–27

Bandoni RJ (1998) On some species of *Mycogloea*. Mycoscience 39:31–36

Bandoni RJ, Boekhout T (2011a) Agaricostilbum Wright (1970). In: Kurtzman CP, Fell JW, Boekhout T (eds) The yeasts, a taxonomic study, 5th edn. Elsevier, Amsterdam, pp 1375–1378

Bandoni RJ, Boekhout T (2011b) *Tremella* Persoon (1794). In: Kurtzman CP, Fell JW, Boekhout T (eds) The yeasts, a taxonomic study, 5th edn. Elsevier, Amsterdam, pp 1567–1590

Bandoni RJ, Johri BN (1972) *Tilletiaria*: a new genus in the Ustilaginales. Can J Bot 50:39–43

Bandoni RJ, Oberwinkler F (1981) *Hyalopycnis blepharistoma*: a pycnidial basidiomycete. Can J Bot 50:2283–2288

Bandoni RJ, Oberwinkler F, Bandoni AA (1991) On species of *Filobasidium* associated with *Yuccas*. Syst Appl Microbiol 14:98–101

Bandoni RJ, Boekhout T, Sampaio JP (2011a) Holtermannia Saccardo & Traverso (1910). In: Kurtzman CP, Fell JW, Boekhout T (eds) The yeasts (fifth edition). Elsevier, Amsterdam, pp 1467–1470

Bandoni RJ, Sampaio JP, Boekhout T (2011b) Sirobasidium de Lagerheim & Patouillard, 1982. In: Kurtzman CP, Fell JW, Boekhout T (eds) The yeasts, a taxonomic study, 5th edn. Elsevier, Amsterdam, pp 1545–1548

Barbisan LF, Spinardi-Barbisan AL, Moreira EL, Salvadori DM, Ribeiro LR, da Eira AF, de Camargo JL (2003) *Agaricus blazei* (Himematsutake) does not alter the development of rat diethylnitrosamine-initiated hepatic preneoplastic foci. Cancer Sci 94:188–192

Baric S, Lindner L, Marschall K et al (2009) Haplotype diversity of *Tilletiopsis* spp. causing white haze in apple orchards in Northern Italy. Plant Pathol 59:535–541. https://doi.org/10.1111/j.1365-3059.2009.02217.x

Baric S, Lindner L, Marschall K, Dalla Via J (2010) Haplotype diversity of *Tilletiopsis* spp. causing white haze in apple orchards in Northern Italy. Plant Pathol 59:535–541

Baroni TJ (2017) Mushrooms of the Northeastern United States and Eastern Canada. Timber Press, Portland

Bas C (1969) Morphology and subdivision of *Amanita* and a monograph of its section *Lepidella*. Persoonia 5:285–579

Bates ST (2004) Arizona members of the Geastraceae and Lycoperdaceae (Basidiomycota, Fungi). Dissertation, Arizona State University

Bau T, Yan J-Q (2021) A new genus and four new species in the /*Psathyrella* s.l. clade from China. MycoKeys 80:115–131

Bauer R (2004) Basidiomycetous interfungal cellular interactions—a synopsis. In: Agerer R, Piepenbring M, Blanz P (eds) Frontiers in basidiomycote mycology. IHW-Verlag, Germany, pp 325–337

Bauer R, Oberwinkler F (1990a) Meiosis, spindle pole body cycle, and taxonomy of the heterobasidiomycete *Pachnocybe ferruginea*. Plant Syst Evol 172:241–261

Bauer R, Oberwinkler F (1990b) Direct cytoplasm-cytoplasm connection: an unusual host-parasite interaction of the tremelloid mycoparasite *Tetragoniomyces uliginosus*. Protoplasma 154:157–160

Bauer R, Oberwinkler F (1991) The symplechosome: a unique cell organelle of some basidiomycetes. Botanica Acta 104(2):93–97

Bauer R, Oberwinkler F, Vánky K (1997) Ultrastructural markers and systematics in smut fungi and allied taxa. Can J Bot 75:1273–1314

Bauer R, Vánky K, Begerow D, Oberwinkler F (1999a) Ustilaginomycetes on *Selaginella*. Mycologia 91:475–484

Bauer R, Oberwinkler F, Vánky K (1999b) Ustilaginomycetes on *Osmunda*. Mycologia 91:669–675

Bauer R, Begerow D, Nagler A, Oberwinkler F (2001a) The Georgefischeriales: a phylogenetic hypothesis. Mycol Res 105:416–424

Bauer R, Begerow D, Oberwinkler E, Piepenbring M, Berbee ML (2001b) Ustilaginomycetes. In: McLaughlin DJ, McLaughlin EG, Lemke PA (eds) Systematics and evolution. The mycota, vol 7B. Springer, Heidelberg. https://doi.org/10.1007/978-3-662-10189-6_3

Bauer R, Begerow D, Oberwinkler F, Marvanová L (2003) *Classicula*: the teleomorph of naadella flutans. Mycologia 95:756–764

Bauer R, Lutz M, Oberwinkler F (2004) Tuberculina-rusts: a unique basidiomycetous interfungal cellular interaction with horizontal nuclear transfer. Mycologia 96(5):960–967

Bauer R, Lutz M, Oberwinkler F (2005) *Gjaerumia*, a new genus in the Georgefischeriales (Ustilaginomycetes). Mycol Res 109:1250–1258

Bauer R, Begerow D, Sampaio JP, Weiss M, Oberwinkler F (2006) The simple-septate basidiomycetes: a synopsis. Mycol Prog 5:41–66

Bauer R, Lutz M, Piątek M, Vanky K, Oberwinkler F (2007) *Flamingomyces* and *Parvulago*, new genera of marine smut fungi (Ustilaginomycotina). Mycol Res 111:1199–1206

Bauer R, Lutz M, Begerow D, Piątek M, Vanky K, Bacigálová K, Oberwinkler F (2008) Anther smut fungi on monocots. Mycol Res 112:1297–1306

Beekman AM, Barrow RA (2014) Syntheses of the fungal metabolites Boletopsins 7, 11, and 12 from the Papua New Guinea Medicinal Mushroom *Boletopsis* sp. J Org Chem 79(3):1017–1024. https://doi.org/10.1021/jo402492d

Beever RE, Lebel T (2014) Truffles of New Zealand: a discussion of bird dispersal characteristics of fruit bodies. Auck Bot Soc 69(2):170–178

Begerow D, McTaggart A (2018) Ustilaginomycotina. In: Begerow D (ed) Syllabus of plant families—A. Engler's Syllabus der Pflanzenfamilien, Part 1/3: Basidiomycota and Entorrhizomycota. Schweizerbart Science Publishers, Stuttgart, pp 92–129

Begerow D, Bauer R, Oberwinkler F (1998) ['1997'] Phylogenetic studies on nuclear large subunit ribosomal DNA sequences of smut fungi and related taxa. Can J Bot 75:2045–2056

Begerow D, Bauer R, Boekhout T (2000) Phylogenetic placements of ustilaginomycetous anamorphs as deduced from nuclear LSU rDNA sequences. Mycol Res 104:53–60. https://doi.org/10.1017/S0953756299001161

Begerow D, Bauer R, Oberwinkler F (2001) *Muribasidiospora*: microstromatales or exobasidiales? Mycol Res 105:798–810

Begerow D, Bauer R, Oberwinkler F (2002a) The exobasidiales: an evolutionary hypothesis. Mycol Progr 1:187–199

Begerow D, Lutz M, Oberwinkler F (2002b) Implications of molecular characters for the phylogeny of the genus *Entyloma*. Mycol Res 106:1392–1399

Begerow D, Göker M, Lutz M, Stoll M (2004) On the evolution of smut fungi on their hosts. In: Agerer R et al (eds) Frontiers in basidiomycote mycology. IHW-Verlag, Eching, pp 81–98

Begerow D, Stoll M, Bauer R (2006) A phylogenetic hypothesis of Ustilaginomycotina based on multiple gene analyses and morphological data. Mycologia 98:906–916

Begerow D, Schäfer AM, Kellner R, Yurkov A, Kemler M, Oberwinkler F, Bauer R (2014) Ustilaginomycotina. In: McLaughlin DJ, Spatafora JW (eds) The Mycota, vol 7, Part A, Systematics and evolution, 2nd edn. Springer, Berlin, pp 295–329

Begerow D, Kemler M, Feige A, Yurkov A (2017) Parasitism in yeasts. In: Buzzini P, Lachance MA, Yurkov A (eds) Yeasts in natural ecosystems: ecology. Springer, Cham, pp 179–210

Begerow D, McTaggart A, Agerer R (2018) Syllabus of plant families—A. Engler's Syllabus der Pflanzenfamilien, Part 1/3: Basidiomycota and Entorrhizomycota. Schweizerbart Science Publishers, Stuttgart

Bellini MF, Giacomini NL, Eira AF, Ribeiro LR, Mantovani MS (2003) Anticlastogenic effect of aqueous extracts of *Agaricus blazei* on CHO k1 cells, studying different developmental phases of the mushroom. Toxicol Vitro 17:465–469

Berbee ML, Wong EYY, Tsui CKM (2016) Phylogenetic evidence places the coralloid jelly fungus*Tremellodendropsis tuberosa* (Tremellodendropsidales) among early diverging Agaricomycetes. Mycol Prog 15:939–946

Berbee ML, James TY, Strullu-Derrien C (2017) Early diverging fungi: diversity and impact at the dawn of terrestrial life. Annu Rev Microbiol 71:41–60

Berkeley MJ (1836) Fungi. In Smith's English Flora vol 5. Part 2

Berkeley MJ (1837) Notices of British fungi (38–58). Mag Zool Bot 1:507–513

Berkeley MJ, Broome CE (1871) Notices of British fungi. Ann Mag Nat Hist IV 7:425–436

Bernicchia A (1990) Polyporaceae s.l. in Italia. Instituto di Patologia Vegetale, Italy

Bernicchia A (2005) Polyporaceae s.l. Fungi Europaei, 10. ed. Candusso, Alassio

Bernicchia A, Gorjón SP (2010) Fungi Europaei, vol 12: Corticiaceae s.l. Edizioni Candusso, Alassio

Besl H, Bresinsky A (1997) Chemosystematics of Suillaceae and Gomphidiaceae (suborder Suillineae). Plant Syst Evol 206:223–242

Besl H, Bresinsky A, Kämmerer A (1986) Chemosystematik der Coniophoraceae. Zeitschrift Für Mykologie 52(2):277–286

Bhanja SK, Rout D, Patra P et al (2013) Structural studies of an immunoenhancing glucan of an ectomycorrhizal fungus *Ramaria botrytis*. Carbohydr Res 374:59–66.https://doi.org/10.1016/j.carres.2013.03.023

Bhardwaj K, Sharma A, Tejwan N, Bhardwaj S, Bhardwaj P, Nepovimova E, Shami A, Kalia A, Kumar A, Abd-Elsalam KA, Kuča K (2020) *Pleurotus* macro fungi-assisted nanoparticle synthesis and its potential applications: a review. J Fungi 6:351

Bhat R, Sharanabasava VG, Deshpande R, Shetti U, Sanjeev G, Venkataraman A (2013) Photo-bio-synthesis of irregular shaped functionalized gold nanoparticles using edible mushroom *Pleurotus florida* and its anti-cancer evaluation. J Photochem B 125:63–69

Bijlani S, Singh NK, Mason CE, Wang CCC, Venkateswaran K (2020) Draft genome sequences of Tremellomycetes strains isolated from the International Space Station. Microbiol Resour Announc 9:e00504-e520

Bilbao-Sainz C, Chiou B-S, Punotai K, Olson D, Williams T, Wood D, Rodov V, Poverenov E, McHugh T (2018) Layer-by-layer alginate and fungal chitosan based edible coatings applied to fruit bars. J Food Sci 83:1880–1887

Binder M (1999) Zur molecularen Systematik der Boletales: Boletineae und Sclerodermatineae subordo nov. Dissertation, University of Regensburg

Binder M, Bresinsky A (2002) Derivation of a polymorphic lineage of Gasteromycetes from boletoid ancestors. Mycologia 94(1):85–98

Binder M, Hibbett DS (2002) Higher level phylogenetic relationships of Homobasidiomycetes (mushroom-forming fungi) inferred from four rDNA regions. Mol Phylogenet Evol 22:76–90

Binder M, Hibbett DS (2006) Molecular systematics and biological diversification of Boletales. Mycologia 98(6):971–981

Binder M, Hibbett DS, Molitoris HP (2001) Phylogenetic relationships of the marine gasteromycete Nia vibrissa. Mycologia 93(4):679–688

Binder M, Hibbett DS, Larsson KH, Larsson E, Langer E, Langer G (2005) The phylogenetic distribution of resupinate forms across the major clades of mushroom-forming fungi (Homobasidiomycetes). Syst Biodivers 3(2):113–157

Binder M, Larsson KH, Matheny PB, Hibbett DS (2010) Amylocorticiales ord. nov. and Jaapiales ord. nov.: early diverging clades of Agaricomycetidae dominated by corticioid forms. Mycologia 102:865–880

Binder M, Justo A, Riley R et al (2013) Phylogenetic and phylogenomic overview of the Polyporales. Mycologia 105(6):1350–1373

Birkebak JM, Mayor JR, Ryberg KM, Matheny PB (2013) A systematic, morphological and ecological overview of the Clavariaceae (Agaricales). Mycologia 105:896–911

Blackwell M, Hibbett DS, Taylor JW, Spatafora JW (2007) Research Cordination Networks: a phylogeny for kingdom Fungi (Deep Hypha). Mycologia 98:829–837

Blumfield M, Abbott K, Duve E, Cassettari T, Marshall S, Fayet-Moore F (2020) Examining the health effects and bioactive components in *Agaricus bisporus* mushrooms: a scoping review. J Nutr Biochem 84:108453

Boa E (2004) Wild edible fungi: a global overview of their use and importance to people. FAO, Rome

Boccone P (1697) Museo di fisica e di esperienze variato, e decorato di osservazioni naturali, note medicinali, e ragionamenti secondo i principij de moderni. I.B. Zuccato, Venecia

Bodensteiner P, Binder M, Moncalvo JM, Agerer R, Hibbett DS (2004) Phylogenetic relationships of cyphelloid homobasidiomycetes. Mol Phylogenet Evol 33(2):501–515

Bodman MC (1952) A taxonomic study of the genus *Heterochaete*. Lloydia 15:193–233

Boedijn KB (1937) A smut causing galls on the leaves of *Hypolytrum*. Bull Jard Bot Buitenzorg 14:368–372

Boekhout T (1991a) A revision of ballistoconidia-forming yeasts and fungi. Stud Mycol 33:1–194

Boekhout T (1991b) Systematics of the genus *Itersonilia*Derx: a comparative phenetic study. Mycol Res 95:135–146

Boekhout T (2011) Tilletiopsis Derx ex Derx. In: Kurtzman CP, Fell JW, Boekhout T (eds) The yeasts, a taxonomic study, 5th edn. Elsevier, Amsterdam, pp 2003–2014

Boekhout T, Fonseca A, Batenburg-van der Vegte WH (1991) *Bulleromyces* genus novum (Tremellales), a teleomorph for *Bullera alba*, and the occurrence of mating in *Bullera variabilis*. Antonie Van Leeuwenhoek 59:81–93

Boekhout T, Fell JW, O'Donnell K (1995) Molecular systematics of some yeast anamorphs belonging to the Ustilaginales and Tilletiales. Stud Mycol 38:175–183

Boekhout T, Theelen BJF, Houbraken J, Robert V, Scorzetti G, Gafni A, Gerson U, Sztejnberg A (2003) Novel anamorphic mite-associated fungi belonging to the Ustilaginomycetes: *Meira geulakonigii* gen. nov., sp. nov., *Meira argovae* sp. nov. and *Acaromyces ingoldii* gen. nov., sp. nov. Int J Syst Evol Microbiol 53:1655–1664

Boekhout T, Gildemacher P, Theelen B, Muller WH, Heijne B, Lutz M (2006) Extensive colonization of apples by smut anamorphs causes a new postharvest disorder. FEMS Yeast Res 6:63–76. https://doi.org/10.1111/j.1567-1364.2005.00002.x

Boekhout T, Fonseca A, Sampaio JP, Bandoni RJ, Fell JW, Kown-Gung KJ (2011) Discussion on teleomorphic and anamorphic basidiomycetous yeasts. The yeasts, a taxonomic study, 5th edn. Elsevier, Amsterdam

Boekhout T, Amend AS, El Baidouri F et al (2022) Trends in yeast diversity discovery. Fungal Divers 114:491–537

Boidin J, Gilles G (1989) Basidiomycètes Aphyllophorales de l'île de la Réunion. XV. Famille des Xenasmataceae Oberw. Bulletin De La Société Mycologique De France 105:151–162

Boidin J, Gilles G (2000) Basidiomycètes Aphyllophorales de l'île de la Réunion XXI-suite. Mycotaxon 75:357–387

Boidin J, Mugnier J, Canales R (1998) Taxonomie moléculaire des Aphyllophorales. Mycotaxon 66:445–492

Bomfleur B, McLoughlin S, Vajda V (2014) Fossilized nuclei and chromosomes reveal 180 million years of genomic statis in royal ferns. Science 343:1376–1377

Bomfleur B, Grimm GW, Stephen McLoughlin S (2017) The fossil Osmundales (Royal Ferns)—a phylogenetic network analysis, revised taxonomy, and evolutionary classification of anatomically preserved trunks and rhizomes. PeerJ 5:e3433

Bonito G, Hameed K, Toome-Heller M et al (2017) *Atractiella rhizophila*, sp. nov., an endorrhizal fungus isolated from the Populus root microbiome. Mycologia 109(1):18–26

Bonorden HF (1851) Handbuch der allgemeinen Mykologie. Schweizerbart, Stuttgart

Boobalan T, Sethupathi M, Sengottuvelan N, Kumar P, Balaji P, Gulyás BZ, Padmanabhan P, Selvan ST, Arun A (2020) Mushroom-derived carbon dots for toxic metal ion detection and as antibacterial and anti-cancer agents. ACS Appl Nano Mater 3:5910–5919

Borda LJ, Wikramanayake TC (2015) Seborrheic dermatitis and dandruff: a comprehensive review. J Clin Investig Dermatol 3(2):10. https://doi.org/10.13188/2373-1044.1000019

Borovička J, Braeuer S, Walenta M, Hršelová H, Leonhardt T, Sácký J, Kaňa A, Goessler W (2022) A new mushroom hyperaccumulator: cadmium and arsenic in the ectomycorrhizal basidiomycete *Thelephora penicillata*. Sci Total Environ 826:154227. https://doi.org/10.1016/j.scitotenv.2022.154227

Botnen S, Kauserud H, Carlsen T et al (2015) Mycorrhizal fungal communities in coastal sand dunes and heaths investigated by pyrosequencing analyses. Mycorrhiza 25:447–456. https://doi.org/10.1007/s00572-014-0624-1

Bougher NL (1995) Diversity of ectomycorrhizal fungi associated with eucalypts in Australia. In: Brundrett M, Dell B, Malajczuk N (eds) Mycorrhizal research for forestry in Asia. Arawang Information Bureau Pty Ltd, Canberra, pp 8–15

Bourdot H, Galzin A (1911) Hyménomycètes de France. Bull Trimest La Société Mycol Fr 27:223–274

Bourdot H, Galzin A (1928) Hyménomycètes de France, Hetérobasidiés—Homobasidiés Gymnocarpes. Bibliotheca Mycologica 23 J Cramer, Lehre

Boyce GR, Gluck-Thaler E, Slot JC, Stajich JE, Davis WJ, James TY, Cooley JR, Panaccione DG, Eilenberg J, De Fine Licht HH, Macias AM, Berger MC, Wickert KL, Stauder CM, Spahr EJ, Maust MD, Metheny AM, Simon C, Kritsky G, Hodge KT, Humber RA, Gullion T, Short DPG, Kijimoto T, Mozgai D, Arguedas N, Kasson MT (2019) Psychoactive plant- and mushroom-associated alkaloids from two behavior modifying cicada pathogens. Fungal Ecol 41:147–164. https://doi.org/10.1016/j.funeco.2019.06.002

Braun U (1995) A monograph of *Cercosporella*, *Ramularia* and allied genera (phytopathogenic Hyphomycetes), vol 1. IHWVerlag, Eching

Brearley FQ (2012) Ectomycorrhizal associations of the Dipterocarpaceae. Biotropica 44(5):637–648

Brefeld O (1888) Untersuchungen aus dem Gesammtgebiete der Mykologie. VII. Basidiomyceten II. Protobasidiomyceten. Arthur Felix, Leipzig

Brefeld O (1895) Untersuchungen aus dem Gesammtgebiete der Mykologie. XII Heft Hemibasidii. Die Brandpilze III. Miinster. Arthur Felix, Leipzig

Bresadola G (1911) Adnotanda mycological. Annales Mycologici 9:425–428

Bresinsky A, Rennschmid A (1971) Pigmentmerkmale, Organisationsstufen und systematische Gruppen bei höheren Pilzen. Ber Dtsch Bot Ges 84:313–329

Bromhead EF (1840) Remarks on the botanical system of Professor Perleb. Mag Nat Hist J Zool Bot Mineral Geol Meteorol 4:329–338

Browne P (1756) The Civil and Natural History of Jamaïca. T Osbourne and J Simpson, London

Bruns TD, Szaro TM, Gardes M et al (1998) A sequence database for the identification of ectomycorrhizal basidiomycetes by phylogenetic analysis. Mol Ecol 7:257–272

Bucholtz F (1901) Hypogaeen aus Russland. Hedwigia 40:304–322

Bucholtz F (1903) Zur morphologie und systematik der fungi hypogaei. Annales Mycologici 1:152–174

Burr B, Barthlott W, Westerkamp C (1996) *Staheliomyces*(Phallales) visited by *Trigona* (Apidae): melittophily in spore dispersal of an Amazon stinkhorn? J Trop Ecol 12:441–445

Buscardo E, Rodríguez-Echeverría S, Freitas H, de Angelis P, Pereira JS, Muller LAH (2015) Contrasting soil fungal communities in Mediterranean pine forests subjected to different wildfire frequencies. Fungal Divers 70(1):85–99. https://doi.org/10.1007/s13225-014-0294-5

Buyck B (2016) Special issue: *Cantharellus*. Cryptogam Mycol 37(3):225–258

Buyck B, Hofstetter V, Eberhardt U, Verbeken A, Kauff F (2008) Walking the thin line between*Lactarius* and *Russula*: the dilemma of*Russula* sect, *Ochricompactae*. Fungal Divers 28:15–40

Buyck B, Duhem B, Eyssartier G, Ducousso M (2012) *Podoserpula miranda* sp. nov. (Amylocorticiales, Basidiomycota) from New Caledonia. Cryptogamie Mycol 33(4):453–461.https://doi.org/10.7872/crym.v33.iss4.2012.453

Buyck B, Zoller S, Hofstetter V (2018) Walking the thin line…ten years later: the dilemma of above versus below-ground fea-tures to support phylogenies in the Russulaceae (Basidiomycota). Fungal Divers 89:267–292

Buzzini P, Lachance MA, Yurkov A (2017) Yeast in natural ecosystems: ecology. Springer, Cham

Buzzini P, Turchetti B, Yurkov A (2018) Extremophilic yeasts: the toughest yeasts around? Yeast 35:487–497

Cabral TS, Marinho P, Goto TB, Baseia IG (2012) *Abrachium*, a new genus in the Clathraceae, and *Itajahya* reassessed. Mycotaxon 119:419–429

Cabral TS, Silva BDB, Martín MP, Clement CR, Hosaka K, Baseia IG (2019) Behind the veil – exploring the diversity in *Phallus indusiatus* s.l. (Phallomycetidae, Basidiomycota). MycoKeys 58:103–127

Cabral TS, Melanda GCS, Assis NM, OvreboC BIG, Martín MP (2022) Loosening the belt: unknown diversity of the strangled stinkhorn genus *Staheliomyces* (Phallales, Basidiomycota). Mycol Prog 21(4):46

Cai L, Giraud T, Zhang N, Begerow D, Cai G, Shivas RG (2011) The evolution of species concepts and species recognition criteria in plant pathogenic fungi. Fungal Divers 50:121–133

Cali V, Spatafora C, Tringali C (2004) Sarcodonins and sarcoviolins, bioactive polyhydroxy p-terphenyl pyrazinediol dioxide conjugates from fruiting bodies of basidiomycete *Sarcodon leucopus*. Eur J Org Chem 3:592–599. https://doi.org/10.1002/ejoc.200300407

Calonge FD (1998) Gasteromycetes. I. Lycoperdales, nidulariales, phallales, sclerodermatales, tulostomales. Flora Mycologica Iberica 3:1–271

Calonge FD (2005) A tentative key to identify the species of *Phallus*. Bol Soc Micologica Madr 29:9–18

Calonge FD, Martín MP (2000) Morphological and molecular data on the taxonomy of *Gymnomyces*, *Martellia* and *Zelleromyces* (Elasmomycetaceae, Russulales). Mycotaxon 76:9–15

Cannon PF, Kirk PM (2007) Fungal families of the world. Wallingford, Oxfordshire

Cao Y, Zhang Y, Yu Z, Wang P, Tang X, He X, Mi F, Liu C, Yang D, Xu J (2015) Genome sequence of*Phlebopus portentosus* strain PP33, a cultivated bolete. Genome Announc 3(2):e00326-e415

Cao Y, Li P-D, Zhao J, Wang H-K, Jeewon R, Bhoyroo V, Aruna B, Lin F-C, Wang Q (2018) Morph-molecular characterization of *Meira nicotianae* sp. nov., a novel basidiomycetous, anamorphic yeast-like fungus associated with growth improvement in tobacco plant. Phytotaxa 365:169–181

Cao T, Hu Y-P, Yu J-R, Wei T-Z, Yuan H-S (2021a) A phylogenetic overview of the Hydnaceae (Cantharellales, Basidiomycota) with new taxa from China. Stud Mycol 99:100121

Cao B, Haelewaters D, Schoutteten N et al (2021b) Delimiting species in Basidiomycota: a review. Fung Divers 109:181–237. https://doi.org/10.1007/s13225-021-00479-5

Capella-Gutiérrez S, Silla-Martínez JM, Gabaldón T (2009) trimAl: a tool for automated alignment trimming in large-scale phylogenetic analyses. Bioinformatics 25:1972–1973. https://doi.org/10.1093/bioinformatics/btp348

Carey AB (2003) Biocomplexity and restoration of biodiversity in temperate coniferous forest: inducing spatial heterogeneity with variable-density thinning. Forestry 76(2):127–136

Carris LM, Castlebury LA, Goates BJ (2006) Nonsystemic bunt fungi–*Tilletia indica* and *T. horrida*: a review of history, systematics, and biology. Annu Rev Phytopathol 44:113–133

Castlebury LA (1998) Morphological characterization of *Tilletia indica* and similar fungi. In: Malik VS, Mathre DE (eds) Bunts and smuts of wheat: International Symposium, Raleigh, North Carolina, August 17–20, 1997. North American Plant Protection Organization, Ottawa, pp 97–105

Castlebury LA, Carris LM, Vánky K (2005) Phylogenetic analysis of *Tilletia* and allied genera in order Tilletiales (Ustilaginomycetes; Exobasidiomycetidae) based on large subunit nuclear rDNA sequences. Mycologia 97:888–900

Castro ML, Freire L (1995) *Gyroporus ammophilus*, a new poisonous bolete from the Iberian Peninsula. Persoonia 16:123–126

Castro-Alves VC, Gomes D, Menolli N Jr, Sforça ML, do Nascimento JR (2017) Characterization and immunomodulatory effects of glucans from *Pleurotus albidus*, a promising species of mushroom for farming and biomass production. Int J Biol Macromol 95:215–223

Cejp K (1958) Nidulariales. Flora ČSR: Gasteromycetes, Houby-Břichatky (Gasteromycetes-Puffballs). Nakladatelstvi Ceskoslovenske Akademie ved, Praha, pp 633–382

Chamuris G (1988) The non-stipitate stereoid fungi in the northeastern United States and adjacent Canada. Mycol Memoir 14:41–45

Chandra A, Huff DR (2008) *Salmacisia*, a new genus of Tilletiales: reclassification of *Tilletia buchloeana* causing induced hermaphroditism in buffalograss. Mycologia 100:81–93

Chang ST, Miles PG (1989) Edible mushrooms and their cultivation. CRC Press, Boca Raton

Chaturvedi VK, Yadav N, Rai NK, Abd Ellah NH, Bohara RA, Rehan IF, Marraiki N, Batiha GES, Hetta HF, Singh MP (2020) *Pleurotus sajor-caju*-mediated synthesis of silver and gold nanoparticles active against colon cancer cell lines: a new era of Herbonanoceutics. Molecules 25:3091

Chen J-J, Shen L-L, Cui B-K (2015) Morphological characters and molecular data reveal a new species of *Hydnocristella* (Gomphales, Basidiomycota) from southwestern China. Nova Hedwig 101:139–146. https://doi.org/10.1127/nova_hedwigia/2015/0255

Chen Z-H, Yang Z-L, Bau T, Li T-H (2016) Poisonous mushrooms: recognition and poisoning treatment. Science Press, Beijing

Chen C-C, Cao B, Hattori T, Cui B-K, Chen C-Y, Wu S-H (2020) Phylogenetic placement of*Paratrichaptum* and reconsideration of Gloeophyllales. Fungal Syst Evol 5:119–129

Chevallier FF (1826) Flore Générale des Environs de Paris. imprimerie de Decourchant rue d'Erfurth, Paris

Chien LH, Deng JS, Jiang WP, Chen CC, Chou YN, Lin JG, Huang GJ (2022) Study on the potential of *Sanghuangporus sanghuang* and its components as COVID-19 spike protein receptor binding domain inhibitors. Biomed Pharmacother 153:113434

Choi J, Détry N, Kim K, Asiegbu F, Valkonen J, Lee Y (2014) fPoxDB: fungal peroxidase database for comparative genomics. BMC Microbiol 14:117

Chowdhary A, Kathuria S, Agarwal K, Meis JF (2014) Recognizing filamentous basidiomycetes as agents of human disease: a review. Med Mycol 52:782–797. https://doi.org/10.1093/mmy/myu047

Cibrián TD, Alvarado-Rosale D, García-Díaz SE (2007) Enfermedades forestales en México/Forest Diseases in Mexico. UACH; Conafor-Semarnat, México; Forest Service USDA, EUA; NRCAN Forest Service, Canadá y Comisión Forestal de América del Norte, COFAN. FAO, Chapingo

Ciferri R et al (1959) Tentative arrangement of the conidial stages of Tilletiaceae. In: Bontea V (ed) Omagiu lui Traian Săvulescu. Edit Acad RP Romîne, Bucureşti, pp 175–180

Cissé OH, Almeida JMGCF, Fonseca Á, Kumar AA et al (2013) Genome sequencing of the plant pathogen *Taphrina deformans*, the causal agent of peach leaf curl. mBio 4:e00055-13

Claridge AW, McNee A, Tanton MT & Davey SM (1992) Ecology of bandicoots in unlogged forest adiacent to logging coupes: A case study from the Eden woodchip agreement area. In: Conservation of 'Kustralia'sForesi Fauna (ed. D. Lunney) Royal Zoological Society of NSW, Mosman.

Claridge AW, May TW (1994) Mycophagy among Australian mammals. Aust J Ecol 19:251–275

Claridge AW, Trappe JM (2004) Managing habitat for mycophagous (fungus-feeding) mammals: a burning issue. Conservation of Australia's Forest Fauna 936–946

Clements FE (1909) The genera of fungi. H.W. Wilson Company, Hackensack

Cockerell TDA (1908) Descriptions of Tertiary plants. Am J Sci 26(156):537–544

Coelho MA, Ianiri G et al (2023) Frequent transitions in mating-type locus chromosomal organization in *Malassezia* and early steps in sexual reproduction. Proc Natl Acad Sci USA 120(32):e2305094120. https://doi.org/10.1073/pnas.2305094120

Cohen L, Persky Y, Hadar R (2002) Biotechnological applications and potential of wood–degrading mushrooms of the genus *Pleurotus*. Appl Microbiol Biotechnol 58:582–594.https://doi.org/10.1007/s00253-002-0930-y

Cole GT (1983) *Graphiola phoenicis*: a taxonomic enigma. Mycologia 75:93–116

Consiglio G, Vizzini A, Cooper J, Marchetti M, Angelini C, Brugaletta E, Setti L (2021) I membri agaricoidi del genere *Porotheleum* (Porotheleaceae, Agaricales), *Porotheleum* emend., Porotheleaceae s. stricto e nuovi generi per *Agaricus floccipes* e *Mycena subalpine*. 99–151; The agaricoid members of the genus *Porotheleum* (Porotheleaceae, Agaricales), *Porotheleum* emend., Porotheleaceae s. stricto, and new genera for *Agaricus floccipes* and *Mycena subalpina*. Rivista di Micologia 64(2):99–190

Cooper J (2016a) Mycological Notes 32: Notes on the Porotheleaceae of New Zealand.https://www.funnz.org.nz/sites/default/files/2016-MycNotes32-Porotheleaceae_7.pdf

Cooper J (2016b) Mycological Notes 33: NZ species in *Mycenella*, *Hemimycena*, *Atheniella*and *Mycena* pp. (suborder Marasmiineae incertae sedis). https://www.funnz.org.nz/sites/default/files/2016-MycNotes33-UnplacedMarasmineae_1.pdf

Corda ACJ (1839) Icones fungorum hucusque cognitorum III. Apud J. G. Calve, Prague

Corda ACJ (1842) Icones Fungorum hucusque cognitorum V. Apud J. G. Calve, Prague

Cordier T, Robin C, Capdevielle X, Fabreguettes O et al (2012) The comparison of phyllosphere fungal assemblages of European beech (*Fagus sylvatica*) varies significantly along an elevation gradient. New Phytol 196:510–519

Corner EJH (1948) *Asterodon*, a clue to the morphology of fungus fruit-bodies, with notes on *Asterostroma* and *Asterostromella*. Trans Br Mycol Soc 31:234–345

Corner EJH (1950) A monograph of *Clavaria* and allied genera. Ann Bot Mem 1:1–740

Corner EJH (1953) Addenda Clavariacea. III. Ann Bot NS 17:347–368

Corner EJH (1966a) A monograph of cantharelloid fungi. Ann Bot Mem 2:1–255

Corner EJH (1966b) The clavarioid complex of *Aphelaria* and*Tremellodendropsis*. Trans Br Mycol Soc 49:205–211

Corner EJH (1968) A monograph of *Thelephora*. Beihefte Zur Nova Hedwig 27:1–110

Corner EJH (1970) Supplement to "A monograph of *Clavaria* and allied genera". Beih Nova Hedwigia 33:1–299

Corner EJH (1972) *Boletus* in Malaysia. Botanic Gardens, Singapore

Corner EJH (1987) Ad Polyporaceas 4. The genera *Daedalea*. Flabellophora Etc Beih Nova Hedwigia 86:1–286

Cornu M (1883) Sur quelques Ustilaginées nouvelles ou peu connues. Ann Sci Nat Bot Sér 6(15):269–296

Corrales A, Koch RA, Vasco-Palacios AM, Smith ME, Ge ZW, Henkel TW (2022) Diversity and distribution of tropical ectomycorrhizal fungi. Mycologia 114:919–933. https://doi.org/10.1080/00275514.2022.2115284

Costa-Rezende DH, Robledo GL, Góes-Neto A, Reck MA, Crespo E, Drechsler-Santos ER (2017) Morphological reassessment and molecular phylogenetic analyses of *Amauroderma* s. lat. raised new perspectives in the generic classification of the Ganodermataceae family. Persoonia 39:254–269

Costa-Rezende DH, Robledo GL, Drechsler-Santos ER et al (2020) Taxonomy and phylogeny of polypores with ganodermatoid basidiospores (Ganodermataceae). Mycol Prog 19:725–741

Couch JN (1938) The genus *Septobasidium*. The University of North Carolina Press, Chapel Hill

Couch JN (1941) A new *Uredinella* from Ceylon. Mycologia 33:405–410

Crawford DA (1954) Studies on New Zealand Clavariaceae. I. Trans R Soc N Z 82:617–631

Cromack K Jr, Sollins P, Graustein WC, Speidel K, Todd AW, Spycher G, Li CY, Todd RL (1979) Calcium oxalate accumulation and soil weathering in mats of the hypogeous fungus *Hysterangium crassum*. Soil Biol Biochem 11(5):463–468

Crous PW, Wingfield MJ, Burgess TI, Hardy GESJ, Gené J et al (2018) Fungal Planet description sheets: 716–784. Persoonia 40:240–393

Cui B-K, Dai Y-C, He S-H, Zhou L-W, Yuan H-S (2015) A novel *Phellinidium* sp. causes laminated root rot on Qilian juniper (*Sabina przewalskii*) in northwest China. Plant Dis 99:39–43

Cui Y-Y, Cai Q, Tang L-P, Liu J-W, Yang Z-L (2018) The family Amanitaceae: molecular phylogeny, high-rank taxonomy and the species in China. Fungal Divers 91:5–230. https://doi.org/10.1007/s13225-018-0405-9

Cui B-K, Li H-J, Ji X, Zhou J-L, Song J, Si J, Yang Z-L, Dai Y-C (2019) Species diversity, taxonomy and phylogeny of Polyporaceae (Basidiomycota) in China. Fungal Divers 97:137–392

Cummins GB, Hiratsuka Y (2003) Illustrated genera of rust fungi, 3rd edn. APS Press, Minesota

Cunningham GH (1931) The gasteromycetes of Australasia X. The Phallales I. Proc Linn Soc NSW 56:1–15

Cunningham GH (1947) New Zealand Polyporaceae. 1. The genus *Poria*. Bull N Z Dept Sci Ind Res 72(1):43

Cunningham JL, Bakshi BK, Lentz PL, Gilliam MS (1976) Two new genera of leaf-parasitic fungi (Basidiomycetidae : Brachybasidiaceae). Mycologia 68:640–654

Daghino S, Martino E, Voyron S, Perotto S (2022) Metabarcoding of fungal assemblages in*Vaccinium* myrtillus endosphere suggests colonization of above-ground organs by some ericoid mycorrhizal and DSE fungi. Sci Rep 12:1–11. https://doi.org/10.1038/s41598-022-15154-1

Dai Y-C (2011) A revised checklist of corticioid and hydnoid fungi in China for 2010. Mycoscience 52:69–79

Dai Y-C (2012a) Polypore diversity in China with an annotated checklist of Chinese polypores. Mycoscience 53:49–80. https://doi.org/10.1007/s10267-011-0134-3

Dai Y-C (2012b) Pathogenic wood-decaying fungi on woody plants in China. Mycosystema 31:493–509

Dai Y-C, Yang Z-L (2008) A revised checklist of medicinal fungi in China. Mycosystema 27(6):801–824

Dai Y-C, Yang Z-L, Cui B-K, Yu C-J, Zhou L-W (2009) Species diversity and utilization of medicinal mushrooms and fungi in China (review). Int J Med Mushrooms 11:287–302. https://doi.org/10.1615/IntJMedMushr.v11.i3.80

Dai Y-C, Zhou L-W, Yang Z-L, Wen H-A, Bao T, Li T-H (2010) A revised checklist of edible fungi in China. Mycosystema 29:1–21

Dai Y-C, Yang Z-L, Cui B-K, Wu G, Yuan H-S, Zhou L-W, He S-H, Ge Z-W, Wu F, Wei Y-L, Yuan Y, Si J (2021) Diversity and systematics of the important macrofungi in Chinese forests. Mycosystema 40:770–805. https://doi.org/10.13346/j.mycosystema.210036

Danell E (1999) Cantharellus. In: Cairney JWG, Chambers SM (eds) Ectomycorrhizal *fungi: key genera in profile*. Springer Verlag, Berlin, pp 253–267

Das SP, Sumayyah MQ et al (2021) The human fungal pathogen *Malassezia* and its role in cancer. Fungal Biol Rev 38:9–24. https://doi.org/10.1016/j.fbr.2021.08.002

David-Palma M, Libkind D, Brito PH et al (2020) The untapped australasian diversity of astaxanthin-producing yeasts with biotechnological potential—*Phaffia australis* sp. nov. and *Phaffia tasmanic*a sp. nov. Microorganisms 8(11):1651

Davoodian N, Halling RE (2013) Validation and typification of *Gyroporus purpurinus*. Mycotaxon 125(1):103–105

Davoodian N, Bougher NL, Fechner NA, Bergemann SE, Halling RE (2019) Three new species of*Gyroporus* (Boletales, Basidiomycota) from Australia. Muelleria 37:101–107

Davoodian N, Lebel T, Castellano MA, Hosaka K (2021) Hysterangiales revisited: expanded phylogeny reveals new genera and two new suborders. Fungal Syst Evol 8:65–80

De LC (2020) Good agricultural practices of commercial orchids. Vigyan Varta 1(5):53–64

de Bary A (1874) *Protomyces microsporus* und seine Verwandten. Bot Zeitung 32:97–108

de Beer ZW, Begerow D, Bauer R, Pegg GS, Crous PW, Wingfield MJ (2006) Phylogeny of the Quambalariaceae fam. nov., including important *Eucalyptus* pathogens in South Africa and Australia. Stud Mycol 55:289–298

de Francesco G, Sannino C, Sileoni V, Marconi O, Filippucci S, Tasselli G, Turchetti B (2018) Mrakia gelida in brewing process: an innovative production of low alcohol beer using a psychrophilic yeast strain. Food Microbiol 76:354–362

de Garcia V, Trochine A, Uetake J, Bellora N, Libkind D (2020) Novel yeast taxa from the cold: description of *Cryolevonia giraudoae* sp. nov. and *Camptobasidium gelus* sp. nov. Int J Syst Evol Microbiol 70(6):3711–3717

de Hoog GS, Smith MTh, Rosa CA (2011) Moniliella Stolk & Dakin, (1966). In: Kurtzman CP, Fell JW, Boekhout T (eds) The yeasts, a taxonomic study, 5th edn. Elsevier, Amsterdam, pp 1837–1846

de Meiras-Ottoni A, Larsson KH, Gibertoni TB (2021) Additions to *Trechispora* and the status of *Scytinopogon*(Trechisporales, Basidiomycota). Mycol Prog 20:203–222. https://doi.org/10.1007/s11557-021-01667-y

de Thümen F (1879) *Vossia* Thüm. Eine Neue Ustilagineen-Gattung Oesterr Bot Z 29:18–20

de Vries R, Lange E, Wösten H, Stalpers J (2008) Control and possible applications of a novel carrot-spoilage basidiomycete, *Fibulorhizoctonia psychrophila*. Antonie Van Leeuwenhoek 93:407–413

Deacon JW (2006) Fungal biology, 4th edn. Blackwell Publishing, Massachusetts

Dearnaley JWD, Perotto S, Selosse MA (2016) Structure and development of orchid mycorrhizas. In: Martin F (ed) Molecular mycorrhizal symbiosis. Wiley-Blackwell, New Jersey, pp 63–86

Denchev CM (2001) Class *Ustomycetes* (Orders *Tilletiales, Ustilaginales,* and *Graphiolales*). In: Fakirova V (ed) Fungi of Bulgaria, Editio Academica 'Prof. Marin Drinov' & Editio Pensoft, Sofia, vol 4, pp 1–286 (**in Bulgarian**)

Denchev CM (2003) *Melanustilospora*, a new genus in the Urocystales (smut fungi). Mycotaxon 87:475–477

Denchev CM, Denchev TT (2013) *Erratomycetaceae,* fam. nov., and validation of some names of smut fungi recently described from India. Mycobiota 1:63–70

Denchev TT, Denchev CM (2016) *Jamesdicksonia anadelphiae-trichaetae* (*Georgefischeriales*) and *Sporisorium anadelphiae-trichaetae* (*Ustilaginales*), new species on*Anadelphia trichaeta* (*Poaceae*) from Guinea. Phytotaxa 252:205–216

Denchev TT, Denchev CM (2018a) *Planetella lironis*—a new record from Greenland. Mycotaxon 133:381–386

Denchev TT, Denchev CM (2018b) Contributions to the smut fungi of Africa. 4. Taxonomic re-examination and emended description of *Bauerago capensis*. Mycobiota 8:1–7

Denchev TT, Denchev CM (2018c) Two new smut fungi on *Ventenata* (Poaceae): *Tilletia elizabethae* from Slovakia and *T. ventenatae* from Turkey. Willdenowia 48:177–183

Denchev TT, Denchev CM (2018d) *Tilletia tripogonellae*(Tilletiaceae), a new smut fungus on *Tripogonella spicata* (Poaceae) from Argentina. Ann Bot Fenn 55:273–277

Denchev CM, Denchev TT (2021) Validation of the generic names *Meira* and *Acaromyces* and nineteen species names of basidiomycetous yeasts. Mycobiota 11:1–10

Denchev CM, Kakishima M (2007) Notes on some Japanese smut fungi. IV. *Mundkurella japonica*, sp. nov. Mycotaxon 102:9–16

Denchev CM, Moore RT (2009) Validation of Malasseziaceae and Ceraceosoraceae (Exobasidiomycetes). Mycotaxon 110:379–382

Denchev TT, Denchev CM, Michikawa M, Kakishima M (2013) The genus *Anthracoidea* (*Anthracoideaceae*) in Japan and some adjacent regions. Mycobiota 2:1–125

Denchev TT, van der Zon APM, Denchev CM (2018) *Tilletia triraphidis* (Tilletiaceae), a new smut fungus on *Triraphis purpurea*(Poaceae) from Namibia. Phytotaxa 375:182–186

Denchev TT, Denchev CM, Kemler M, Begerow D (2020a) *Kalmanago* gen. nov. (*Microbotryaceae*) on *Commelina* and *Tinantia* (*Commelinaceae*). Mycobiota 10:21–37

Denchev TT, Knudsen H, Denchev CM (2020b) The smut fungi of Greenland. Mycokeys 64:1–164

Denchev TT, Denchev CM, Kemler M, Begerow D (2021) *Entyloma eranthidis* sp. nov. on *Eranthis longistipitata* from Uzbekistan. Mycotaxon 136:373–385

Deng C-Y, Shi L-Y, Wang J, Xiang Z, Li S-M, Li G-J, Yang H (2020) Species diversity of the*Russula virescens* complex "qingtoujun" in southern China. Mycosystema 39(9):1661–1683

Dennis RWG (1970) Fungus flora of Venezuela and adjacent countries. Kew Bull Addit Ser 3:1–531

Dentinger BTM, Gaya E, O'Brien H, Suz LM, Lachlan R, Díaz-Valderrama JR, Koch RA, Aime MC (2016) Tales from the crypt: genome mining from fungarium specimens improves resolution of the mushroom tree of life. Biol J Lin Soc 117(1):11–32

Derx HC (1930) Étude sur les Sporobolomycètes. Ann Mycol 28:1–23

Derx HG (1948) *Itersonilia* nouveau genre de Sporobolomycètes à mycelium bouclé. Bull Jard Bot Buitenzorg 17:465–472

Desjardin DE, Perry BA (2015) A new species of *Scytinopogon*from the island of Príncipe, Republic of São Tomé and Príncipe, West Africa. Mycosphere 6(4):434–441

Desvaux NA (1809) Observations sur quelques genres à établir dans la famille del Champignons. Journal De Botanique 2:88–105

Díaz-Moreno R, Marmolejo JG, Valenzuela R (2005) Flora micológica de bosques de pino y pino-encino en durango, México. Ciencia UANL 7:362–369

Diederich P, Millanes AM, Etayo J, van den boom P, Wedin M (2022a) Finding the needle in the haystack: a revision of *Critendenia*, a surprisingly diverse lichenocolous genus of Agaricostilbomycetes, Pucciniomycotina. The Bryologist 125(2):248–293

Diederich P, Millanes A, Wedin M, Lawrey JD (2022b) Flora of Lichenicolous Fungi. Basidiomycota, vol 1. National Museum of Natural History, Luxembourg

Ding X-X, Xu X, Cui Y-Y (2022) A fifty-locus phylogenetic analysis provides deep insights into the phylogeny of *Tricholoma* (Tricholomataceae, Agaricales). Persoonia 50:1–26

Domínguez de Toledo LS, Castellano MA (1998) A revision of the genera *Radiigera* and *Pyrenogaster*. Mycologia 88:863–884

Dong M, Hou Y, Ding X (2020) Structure identification, antitumor activity and mechanisms of a novel polysaccharide from *Ramaria flaccida* (Fr.) Quel. Oncol Lett 20(3):2169–2182. https://doi.org/10.3892/ol.2020.11761

Donk MA (1933) Revision der Niederlandischen Homobasidiomycetes. Aphyllophoraceae 2. Mededelingen Van Het Botanisch Museum En Herbarium Van De Rijksuniversiteit Utrecht 9:1–278

Donk MA (1948) Notes on Malesian fungi. I. Bulletin Du Jardin Botanique De Buitenzorg 17:473–482

Donk MA (1949) New and revised nomina generica conservanda proposed for Basidiomycetes (Fungi). Bull Du Jard Bot Buitenzorg 3:83–168

Donk MA (1956) Notes on resupinate Hymenomycetes II. Tulasnelloid Fungi Reinwardtia 3(3):363–379

Donk MA (1957) The Generic Names Proposed for Hymenomycetes. VII: " Thelephoraceae." Taxon 6:17–28

Donk MA (1960) *Tylospora* nom. nov. Taxon 9:220

Donk MA (1961) Four new families of Hymenomycetes. Persoonia 1(4):405–407

Donk MA (1964) A conspectus of the families of Aphyllophorales. Persoonia 3(2):199–324

Donk MA (1966) Check list of European hymenomycetous Heterobasidiae. Persoonia 4(2):145–244

Donk MA (1971) Progress in the study of the classification of the higher Basidiomycetes. In: Petersen RH (ed) Evolution in the higher Basidiomycetes. University of Tennessee Press, Knoxville

Dörfelt H (1979) Taxonomische Studien in der Gattung Xerula R. Mre Feddes Repertorium 90:363–388

Dörfelt H (1980a) Taxonomische Studien in der Gattung Xerula R. Mre. (II). Feddes Repertorium 91:209–223

Dörfelt H (1980b) Taxonomische Studien in der Gattung Xerula R. Mre. (III). Feddes Repertorium 91:415–438

Dörfelt H (1981a) Taxonomische Studien in der Gattung Xerula R. Mre. (IV). Feddes Repertorium 92:255–291

Dörfelt H (1981b) Taxonomische Studien in der Gattung Xerula R. Mre. (V). Feddes Repertorium 92:631–634

Dörfelt H (1983a) Taxonomische Studien in der Gattung Xerula R. Mre. (VI). Feddes Repertorium 94:43–85

Dörfelt H (1983b) Taxonomische Studien in der Gattung Xerula R. Mre. (VII). Feddes Repertorium Specierum 94:251–262

Dörfelt H (1983c) Taxonomische Studien in der Gattung Xerula R. Mre. (VII). Feddes Repertorium Specierum 95:549–561

Dörfelt H (1984) Taxonomische Studien in der Gattung Xerula R. Mre. (IX). Feddes Repertorium Specierum 95:189–200

Dörfelt H (1985) Taxonomische Studien in der Gattung Xerula R. Mre. (X). Feddes Repertorium 96:235–240

Douanla-Meli C, Langer E, Calonge FD (2005) *Geastrum pleosporus* sp. nov., a new species of Geastraceae identified by morphological and molecular phylogenetic data. Mycol Prog 4:239–250

Douglas SM (2010) Sphaerobolus spp.—the artillery fungus. The Connecticut Agricultural Experiment Station. https://portal.ct.gov/-/media/CAES/DOCUMENTS/Publications/Fact_Sheets/Plant_Pathology_and_Ecology/SPHAEROBOLUSSPPTHEARTILLERYFUNGUS050310Rpdf.pdf

Doweld A (2001) Prosyllabus Tracheophytorum, Tentamen systematis plantarum vascularium (Tracheophyta). GEOS, Moscow

Dring DM (1973) Gasteromycetes. In: Ainsworth GC, Sparrow FK, Sussman AS (eds) The fungi: an advanced treatise, vol IVB. Academic Press, New York, pp 451–478

Dring DM (1980) Contributions towards a rational arrangement of the Clathraceae. Kew Bull 35:1–96

Du H, Hu Q, Yang W, Pei F, Kimatu BM, Ma N, Zhao L (2016) Development, physiochemical characterization and forming mechanism of *Flammulina velutipes*polysaccharide-based edible films. Carbohydr Polym 152:214–221

Durán R (1987) Ustilaginales of Mexico. Taxonomy, symptomatology, spore germination, and basidial cytology. Washington State University Press, Pullman

Durán R, Fischer GW (1961) The genus *Tilletia*. Washington State University Press, Pullman

Eberhardt U, Schütz N, Krause C, Beker HJ (2018) *Hebelomina*(Agaricales) revisited and abandoned. Plant Ecol Evol 151:96–109

Ebihara A (2016) The standard of ferns and lycophytes in Japan I. Gakken Plus, Tokyo

Ekowati N, Yuniati NI, Hernayanti H, Ratnaningtyas NI (2018) Antidiabetic potentials of button mushroom (*Agaricus bisporus*) on Alloxan-induced diabetic rats. Biosaintifika J Biol Biol Educ 10:655–662

Eliescu A, Georgescu AA, Nicolescu CM, Bumbac M, Cioateră N, Mureseanu M, Buruleanu LC (2020) Biosorption of Pb(II) from aqueous solution using mushroom (*Pleurotus ostreatus*) biomass and spent mushroom substrate. Anal Lett 53:2292–2319

Elliott WT (1922) Some observations on the mycophagous propensities of slugs. Trans Br Mycol Soc 8:84–90

Elliott TF, Trappe JM (2018) A worldwide nomenclature revision of sequestrate *Russula* species. Fungal Syst Evol 1:229–242

Engler A, Prantl KAE (1900) Die Natürlichen Pflanzenfamilien nebst ihren Gattungen und wichtigeren Arten. W. Engelmann, Leipzig

Eriksson J (1958) Studies of the Swedish Heterobasidiomycetes and Aphyllophorales with special regard to the familiy Corticiaceae. Almqvist & Wiksells, Uppsala

Eriksson J, Ryvarden L (1973) The Corticiaceae of North Europe, vol 2. *Aleurodiscus-Confertobasidium*. Fungiflora, Oslo

Eriksson J, Ryvarden L (1976) The Corticiaceae of North Europe, vol. 4. *Hyphodermella-Mycoacia*. Fungiflora, Oslo

Eriksson J, Hjortstam K, Ryvarden L (1981) The Corticiaceae of North. Europe 6:1048–1276

Ertz D, Lawrey JD, Sikaroodi M, Gillevet PM, Fischer E, Killmann D, Sérusiaux E (2008) A new lineage of lichenized basidiomycetes inferred from a two-gene phylogeny: the Lepidostromataceae with three species from the tropics. Am J Bot 95:1548–1556

Estrada-Torres A, Gaither TW, Miller D, Lado C, Keller HW (2005) The myxomycete genus *Schenella*: Morphological and DNA sequence evidence for synonymy with the gasteromycete genus *Pyrenogaster*. Mycologia 37:139–149

Fan L-F, Wu Y-D, Wu F, Dai Y-C (2021) *Calocera tibetica* sp. nov. (Dacrymycetaceae, Dacrymycetales) from southwestern China. Phytotaxa 500:133–141. https://doi.org/10.11646/phytotaxa.500.2.6

Fangfuk W, Fukuda M, Yamada A, Petchang R, To-anun C (2010) Identification of Japanese Astraeus, based on morphological and phylogenetic analyses. Mycoscience 51(4):291–299

Farr DF, Rossman AY (2015) Fungal Databases. Systematic Mycology and Microbiology Laboratory, ARS, USDA. http://nt.ars-grin.gov/fungaldatabases/

Fayod V (1889) Prodrome d'une histoire naturelle des Agaricinées. Annls Sci Nat Bot Sér VII 9:181–411

Fell JW (1995) rDNA targeted oligonucleotide primers for the identification of pathogenic yeasts in a polymerase chain reaction. J Ind Microbiol Biotechnol 14(6):475–477

Fell JW, Johnson EA (2011) Phaffia M.W. Miller, Yoneyama & Soneda, 1976. In: Kurtzman CP, Fell JW, Boekhout T (eds) The yeasts, a taxonomic study, 5th edn. Elsevier, Amsterdam, pp 1853–1855

Fell JW, Scorzetti G (2004) Reassignment of the basidiomycetous yeasts *Trichosporon pullulans* to *Guehomyces pullulans* gen. nov., comb. nov. and *Hyalodendron lignicola* to *Trichosporon lignicola* comb. nov. Int J Syst Evol Microbiol 54(3):995–998. https://doi.org/10.1099/ijs.0.03017-0

Fell JW, Hunter IL, Tallman AS (1973) Marine basidiomycetous yeasts (*Rhodosporidium* spp. n.) with tetrapolar and multiple allelic bipolar mating systems. Can J Microbiol 19:643–657

Fell JW, Roeijmans H, Boekhout T (1999) Cystofilobasidiales, a new order of basidiomycetous yeasts. Int J Syst Evol Microbiol 49:907–913

Fell JW, Boekhout T, Fonseca A, Scorzetti G, Statzell-Tallman A (2000) Biodiversity and systematics of basidiomycetous yeasts as determined by large-subunit rDNA D1/d2 domain sequence analysis. Int J Syst Evol Microbiol 50:1351–1371

Feng B, Xu J, Wu G, Zeng N-K, Li Y-C, Tolgor B, Kost GW, Yang Z-L (2012) DNA sequence analyses reveal abundant diversity, endemism and evidence for Asian origin of the porcini mushrooms. PLoS ONE 7(5):e37567

Feng W-L, Jin Q-L, Shen Y-Y, Wei H-L, Cai W-M (2023) Breeding new cultivars of *Flammulina filiformis* 'Zhejin 102', Lentinula edodes 'L901' and *Hericium erinaceus* 'Zhelinhou No. 2.' Mycosystema 42(10):2152–2156.https://doi.org/10.13346/j.mycosystema.220495

Fernández NV, Mestre MC, Marchelli P, Fontenla SB (2011) Yeast and yeast-like fungi associated with dry indehiscent fruits of *Nothofagus nervosa* in Patagonia, Argentina. FEMS Microbiol Ecol 89:179–192

Fiasson JL (1982) Distribution of styrylpyrones in the basidiocarps of various Hymenochaetaceae. Biochem Syst Ecol 10(4):289–296

Fiasson JL, Niemelä T (1984) The Hymenochaetales: a revision of the European poroid taxa. Karstenia 24:14–28

Findley K, Oh J et al (2013) Topographic diversity of fungal and bacterial communities in human skin. Nature 498(7454):367–370. https://doi.org/10.1038/nature12171

Firenzuoli F, Gori L, Lombardo G (2008) The medicinal mushroom *Agaricus blazei* Murrill: review of literature and pharmaco-toxicological problems. Evid Based Complement Altern Med 5:3–15

Fischer E (1898) Phallineae. In: Engler A, Prantl K (eds) Die natürlichen Pflanzenfamilien. Teil 1. Abteilung 1**. W. Engelmann, Leipzig, pp 276–296

Fischer E (1899) Hymenogastrineae. In: Engler A, Prantl K (eds) Die natürlichen Pflanzenfamilien. Teil 1. Abteilung 1**. W. Engelmann, Leipzig

Fischer E (1933) Gastromyceteae. In: Engler A, Prantl K, Harms H (eds) Die Natürlichen Pflanzenfamilien. Engelmann, Leipzig

Floudas D, Hibbett DS (2015) Revisiting the taxonomy of *Phanerochaete* (Polyporales, Basidiomycota) using a four gene dataset and extensive ITS sampling. Fungal Biol 119(8):679–719

Floudas D, Binder M, Riley R et al (2012) The Paleozoic origin of enzymatic lignin decomposition reconstructed from 31 fungal genomes. Science 336:1715–1719. https://doi.org/10.1126/science.1221748

Floudas D, Held BW, Riley R, Nagy LG, Koehler G, Ransdell AS, Younus H, Chow J, Chiniquy J, Lipzen A, Tritt A, Sun H, Haridas S, LaButti K, Ohm RA, Kües U, Blanchette RA, Grigoriev IV, Minto RE, Hibbett DS (2015) Evolution of novel wood decay mechanisms in Agaricales revealed by the genome sequences of*Fistulina hepatica* and *Cylindrobasidium torrendii*. Fungal Genet Biol 76:78–92. https://doi.org/10.1016/j.fgb.2015.02.002

Flyen A-C, Thuestad AE (2023) A review of fungal decay in historic wooden structures in polar regions. Conserv Manag Archaeol Sites 1–33. https://doi.org/10.1080/13505033.2022.2156145

Fogel R, Trappe JM (1978) Fungus consumption (mycophagy) by small mammals. Northwest Sci 52(1):1–31

Fonseca A (1992) Utilization of tartaric acid and related compounds by yeasts: taxonomic implications. Can J Microbiol 38:1242–1251

Fonseca A, Inácio J (2006) Phylloplane yeast. In: Rosa CA, Peter G (eds) The yeast handbook Biodiversity and ecophysiology of yeast. Springer, Berlin

Fonseca A, Boekhout T, Fell JW (2011) Cryptococcus Vuillemin (1901). In: Kurtzman CP, Fell JW, Boekhout T (eds) The yeasts, a taxonomic study, 5th edn. Elsevier, Amsterdam

Frank JL, Coffan RA, Southworth D (2010) Aquatic gilled mushrooms: *Psathyrella* fruiting in the Rogue River in Southern Oregon. Mycologia 102(1):93–107.https://doi.org/10.3852/07-190

Fries EM (1815–1818) Observationes mycologicae. sumptibus G. Bonnieri, Havniae

Fries EM (1821) Systema mycologicum, vol. 1. Ex Officina Berlingiana, Lundae

Fries EM (1822) Systema mycologicum. Officina Berlingiana, Lund

Fries EM (1825) Systema orbis vegetabilis. Typographia academica, Lund

Fries EM (1828) Elenchus Fungorum vol. 1–2. Sumptibus Ernesti Mauritii, Gryphiswaldiae

Fries EM (1838) Epicrisis systematis mycologici. e Typographia Academica, Upsaliae

Fries EM (1851) Novae symbolae mycologicae, vol. 1. Excudit CA Leffler Reg Acad Typographus, Upsaliae

Fries EM (1855) Novae symbolae mycologicae, vol. 2. Nova Acta Regii Societatis Scientia Upsaliensis 3:17–136

Fries EM (1874) Hymenomycetes Europaei. Offinina Berlngiana, Upsaliae

Fröde R, Bröckelmann M, Steffan B, Steglich W, Marumoto R (1995) A novel type of triterpenoid quinone methide pigment from the toadstool *Russula flavida* (Agaricales). Tetrahedron 51(9):2553–2560

Fuentes-Davila G (1996) Karnal bunt of wheat. In: Wilcoxson RD, Saari EE (eds) Bunt and smut diseases of wheat: concepts and methods of disease management. CIMMYT, Mexico, pp 26–32

Fukasawa Y (2021) Ecological impacts of fungal wood decay types: a review of current knowledge and future research directions. Ecol Res 36(6):910–931

Fu YP, Dai YT, Chethana KW, Li ZH, Sun L, Li CT, Yu HL, Yang RH, Tan Q, Bao DP, Deng YJ (2022) Large-scale genome investigations reveal insights into domestication of cultivated mushrooms. Mycosphere 1(13):86–133

Gafforov Y, Rašeta M, Rapior S, Yarasheva M, Wang X, Zhou L, Wan-Mohtar WAAQI, Zafar M, Lim YW, Wang M, Abdullaev B, Bussmann RW, Zengen G, Chen JJ (2023) Macrofungi as medicinal resources in Uzbekistan: biodiversity, ethnomycology, and ethnomedicinal practices. J Fungi 9(9):922. https://doi.org/10.3390/jof9090922

Galappaththi MCA, Dauner L, Madawala S, Karunarathna SC (2021) Nutritional and medicinal benefits of oyster (*Pleurotus*) mushrooms: a review. Fungal Biotec 1:65–87. https://doi.org/10.5943/funbiotec/1/2/5

Gamal A, Elshaer M et al (2022) The mycobiome: cancer pathogenesis, diagnosis, and therapy. Cancers 14(12):2875. https://doi.org/10.3390/cancers14122875

Gan T, Luo T, Pang K et al (2021) Cryptic terrestrial fungus-like fossils of the early Ediacaran period. Nat Commun 12(1):641

Gandia A, van den Brandhof JG, Appels FV, Jones MP (2021) Flexible fungal materials: shaping the future. Trends Biotechnol 39(12):1321–1331

Gao C, Zhang Y, Shi N-N, Zheng Y, Chen L et al (2015) Community assembly of ectomycorrhizal fungi along a subtropical secondary forest succession. New Phytol 205:771–785. https://doi.org/10.1111/nph.13068

Garcia J, Costa VM, Carvalho A, Baptista P, de Pinho PG, de Lourdes BM, Carvalho F (2015)*Amanita phalloides* poisoning: mechanisms of toxicity and treatment. Food Chem Toxicol 86:41–55. https://doi.org/10.1016/j.fct.2015.09.008

García-Sandoval R, Wang Z, Binder M, Hibbett DS (2011) Molecular phylogenetics of the Gloeophyllales and relative ages of clades of Agaricomycotina producing a brown rot. Mycologia 103:510–524

Gardes M, Dahlberg A (1996) Mycorrhizal diversity in arctic and alpine tundra: an open question. New Phytol 133(1):147–157

Gareth Jones EB, Pang K-L, Abdel-Whag MA, Scholz B, Hyde KV, Boekhout T, Ebel R, Rateb ME, Henderson L, Skayaroj J, Suetrong S, Dayarathne MC, Kumar V, Raghukumar S, Sridhar KR, Bahkali AHA, Gleason FH, Norphanphoun C (2019) An online resource for marine fungi. Fungal Divers 96:347–433

Garnica S, Riess K, Schön ME, Oberwinkler F, Setaro SD (2016) Divergence times and phylogenetic patterns of Sebacinales, a highly diverse and widespread fungal lineage. PLoS ONE 11:e0149531

Garnica S, Sandoval-Leiva P, Riess K (2021) Phylogenetic relationships in the genus *Podoserpula* and description of *P. aliweni*, a new species from Chile. Mycologia 113(5):1110–1121. https://doi.org/10.1080/00275514.2021.1927422

Gäumann E (1926) Vergleichende Morphologie Der Pilze. Verlag Von Gustav Fischer, Jena

Geml J, Davis DD, Geiser DM (2005a) Systematics on the genus *Sphaerobolus* based on molecular and morphological data, with the description of *Sphaerobolus ingoldii* sp. nov. Mycologia 97:680–694

Geml J, Davis DD, Geiser DM (2005b) Phylogenetic analyses reveal deeply divergent species lineages in the genus *Sphaerobolus* (Phallales: Basidiomycota). Mol Phylogenet Evol 35:313–322

Ghobad-Nejhad M, Nilsson RH, Hallenberg N (2010) Phylogeny and taxonomy of the genus *Vuilleminia* (Basidiomycota) based on molecular and morphological evidence, with new insights into Corticiales. Taxon 59:1519–1534

Ghobad-Nejhad M, Langer E, Nakasone K, Diederich P, Nilsson RH, Rajchenberg M, Ginns J (2021) Digging up the roots: taxonomic and phylogenetic disentanglements in *Corticiaceae* s.s. (*Corticiales, Basidiomycota*) and evolution of nutritional modes. Front Microbiol 12:704802

Giachini AJ, Oliveira VL, Castellano MA, Trappe JM (2000) Ectomycorrhizal fungi in *Eucalyptus* and *Pinus* plantations in southern Brazil. Mycologia 92(6):1166–1177

Giachini AJ, Hosaka K, Nouhra E et al (2010) Phylogenetic relationships of the Gomphales based on nuc-25S-rDNA, mit-12S-rDNA, and mit-atp6-DNA combined sequences. Fungal Biol 114:224–234. https://doi.org/10.1016/j.funbio.2010.01.002

Gilbert E-J (1931) Les Livres du Mycologue, Tome I-IV. Tom. III, Les Bolets: 83. Librairie E. Le François, Paris

Gilbertson RL, Ryvarden L (1986) North American polypores. Fungiflora, Oslo

Gilbertson RL, Ryvarden L (1987) North American Polypores. Megasporoporia-Wrigthoporia. vol 2: Fungiflora. Noruega, Oslo

Gill M, Steglich W (1987) Pigments of fungi (Macromycetes). Prog Chem Org Nat Prod 51:1–317

Gillet CC (1878) Champignons (Fungi, Hymenomycetes) qui croissant en France. Description et iconographie. JB Baillière, Paris

Ginns J (1986) The genus *Syzygospora* (Heterobasidiomycetes: Syzygosporaceae). Mycologia 78(4):619–636

Ginns J (1998) Genera of the North American Corticiaceae sensu lato. Mycologia 90:1–35

Ginns J, Lefebvre MNL (1993) Lignicolous corticioid fungi (Basidiomycota) of North America. Mycol Soc Am Mycol Memoir 19:1–247

Girlanda M, Selosse M-A, Cafasso D, Brilli F, Delfine S, Fabbian R, Ghignone S, Pinelli R, Segreto R, Loreto F, Cozzolino S, Perotto S (2005) Inefficient photosynthesis in the Mediterranean orchid Limodorum abortivum is mirrored by specific association to ectomycorrhizal Russulaceae. Mol Ecol 15:491–504

Goates BJ (1996) Common bunt and dwarf bunt. In: Wilcoxson RD, Saari EE (eds) Bunt and smut diseases of wheat: concepts and methods of disease management. CIMMYT, Mexico, pp 12–25

Góes-Neto A, Groposo C (2005) Hymenochaetales. Hymenochaetoid clade. Hymenochaetaceae. Version 10 June 2005. http://tolweb.org/Hymenochaetoid_clade/20547

Gokhale AA (1972) Studies on the genus *Tilletiopsis*. Nova Hedwigia 23:795–809

Golubev WI (2011) Mastigobasidium Golubev, 1999. In: Kurtzman CP, Fell JW, Boekhout T (eds) The yeasts, a taxonomic study, 5th edn. Elsevier, Amsterdam, pp 145–1497

González A, Cruz M, Losoya C, Nobre C, Loredo A, Rodríguez R, Contreras J, Belmares R (2020) Edible mushrooms as a novel protein source for functional foods. Food Funct 11:7400–7414. https://doi.org/10.1039/d0fo01746a

González-Ávila PA, Luna-Vega I, García-Sandoval R et al (2016) Distributional patterns of the order Gomphales (Fungi: Basidiomycota) in Mexico. Trop Conserv Sci 9(4):1940082916667140. https://doi.org/10.1177/1940082916667140

González-Ávila PA, Martínez-González CR, Alvarado-Sizzo H et al (2020) Three new combinations in *Gloeocantharellus* (Gomphales, Agaricomycetes) from Mexico based on molecular evidence. Phytotaxa 447(1):42–50. https://doi.org/10.11646/phytotaxa.447.1.4

Goodell B, Winandy JE, Morrell JJ (2020) Fungal degradation of wood: emerging data, new insights and changing perceptions. Coatings 10(12):1210

Gorjón SP, Greslebin AG, Rajchenberg MP (2011) Notes on *Amylocorticiellum* (Amylocorticiales, Basidiomycota), with some new combinations. Mycotaxon 116:283–293. https://doi.org/10.5248/116.283

Gorjón SP, Greslebin AG, Rajchenberg M (2012) *Uncobasidium roseocremeum* sp. nov. and other corticioid basidiomycetes from Patagonian Andes of Argentina. Mycotaxon 121:349–364

Goyette S, Spirin V, Spribille T, Goyette S (2023) Systemic infection of *Bryoria* (Lecanoromycetes, Ascomycota) by *Athelia* (Agaricomycetes, Basidiomycota) in western North America. Mycologia 115:299–316

Gray SF (1821) A natural arrangement of British plants, vol I. Baldwin Cradock and Joy, London

Greis VH (1935) *Nidulariopsis melanocarpa* Greis nov. gen. spec. und eine neue Form von Sphaerobolus iowensis. Hedwigia 75:255–266

Greville RK (1825) Scottish cryptogamic flora, vol III. MacLachlan & Stewart, Edinburgh

Grewe F, Ametrano C, Widhelm TJ, Leavitt S, Distefano I, Polyiam W, Pizarro D, Wedin M, Crespo A, Divakar PK, Lumbsch HT (2020) Using target enrichment sequencing to study the higher-level phylogeny of the largest lichen-forming fungi family: Parmeliaceae (Ascomycota). IMA Fungus 11:1

Grimm GW, Kapli P, Bomfleur B, McLoughlin S, Renner S (2015) Using more than the old fossils: dating Osmundaceae with three Bayesian clock approaches. Syst Biol 64:396–405

Gruhn G, Alvarado P, Hallenberg N, Roy M, Courtecuisse R (2018) Contribution to the taxonomy of Sistotremastrum (Trechisporales, Basidiomycota) and the description of two new species, *S. Fibrillosum* and *S. Aculeocrepitans*. Phytotaxa 379(1):27–38

Guarnaccia V, Remolif GM, Nari L, Gualandri V, Angeli D, Oettl S, Dijksterhuis J, Boekhout T, Spadaro D (2024) Characterization of fungal species involved in white haze disorder on apples in Northern Italy and description of *Golubevia mali* sp. nov. and *Entyloma mali* sp. nov. Postharvest Biol Technol 209:112678

Guého-Kellermann E, Boekhout T, Begerow D (2010) Biodiversity, phylogeny and ultrastructure. In: Boekhout T, Mayser P, Guého-Kellermann E, Velegraki A (eds) *Malassezia* and the skin: science and clinical practice. Springer, Berlin, pp 1–16

Guého-Kellermann E, Batra R, Boekhout T (2011) Malassezia Baillon, 1889. In: Kurtzman C, Fell JW, Boekhout T (eds) The yeasts, a taxonomic study, vol 3, 5th edn. Elsevier, Amsterdam, pp 1807–1832

Guevara-Guerrero G, Castellano MA, García Jiménez J, Cázares González E, Trappe JM (2008) *Hysterangium* (Hysterangiales, Hysterangiaceae) del norte de México. Revista Mexicana De Micología 28:95–100

Guevara-Guerrero G, Montalvo Martínez MA, Gómez Reyes VM, Ge ZW, Castellano MA et al (2021) New molecular data in the truffle-like fungus, *Aroramyces herrerae*, reveal a novel cryptic ancestral taxon, *Pterosporomyces herrerae* gen. nov. & comb. nov. (Trappeacea, Phallales). Glob J Sci Front Res 21(3):1–6

Guillot J, Bond R (2020) *Malassezia* yeasts in veterinary dermatology: an updated overview. Front Cell Infect Microbiol 10:79. https://doi.org/10.3389/fcimb.2020.00079

Guo L (2015) Exobasidiales Septobasidiales. In: Flora Fungorum Sinicorum, vol 50. Science Press, Beijing, p 99

Gupta N, Dubey A, Prasad P, Roy M (2015) Formulation and evaluation of herbal fairness cream comprising hydroalcoholic extracts of *Pleurotus ostreatus*, *Glycyrrhiza glabra* and *Camellia sinensis*. UK J Pharm Biosci 3:41

Gupta S, Summuna B, Gupta M, Annepu SK (2018) Edible mushrooms: cultivation, bioactive molecules, and health benefits. In: Mérillon JM, Ramawat K (eds) Bioactive molecules in food: reference series in phytochemistry. Springer, Cham. https://doi.org/10.1007/978-3-319-54528-8_86-1

Gurgel FE, Silva BDB, Baseia IG (2008) New records of *Scleroderma* from Northeastern Brazil. Mycotaxon 105:399–405

Guzmán G (1971) A new delimitation and probable phylogeny of the family Sclerodermataceae. Trans Br Mycol Soc 56(2):195–199

Habtemariam S (2019) The chemistry, pharmacology and therapeutic potential of the edible mushroom *Dictyophora indusiata* (Ventex. Pers.) Fischer (synn. *Phallus indusiatus*). Biomedicines 7:98

Haeckel E (1894) Systematische Phylogenie. Systematische Phylogenie der Protisten und Pflanzen, vol 1. G. Reimer Verlag, Berlin

Haelewaters D, Dirks AC, Kappler LA, Mitchell JK (2018) A preliminary checklist of fungi at the Boston Harbor Islands. Northeast Nat 25:45–76

Haelewaters D, Dima B, Abdel-Hafiz BII, Abdel-Wahab MA, Abul-Ezz SR, Acar I, Aguirre-Acosta E, Aime MC, Aldemir S, Ali M, Ayala-Vásquez O, Bakhit MS, Bashir H, Battistin E, Bendiksen E, Castro-Rivera R, Çolak ÖF, De Kesel A, de la Fuente JI, Dizkırıcı A, Hussain S, Jansen GM, Kaygusuz O, Khalid AN, Khan J, Kiyashko AA, Larsson E, Martínez-González CR, Morozova OV, Niazi AR, Noordeloos ME, Pham THG, Popov ES, Psurtseva NV, Schoutteten N, Sher H, Türkekul İ, Verbeken A, Ahmad H, Afshan NS, Christe P, Fiaz M, Glaizot O, Liu J, Majeed J, Markotter W, Nagy A, Nawaz H, Papp V, Péter Á, Pfliegler WP, Qasim T, Riaz M, Sándor AD, Szentiványi T, Voglmayr H, Yousaf N, Krisai-Greilhuber I (2020) Fungal systematics and evolution: FUSE 6. Sydowia 72:231–356

Hagen F, Khayhan K, Theelen B, Kolecka A, Polacheck I, Sionov E, Falk R, Parnmen S, Lumbsch HT, Boekhout T (2015) Recognition of seven species in the *Cryptococcus gattii*/*Cryptococcus neoformans* species complex. Fungal Genet Biol 78:16–48

Hamamoto M (2011a) Bannoa Hamamoto (2002). In: Kurtzman CP, Fell JW, Boekhout T (eds) The yeasts, a taxonomic study, 5th edn. Elsevier, Amsterdam, pp 1383–1386

Hamamoto M (2011b) Erythrobasidium Hamamoto, Sugiyama, Komagat (1991). In: Kurtzman CP, Fell JW, Boekhout T (eds) The yeasts, a taxonomic study, 5th edn. Elsevier, Amsterdam, pp 1433–1435

Hamamoto M, Sugiyama J, Komagata K (1988) Transfer of *Rhodotorula hasegawae* to a new basidiomycetous genus *Erythrobasidium*as *Erythrobasidium hasegawae* comb. nov. J Gener Appl Microbiol Tokyo 34(3):279–287

Hamamoto M, Boekhout T, Nakase T (2011) Sporobolomyces Kluyver & van Niel (1924). In: Kurtzman CP, Fell JW, Boekhout T (eds) The yeasts, a taxonomic study, 5th edn. Elsevier, Amsterdam, pp 1929–1990

Hao Y-J, Qui J, Yang Z-H (2014) *Cibaomyces*, a new genus of Physalacriaceae from East Asia. Phytotaxa 162:198–210. https://doi.org/10.11646/phytotaxa.162.4.2

Hapsari R, Elya B, Amin J (2012) Formulation and evaluation of antioxidant and tyrosinase inhibitory effect from gel containing the 70% ethanolic *Pleurotus ostreatus* extract. Int J Med Arom Plants 2:135–140

Harmon AD, Weisgraber KH, Weiss U (1979) Preformed azulene pigments of *Lactarius indigo* (Schw.) Fries (Russulaceae, Basidiomycetes). Cell Mol Life Sci 36(1):54–56

Hashimoto I (2003) Wild food lexicon, Japan: a unique photographic guide to finding, cooking, and eating wild plants, ferns, and lichen. Kashiwa Shobo, Tokyo

Hashimoto Y, Fukukawa S, Kunishi A, Suga H, Richard F, Sauve M, Selosse M-A (2012) Mycoheterotrophic germination of *Pyrola asarifolia* dust seeds reveals convergences with germination in orchids. New Phytol 195:620–630

Haskins RH, Spencer JFT (1967) *Trichosporonoides oedocephalis* n. gen., n. sp. I. Morphology, development, and taxonomy. Can J Bot 53:1139–1148

Hattori T (2003) Type studies of the polypores described by EJH Corner from Asia and West Pacific Areas. VI. Species described in *Tyromyces* (3), *Cristelloporia*, *Grifola*, *Hapalopilus*, *Heterobasidion*, *Ischnoderma*, *Loweporus*, and *Stecchericium*. Mycoscience 44(6):453–463

Hauerslev K (1999) New and rare species of Heterobasidiomycetes. Mycotaxon 72:465–486

Haug I, Weiss M, Homeier J, Oberwinkler F, Kottke I (2005) Russulaceae and Thelephoraceae form ectomycorrhizas with members of the Nyctaginaceae (Caryophyllales) in the tropical mountain rain forest of southern Ecuador. New Phytol 165(3):923–936

Hawksworth DL, Grube M (2020) Lichens redefined as complex ecosystems. New Phytol 227(5):1281

Hawksworth DL, Lücking R (2017) Fungal diversity revisited: 2.2 to 3.8 million species. Microbiol Spectrum 5(4):FUNK-0052-2016

Hawksworth DL, Kirk PM, Sutton BC, Pegler DN (1995) Dictionary of Fungi. International Mycological Institute CAB International, Wallingford

Hay RJ, Midgley G (2010) Introduction: *Malassezia* yeasts from a historical perspective. In: Boekhout T, Mayser P, Guého-Kellermann E, Velegraki A (eds) *Malassezia* and the skin: Science and clinical practice. Springer, Berlin, pp 1–16

Hayes JP, Cross SP, McIntire PW (1986) Seasonal variation in mycophagy by the western red-backed vole, *Clethrionomys californicus*, in southwestern Oregon. Northwest Sci 60(4):250–257

He S-H, Li H-J (2013) *Veluticeps microspora* sp. nov. and*V. ambigua* new to Asia with a preliminary phylogenetic study on the genus. Mycol Progress 12:367–374

He Z-M, Yang Z-L (2021) A new clitocyboid genus Spodocybe and a new subfamily Cuphophylloideae in the family Hygrophoraceae (Agaricales). MycoKeys 79:129

He S-H, Vlasák J, Dai Y-C (2014) *Hispidaedalea* gen. nov. and*Griseoporia taiwanense* sp. nov. (Gloeophyllales, Basidiomycota) based on morphological and molecular characters. Mycol Progress 13:833–839

He M-Q, Zhao R-L, Hyde KD et al (2019a) Notes, outline and divergence times of Basidiomycota. Fungal Divers 99:105–367

He J, Duan K-T, Li Z-H, Ai H-L, Feng T, Liu J-K (2019b) Vibralactone Z4, the first chain-like vibralactone derivative from cultures of the basidiomycete *Boreostereum vibrans*. Nat Prod Res 33(19):2744–2749

He X, Shi ZJ, Zhao C-L (2020) Morphological and molecular identification of two new species of*Tubulicrinis* (Hymenochaetaceae, Hymenochaetales) from southern China. Mycoscience 61:184–189

He M-Q, Zhao R-L, Liu D-M et al (2022) Species diversity of basidiomycota. Fungal Divers 114(1):281–325

He Z-M, Chen Z-H, Bau T, Wang G-S, Yang Z-L (2023a) Systematic arrangement within the family Clitocybaceae (Tricholomatineae, Agaricales): phylogenetic and phylogenomic evidence, morphological data and muscarine-producing innovation. Fungal Divers 27:1–47

He K-X, Cheng Y-F, Yun S-J, Cheng F-E, Cao J-L, Feng C-P (2023b) The regulatory mechanism of*Sparassis latifolia* polysaccharides in response to immune mediated by CD8+T cells in mice. Mycosystema 42(5):1163–1174

Heads SW, Miller AN, Crane J, Leland TMJ, Ruffatto DM, Methven AS, Raudabaugh DB, Wang Y (2017) The oldest fossil mushroom. PLoS ONE 12(6):e0178327

Held BW, Salomon CE, Blanchette RA (2020) Diverse subterranean fungi of an underground iron ore mine. PLoS ONE 15:e0234208. https://doi.org/10.1371/journal.pone.0234208

Hemmes DE, Desjardin DE (2011) Earthstars (*Geastrum*,*Myriostoma*) of the Hawaiian Islands including two new species, *Geastrum litchiforme* and *Geastrum reticulatum*. Pac Sci 65:477–496

Hendrichs MR, Oberwinkler F (2003) The Cryptobasidiaceae of tropical Central and South America. Sydowia 55:33–64

Hendrichs M, Begerow D, Bauer R, Oberwinkler F (2005) The genus *Anthracoidea* (Basidiomycota, Ustilaginales): a molecular phylogenetic approach using LSU rDNA sequences. Mycol Res 109:31–40

Henk DA. (2005) New species of *Septobasidium* from southern Costa Rica and the southeastern United States. Mycologia 97(4):908-913

Henk DA, Vilgalys R (2007) Molecular phylogeny suggests a single origin of insect symbiosis in the Pucciniomycetes with support for some relationships within the genus Septobasidium. Am J Bot 94(9):1515–1526

Hennings P (1898) Exobasidiineae. In: Engler A, Prantl K (eds) Die natürlichen Pflanzenfamilien. Teil 1. Abteilung 1**. W. Engelmann, Leipzig, pp 103–105

Hennings P (1900) Hymenomycetineae. Die Natürlichen Pflanzenfamilien, vol. I, 1a. Engelmann, Leipzig

Hernández Caffot ML, Robledo G, Domínguez de Toledo LS (2013) Gasteroid mycobiota (Basidiomycota) from Polylepis australis woodlands of central Argentina. Mycotaxon 123:491

Herz S, Weber RW, Anke H, Mucci A, Davoli P (2007) Intermediates in the oxidative pathway from torulene to torularhodin in the red yeasts *Cystofilobasidium infirmominiatum* and *C. capitatum* (Heterobasidiomycetes, Fungi). Phytochemistry 68(20):2503–2511. https://doi.org/10.1016/j.phytochem.2007.05.019

Hesler LR, Smith AH (1963) North American species of *Hygrophorus*. Univ Tennessee Press, Knoxville

Hesse R (1891) Hypogaeen Deutschlands 1. Die Hymenogastreen. Halle a. S. Verlag von Ludw, Hofstetter

Hibbett DS (2004) Trends in morphological evolution in homobasidiomycetes inferred using maximum likelihood: a comparison of binary and multistate approaches. Syst Biol 53(6):889–903

Hibbett DS (2006) A phylogenetic overview of the Agaricomycotina. Mycologia 98(6):917–925

Hibbett DS, Binder M (2002) Evolution of complex fruiting-body morphologies in homobasidiomycetes. Proc R Soc B 269:1963–1969. https://doi.org/10.1098/rspb.2002.2123

Hibbett DS, Donoghue MJ (1995) Progress toward a phylogenetic clasification of the Polyporaceae through parsimony analysis of mitochondrial ribosomal DNA sequences. Can J Bot 73:S853–S861

Hibbett DS, Donoghue MJ (2001) Analysis of character correlations among wood decay mechanisms, mating systems and substrate ranges in homobasidiomycetes. Syst Biol 50(2):215–242

Hibbett DS, Thorn RG (2001) Basidiomycota: Homobasidiomycetes. In: McLaughlin DJ, McLaughlin EG, Lemke PA (eds) The Mycota. vol VII. Part B. Systematics and evolution. Springer, Berlin

Hibbett DS, Pine EM, Langer E, Langer G, Donoghue MJ (1997) Evolution of gilled mushrooms and puffballs inferred from ribosomal DNA sequences. Proc Natl Acad Sci USA 94:12002–12006

Hibbett DS, Gilbert LB, Donoghue MJ (2000) Evolutionary instability of ectomycorrhizal symbioses in basidiomycetes. Nature 407(6803):506–508

Hibbett DS, Binder M, Wang Z, Goldman Y (2003) Another Fossil Agaric from Dominican Amber. Mycologia 95(4):685–687

Hibbett DS, Binder M, Bischoff JF et al (2007) A higher-level phylogenetic classification of the Fungi. Mycol Res 111(5):509–547

Hibbett DS, Bauer R, Binder M, Giachini AJ, Hosaka K, Justo A, Larsson E, Larsson KH, Lawrey JD, Miettinen O, Nagy LG, Nilsson RH, Weiss M, Thorn RG (2014) 14 Agaricomycetes. In: McLaughlin D, Spatafora J (eds) Systematics and evolution. The Mycota (A comprehensive treatise on fungi as experimental systems for basic and applied research), vol 7A. Springer, Berlin, pp 373–429

Hilszczanska D, Sierota Z (2006) Persistence of ectomycorrhizas by *Thelephora terrestris* on outplanted Scots pine seedlings. Acta Mycol 41:313–318

Hirota M, Morimura K, Shibata H (2002) Anti-inflammatory compounds from the bitter mushroom. Sarcodon Scabrosus Biosci Biotechnol Biochem 66(1):179–184. https://doi.org/10.1271/bbb.66.179

Hjortstam K (1987) Studies in tropical Corticiaceae (Basidiomycetes) VII. Specimens from East Africa, collected by L. Ryvarden II. Mycotaxon 28:19–37

Hjortstam K, Larsson KH (1976) *Pseudoxenasma*, a new genus of Corticiaceae (Basidiomycetes). Mycotaxon 4(1):307–311

Hjortstam K, Larsson KH (1987) Additions to *Phlebiella*(Corticiaceae, Basidiomycetes) with notes on *Xenasma* and *Sistotrema*. Mycotaxon 29:315–319

Hjortstam K, Ryvarden L (2007) Studies in corticioid fungi from Venezuela III (Basidiomycotina, Aphyllophorales). Synopsis Fungorum 23:56–107

Hjortstam K, Ryvarden L (2008) Some corticioid fungi (Basidiomycotina) from Ecuador. Syn Fung 25:14–27

Hodkinson BP, Moncada B, Lücking R (2014) Lepidostromatales, a new order of lichenized fungi (Basidiomycota, Agaricomycetes), with two new genera, *Ertzia* and*Sulzbacheromyces*, and one new species, *Lepidostroma winklerianum*. Fungal Divers 64:165–179. https://doi.org/10.1007/s13225-013-0267-0

Höhnel F (1916) Mykologisches. Österr Bot Z 66:94–112

Höhnel F (1924) Beitrag zur Kenntnis der Gattung *Cylindrosporium* Grev. Ann Mycol 22:191–203

Horak E (1968) Synopsis generum Agaricalium (Die Gattungstypen der Agaricales). Beiträge zur Kryptogamenflora der Schweiz, Band

Hosaka K (2005) Systematics, phylogeny, and biogeography of the Hysterangiales and related taxa (Phallomycetidae, Homobasidiomycetes). Dissertation, Oregon State University

Hosaka K (2014) Phylogenetic analyses of a truffle-like genus, *Boninogaster*, from Hahajima Island, the Bonin Islands, Japan. Bull Natl Museum Nat Sci Ser B 40:61–67

Hosaka K, Bates ST, Beever RE, Castellano MA, Colgan W III, Domínguez LS, Nouhra ER, Geml J, Giachini AJ, Kenney SR, Simpson NB (2006) Molecular phylogenetics of the gomphoid-phalloid fungi with an establishment of the new subclass Phallomycetidae and two new orders. Mycologia 98(6):949–959

Hosaka K, Castellano MA (2008) Molecular phylogenetics of Geastrales with special emphasis on the position of *Sclerogaster*. Bull Natl Museum Nat Sci Ser B 34:161–173

Hosaka K, Uno K (2012) A preliminary survey on larval diversity in mushroom fruitbodies. Bull Natl Museum Nat Sci Ser B 38(3):77–85

Hosaka K, Castellano MA, Spatafora JW (2008) Biogeography of Hysterangiales (Phallomycetidae, Basidiomycota). Mycol Res 112(4):448–462

Huang R-X, Chen J-Z, Wu J-R, Zhao C-L (2019) *Phlebiella ailaoshanensis* sp. nov. (Polyporales, Basidiomycota) described from China. Phytotaxa 419(1):105–109

Huang H-Y, Zhao J, Zhang P et al (2020) The genus *Clavariadelphus* (Clavariadelphaceae, Gomphales) in China. MycoKeys 70:89–121. https://doi.org/10.3897/mycokeys.70.54149

Hudson HJ, Ingold CT (1960) *Aquatic hyphomycetes* from Jamaica. Trans Br Mycol Soc 43:469–478

Hughes SJ, Cavalcanti WA (1983) *Janetia mangiferae* n.sp., and the *Johncouchia* n.gen. anamorph of *Septobasidium pilosum* from Brasil. Can J Bot 61:2224–2230

Humber RA (2008) Evolution of entomopathogenicity in fungi. J Invertebr Pathol 98:262–266

Humpert AJ, Muench EL, Giachini AJ et al (2001) Molecular phylogenetics of *Ramaria* and related genera: evidence from nuclear large subunit and mitochondrial small subunit rDNA sequences. Mycologia 93:465–477. https://doi.org/10.2307/3761733

Hussain S, Al-Kharousi M, Al-Muharabi MA et al (2022) Phylogeny of Agaricus subgenus *Pseudochitonia* with the description of a new section and a new species from Oman. Mycol Prog 21(8):72

Hwang JS, Song KS, Kim WG, Lee TH, Koshino H, Yoo ID (1997) Polyozellin, a new inhibitor of prolyl endopeptidase from *Polyozellus multiplex*. J Antibiot 50(9):773–777. https://doi.org/10.7164/antibiotics.50.773

Hyde KD, Bahkali AH, Moslem MA (2010) Fungi—an unusual source for cosmetics. Fungal Divers 43:1–9

Ianiri G, LeibundGut-Landmann S, Dawson TL (2022) *Malassezia*: a commensal, pathogen, and mutualist of human and animal skin. Annu Rev Microbiol 76:757–782.https://doi.org/10.1146/annurev-micro-040820-010114

Ingold CT (1972) Presidential Address. Sphaerobolus: the story of a fungus. Trans Br Mycol Soc 58:179–195

Ingold CT (1995) Products of teliospore germination in *Tilletia hyalospora*. Mycol Res 99:1247–1248

Irwin NA, Twynstra CS, Mathur V, Keeling PJ (2021) The molecular phylogeny of Chionaster nivalis reveals a novel order of psychrophilic and globally distributed Tremellomycetes (Fungi, Basidiomycota). PLoS ONE 16(3):e0247594

Ishihara A, Ide Y, Bito T, Ube N, Endo N, Sotome K, Maekawa N, Ueno K, Nakagiri A (2018) Novel tyrosinase inhibitors from liquid culture of *Neolentinus lepideus*. Biosci Biotechnol Biochem 82(1):22–30

Ito S (1964) Mycological flora of Japan, vol 3 Ascomycetes, No. 1 (Saccharomycetales, Cryptococcales, Taphrinales). Yokendo, Tokyo

Iwanski M, Rudawski M, Leski T (2006) Mycorrhizal associations of nursery grown scots pine (*Pinus sylvestris* L.) seedlings in Poland. Ann for Sci 63:715–723.https://doi.org/10.1051/forest:2006052

Iwatsuki K (1992) Wild plants of Japan: ferns and fern allies of Japan. Heibonsha Ltd., Tokyo

James TY, Stajich JE, Hittinger CT, Rokas A (2020) Toward a fully resolved fungal tree of life. Annu Rev Microbiol 74:291–313

Jančič S, Nguyen HDT, Frisvad J, Zalar P, Scheors H-J, Seifert KA, Gunde-Cimerman N (2015) A taxonomic revision of the *Wallemia sebi* species complex. PLoS ONE 10(5):e0125933

Jančič S, Frisvad JC, Kocev D, Gostinčar C, Džeroski S, Gunde-Cimerman N (2016) Production of secondary metabolites in extreme environments: food- and airborne Wallemia spp. produce toxic metabolites at hypersaline cnditions. PLoS ONE 11(12):e0169116

Jarosch M (2001) Zur molekylaren Systematik der Boletales: Coniophorineae, Paxillineae und Suillineae. Bibl Mycol 191:1–158

Jayawardena RS, Hyde KD, Jeewon R, Ghobad-Nejhad M, Wanasinghe DN, Liu N, Phillips AJ, Oliveira-Filho JR, da Silva GA, Gibertoni TB, Abeywikrama P (2019) One stop shop II: taxonomic update with molecular phylogeny for important phytopathogenic genera: 26–50 (2019). Fungal Divers 94:41–129

Jayawardena RS, Hyde KD, Chen YJ, Papp V, Palla B, Papp D, Bhunjun CS, Hurdeal VG, Senwanna C, Manawasinghe IS, Harischandra DL (2020) One stop shop IV: taxonomic update with molecular phylogeny for important phytopathogenic genera: 76–100 (2020). Fungal Divers 103:87–218

Ji J-X, Li Z, Li Y, Kakishima M (2022a) Phylogenetic approach for identification and life cycles of *Puccinia* (Pucciniaceae) species on *Poaceae* from northeastern China. Phytotaxa 533(1):1–48. https://doi.org/10.11646/phytotaxa.533.1.1

Ji J-X, Li Z, Li Y, Kakishima M (2022b) Phylogenetic approach for identification and life cycles of *Puccinia* (Pucciniaceae) species on *Carex* (Cyperaceae) from northeastern China. Phytotaxa 542(3):221–255. https://doi.org/10.11646/phytotaxa.542.3.1

Ji X, Sun Y-F, Wu D-M, Gao N, Cui B-K (2023) An updated phylogenetic assessment and taxonomic revision of Perenniporia sensu lato (Polyporales, Basidiomycota). J Fungi 9:173

Johansen I, Ryvarden L (1979) Studies in the Aphyllophorales of Africa 7. Some new genera and species in the Polyporacea. Trans Brit Mycol Soc 72(2):189–199

Jong SC, Birmingham JM, Pai SH (1991) Immuno-modulatory substances of fungal origin. J Immunol Immunopharmacol 11:788–881

Jülich W (1969) Über die Gattungen Piloderma gen. nov. und Subulicystidium Parm. (Corticiaceae, Aphyllophorales, Basidiomycetes). Berichte Der Deutschen Botanischen Gesellschaft 81:414–421

Jülich W (1972) Monographie der Athelieae (Corticiaceae, Basidiomycetes). Willdenowia, Beih

Jülich W (1978) A new lichenized *Athelia* from Florida. Persoonia 10:149–151

Jülich W (1981) Higher taxa of Basidiomycetes. Biblioth Mycol 85:1–185

Jülich W (1982) Basidiomycetes of south-east Asia 1. The genus *Paraphelaria*. Persoonia 11:397–406

Justo A, Hibbett DS (2011) Phylogenetic classification of *Trametes* (Basidiomycota, Polyporales) based on a five-marker dataset. Taxon 60:1567–1583

Justo A, Vizzini A, Minnis AM, Menolli N Jr, Capelari M, Rodríguez O, Malysheva E, Contu M, Ghignone S, Hibbett DS (2011a) Phylogeny of the *Pluteaceae* (Agaricales, Basidiomycota): taxonomy and character evolution. Fungal Biol 115(1):1–20

Justo A, Minnis AM, Ghignone S, Menolli N, Capelari M, Rodríguez O, Malysheva E, Contu M, Vizzini A (2011b) Species recognition in *Pluteus* and *Volvopluteus* (Pluteaceae, Agaricales): morphology, geography and phylogeny. Mycol Prog 10:453–479

Justo A, Miettinen O, Floudas D, Ortiz-Santana B, Sjökvist E, Lindner D, Nakasone K, Niemelä T, Larsson KH, Ryvarden L, Hibbett DS (2017) A revised family-level classification of the Polyporales (Basidiomycota). Fungal Biol 121(9):798–824

Kobata K, Kano S, Shibata H (1995) New lactarane sesquiterpenoid from the fungus *Russula emetica*. Biosci Biotechnol Biochem 59(2):316–318

Kachalkin AV (2014) Yeasts of the White Sea intertdal zone and description of *Glaciozyma littorale* sp. nov. Antonie Van Leeuwenhoek 105:1073–1083.https://doi.org/10.1007/s10482-014-0165-9

Kachalkin AV, Turchetti B, Inácio J et al (2019) Rare and undersampled dimorphic basidiomycetes. Mycol Prog 18:945–971. https://doi.org/10.1007/s11557-019-01491-5

Kakishima M, Nagao H, Denchev CM (2017a) *Laurobasidium hachijoense,* comb. nov. (*Cryptobasidiaceae*) causing aerialroot-like galls on *Cinnamomum japonicum* in Japan. Phytotaxa 303:97–100

Kakishima M, Nagao H, Ji J-X, Sun Y, Denchev CM (2017b) *Clinoconidium onumae* comb. nov. (*Cryptobasidiaceae*), producing galls on shoot buds of *Cinnamomum tenuifolium* in Japan. Phytotaxa 313:175–184

Kakishima M, Shibata S, Hirooka Y (2020) *Clinoconidium inouyei* comb. nov. (Cryptobasidiaceae), producing galls on shoot buds of *Machilus japonica* in Japan. Phytotaxa 450:199–208

Kalichman J, Kirk PM, Matheny PB (2020) A compendium of generic names of *Agarics* and Agaricales. Taxon 69:425–447. https://doi.org/10.1002/tax.12240

Kalntremtziou M, Papaioannou IA, Vangalis et al (2023) Evaluation of the lignocellulose degradation potential of Mediterranean forests soil microbial communities through diversity and targeted functional metagenomics. Front Microbiol. https://doi.org/10.3389/fmicb.2023.1121993

Kämmerer A, Besl H, Bresinsky A (1985) Omphalotaceae fam. nov. und Paxillaceae, ein chemotaxonomischer Vergleich zweier Pilzfamilien der Boletales. Plant Syst Evol 150:101–117

Kaneko A, Tsukada M, Fukai M, Suzuki T, Nishio K, Miki K, Kinoshita K, Takahashi K, Koyama K (2010) KDR Kinase Inhibitor Isolated from the Mushroom *Boletopsis leucomelas*. J Nat Prod 73(5):1002–1004. https://doi.org/10.1021/np100113e

Karsten PA (1879) Symbolae ad Mycologicam Fennicam V. Meddeland Soc Fauna Fl Fenn 5:15–46

Karsten PA (1890) Fragmenta mycologica XXIX. Hedwigia 29:147–149

Kasuya T, Uzawa M, Hosaka K (2022) *Scleroderma capeverdeanum*, a subhypogeous fungus new to Japan, collected from the Eucalyptus plantation in Ibaraki Prefecture. Truffology 5:23–32

Kato M (2007) Distribution of Osmundaceae. Bull Natl Museum Nat Sci Ser B 33:81–90

Katoh K, Standley DM (2013) MAFFT multiple sequence alignment software version 7: improvements in performance and usability. Mol Biol Evol 30:772–780. https://doi.org/10.1093/molbev/mst010

Kellerman WA, Swingle WT (1889) New species of Kansas fungi. J Mycol 5:11–14

Kemler M, Witfeld F, Begerow D, Yurkov A (2017) Phylloplane yeasts in temperate climates. In: Buzzini P, Lachance MA, Yurkov A (eds) Yeasts in natural ecosystems: diversity. Springer, Cham.https://doi.org/10.1007/978-3-319-62683-3_6

Kemler M, Denchev TT, Denchev CM, Begerow D, Piątek M, Lutz M (2020) Host preference and sorus location correlate with parasite phylogeny in the smut fungal genus *Microbotryum* (Basidiomycota, Microbotryales). Mycol Progr 19:481–493

Khanna JM, Malone MH, Euler KL, Brady LR (1965) Atromentin—anticoagulant from *Hydnellum diabolus*. J Pharm Sci 54(7):1016–1020. https://doi.org/10.1002/jps.2600540714

Kibby G (2021) Fungal portraits: No. 87: Three white *Clitocybe* species: *C. phyllophila*, *C. rivulosa* & *C. leucodiatreta*. Field Mycol 22(3):75–77

Kijpornyongpan T, Aime MC (2016) Rare or rarely detected? Ceraceosorus guamensis sp. nov.: a second described species of Ceraceosorales and the potential for underdetection of rare lineages with common sampling techniques. Antonie Van Leeuwenhoek 109:1127–1139

Kijpornyongpan T, Aime MC (2017) Taxonomic revisions in the microstromatales: two new yeast species, two new genera, and validation of *Jaminaea* and two *Sympodiomycopsis* species. Mycol Prog 16:495–505

Kijpornyongpan T, Mondo SJ, Barry K et al (2018) Broad genomic sampling reveals a smut pathogenic ancestry of the fungal clade ustilaginomycotina. Mol Biol Evol 35:1840–1854. https://doi.org/10.1093/molbev/msy072

Kim HK, Park JS, Cha DY, Kim YS, Moon B (1994) Study on the artificial cultivation of *Lentinus lepideus* (Fr. ex Fr.) Fr. -investigation of mycelial growth conditions. Kor J Mycol 22:145–152

Kim JH, Lee JS, Song KS, Kwon CS, Kim YK, Kim JS (2004) Polyozellin isolated from *Polyozellus multiplex* induces phase 2 enzymes in mouse hepatoma cells and differentiation in human myeloid leukaemic cell lines. J Agric Food Chem 52:451–455. https://doi.org/10.1021/jf034748n

Kim MS, Jeon SM, Ka KH, Bak WC (2013) Cultivation charateristics of *Neolentinus lepideus* strains on Sawdust media. Kor J Mycol 41:225–230

Kirk PM, Cannon PF, David JC, Stalpers JA (2001) Ainsworth and Bisby's dictionary of the Fungi, 9th edn. CABI, Wallingford

Kirk PM, Cannon PF, Minter DW, Stalpers JA (2008) Ainsworth & Bisby's dictionary of the Fungi, 10th edn. CABI, Wallingford

Kirschner R (2004) Sporodochial anamorphs of species of *Helicogloea*. In: Agerer R, Piepenbring M, Blanz P (eds) Frontiers in basidiomycote mycology. IHW-Verlag, Eching, pp 165–178

Kirschner R, Yang ZL (2005) *Dacryoscyphus chrysochilus*, a new staurosporous anamorph with cupulate conidiomata from China and with affinities to the Dacrymycetales (Basidiomycota). Antonie Van Leeuwenhoek 87:329–337. https://doi.org/10.1007/s10482-004-6784-9

Kirschner R, Bauer R, Oberwinkler F (2001) *Colacosiphon*: a new genus described for a mycoparasitic fungus. Mycologia 93:634–644

Kirschner R, Sampaio JP, Begerow D, Chen ZC, Oberwinkler F (2002) Mycogloea nipponica-the first known teleomorph in the heterobasidiomycetous yeast genus *Kurtzmanomyces*. Antonie Van Leeuwenhoek 84:109–114

Kitabayashi K, Kitamura S, Tuno N (2022) Fungal spore transport by omnivorous mycophagous slug in temperate forest. Ecol Evol 12(2):e8565

Klecan AL, Hippe S, Somerville SC (1990) Reduced growth of *Erysiphe graminis* f. sp. *hordei* induced by *Tilletiopsis pallescens*. Phytopathology 80:325–331

Knijn A, Saar I, Ferretti A (2019) Biological characteristics of *Punctularia atropurpurascens* through morphological and molecular analyses during development. Italian J Mycol 48:39–49

Knudsen H, Vesterholt J (2018) Funga Nordica, 2nd revised edition. Nordsvamp, Copenhagen

Ko KS, Hong SG, Jung HS (1997) Phylogenetic analysis of Trichaptum based on nuclear 18S, 5.8S and ITS ribosomal DNA sequences. Mycologia 89:727–734

Kobayasi Y (1937a) Fungi Austro-Japoniae et Micronesiae. I. Bot Mag 51:749–758

Kobayasi Y (1937b) On the genus *Holtermannia* of Tremellaceae. Sci Rep Tokyo Bunrika Daigaky Sect B 3:75–81

Köhl J, de Geijn HG, Haas LG et al (2019) Stepwise screening of candidate antagonists for biological control of *Blumeria graminis* f. sp. *tritici*. Biol Control 136:104008

Kohler A, Kuo A, Nagy L, Morin E, Barry KW, Buscot F, Canbäck B, Choi C et al (2015) Convergent losses of decay mechanisms and rapid turnover of symbiosis genes in mycorrhizal mutualists. Nat Genet 47:410–415

Kolařik M, Wi I-C, Hsieh S-Y, Piepenbring M, Kirschner R (2021) Nucleotide composition bias of rDNA sequences as a source of phylogenetic artifacts in Basidiomycota—a case of a new lineage of a uredinicolous Ramularia-like anamorph with affinities to Ustilaginomycotina. Mycol Pror 20:1553–1571

Kõljalg U, Dahlberg A, Taylor AF, Larsson E, Hallenberg N et al (2000) Diversity and abundance of resupinate thelephoroid fungi as ectomycorrhizal symbionts in Swedish boreal forests. Mol Ecol 9(12):1985–1996. https://doi.org/10.1046/j.1365-294X.2000.01105.x

Kõljalg U, Nilsson RH, Abarenkov K, Tedersoo L, Taylor AF et al (2013) Towards a unified paradigm for sequence-based identification of fungi. Mol Ecol 22(21):5271–5277. https://doi.org/10.1111/mec.12481

Komagata Y, Fukasawa Y, Matsuura K (2022) Low temperature enhances the ability of the termite-egg-mimicking fungus *Athelia termitophila* to compete against wood-decaying fungi. Fungal Ecol 60:101178. https://doi.org/10.1016/j.funeco.2022.101178

Konkel Z, Scott K, Slot J (2021) Draft genome sequence of the termite-associated "Cuckoo Fungus", *Athelia* (Fibularhizoctonia) sp. TMB Strain TB5. Microbiol Resour Announc 10:e01230-e1320

Körnicke F (1879) Neovossia Kcke. Oesterr Bot Z 29:217–218

Korotkin HB, Swenie RA, Miettinen O, Budke JM, Chen KH, Lutzoni F, Smith ME, Matheny PB (2018) Stable isotope analyses reveal previously unknown trophic mode diversity in the Hymenochaetales. Am J Bot 105(11):1869–1887

Koske RE (1972) Two unusual tremellas from British Columbia. Can J Bot 50(12):2565–2567

Kotiranta H, Niemelä T (1996) Threatened polypores in Finland. 2nd ed. Edita, Helsinki

Kotlaba F, Pouzar Z (1964) Preliminary results of staining spores. Trans Brit Mycol Soc 64:822–829

Kottke I, Beiter A, Weiss M, Haug I, Oberwinkler F, Nebel M (2003) Heterobasidiomycetes form symbiotic associations with hepatics: Jungermanniales have sebacinoid mycobionts while *Aneura pinguis* (Metzgeriales) is associated with a *Tulasnella* species. Mycol Res 107:957–968

Kottke I, Suárez JP, Herrera P et al (2010) Atractiellomycetes belonging to the 'rust'lineage (Pucciniomycotina) form mycorrhizae with terrestrial and epiphytic neotropical orchids. Proc R Soc B 277(1685):1289–1298

Koukol ON, Lotz-Winter HE (2016) Secondary conidia observed in *Bartheletia paradoxa*. Czech Mycol 68(1):79–84

Kramer CL (1959) A new genus in the Protomycetaceae. Mycologia 50:916–926

Kramer CL (1973) Protomycetales and Taphrinales. In: Ainsworh GC, Sparrow FK, Sussman AS (eds) The fungi, an advanced treatise, vol IVA. Academic Press, New York, pp 33–41

Kramer CL (1987) The Taphrinales. In: de Hoog GS, Smith MT, Weijman ACM (eds) The expanding realm of yeast-like fungi. Elsevier, Amsterdam, pp 151–166

Krassilov VA, Makulbekov NM (2003) The first finding of Gasteromycetes in the Cretaceous of Mongolia. Paleontol J 37:422–439

Kreisel H (1969) Grundzüge eines natürlichen systems der Pilze. Gustav Fischer Verlag/Cramer, Jena

Kretzer A, Li Y, Szaro T, Bruns TD (1996) Internal transcribed spacer sequences from 38 recognized species of *Suillus* sensu lato: phylogenetic and taxonomic implications. Mycologia 88(5):776–785

Kropp BR, Corden ME (1986) Morphology and taxonomy of *Pachnocybe ferruginea*. Mycologia 78(3):334–342

Krüger D, Binder M, Fischer M, Kreisel H (2001) The Lycoperdales. A molecular approach to the systematics of some gasteroid mushrooms. Mycologia 93:947–957

Kruppa MD, Lowman DW et al (2009) Identification of (1–>6)-beta-D-glucan as the major carbohydrate component of the Malassezia sympodialis cell wall. Carbohydr Res 344(18):2474–2479.https://doi.org/10.1016/j.carres.2009.09.029

Kruse J, Piątek M, Lutz M, Thines M (2018) Broad host range species in specialised pathogen groups should be treated with suspicion—a case study on *Entyloma* infecting *Ranunculus*. Persoonia 41:175–201

Kües U, Khonsuntia W, Subba S, Dörnte B (2018) Volatiles in communication of Agaricomycetes. In: Anke T, Schüffler A (eds) The mycota XV. Physiology and genetics, vol 2. Springer, New York, pp 149–212

Kuhar F, Papinutti L (2009) *Geastrum episcopale*: a new noticeable species with red violet exoperidium. Mycologia 101:535–538

Kuhar F, Castiglia V, Papinutti L (2013) *Geastrum* species of the La Rioja province, Argentina. Mycotaxon 122:145–156

Kuhar F, Barroetaveña C, Rajchenberg M (2016a) New species of *Tomentella* (Thelephorales) from the Patagonian Andes forests. Mycologia 108(4):780–790.https://doi.org/10.3852/15-244

Kuhar F, Castiglia VC, Zamora JC (2016b) Detection of manganese peroxidase and other exoenzymes in four isolates of *Geastrum* (Geastrales) in pure culture. Rev Argent Microbiol 48:274–278

Kühn J (1882) *Paipalopsis irmischiae*, ein neuer Pilzparasit unseres Florengebietes. Irmischia 7:39–40

Kühner R (1980) Les Hyménomycètes agaricoides. Bulletin Mensuel de la Société Linnéenne de Lyon, Lyon

Kühner R (1984) Some mainlines of classification in the gilled fungi. Mycologia 76:1059–1074

Kukkonen I (1963) Taxonomic studies on the genus *Anthracoidea* (Ustilaginales). Ann Bot Soc Zool-Bot Fenn 34:1–122

Kumar AK, Sharma S (2017) Recent updates on different methods of pretreatment of lignocellulosic feedstocks: a review. Bioresour Bioprocess 4:7. https://doi.org/10.1186/s40643-017-0137-9

Kumar TKA, Celio GJ, Matheny PB, McLaughlin DJ, Hibbett DS, Manimohan P (2007) Phylogenetic relationships of *Auriculoschypha* based on ultrastructural and molecular studies. Mycol Res 111:268–274

Kumar P, Barrett DM, Delwiche MJ, Stroeve P (2009) Methods for pretreatment of lignocellulosic biomass for efficient hydrolysis and biofuel production. Ind Eng Chem Res 48:3713–3729. https://doi.org/10.1021/ie801542g

Kumar H, Bhardwaj K, Sharma R, Nepovimova E, Cruz-Martins N, Dhanjal DS, Singh R, Chopra C, Verma R, Abd-Elsalam KA, Tapwal A, Musilek K, Kumar D, Kuča K (2021) Potential usage of edible mushrooms and their residues to retrieve valuable supplies for industrial applications. J Fungi 7:427. https://doi.org/10.3390/jof7060427

Kumla J, Suwannarach N, Tanruean K, Lumyong S (2021) Comparative evaluation of chemical composition, phenolic compounds, and antioxidant and antimicrobial activities of tropical black bolete mushroom using different preservation methods. Foods 10(4):781

Kurtzman RH (1997) Nutrition from mushrooms, understanding and reconciling available data. Mycoscience 38:247–253

Kurtzman CP, Fell JW, Boekhout T (2011) The yeasts, a taxonomic study, vol 1–3. Elsevier, Amsterdam

Kusuma HI, Harnelly E, Thomy Z (2021) Agaricales: the most dominated macroscopic fungi in Tahura Pocut Meurah Intan forest park. J Phys 1882:012096. https://doi.org/10.1088/1742-6596/1882/1/012096

Kwak JY, Rhee IK, Lee KB, Hwang JS, Yoo ID, Song KS (1999) Thelephoric acid and kynapcin-9 in mushroom *Polyozellus multiplex* inhibit prolyl endopeptidase in vitro. J Microbiol Biotechnol 9(6):798–803

Kwon-Chung KJ (1977) Perfect state of *Cryptococcus uniguttulatus*. Int J Syst Bacteriol 27:293–299

Kwon-Chung KJ (2011) Filobasidium Olive (1968). In: Kurtzman CP, Fell JW, Boekhout T (eds) The yeasts (fifth edition). Elsevier, Amsterdam, pp 1457–1465

Lalitha CR, Leelavathy KM (1990) A coccid-association in *Auriculoscypha* and its taxonomic significance. Mycol Res 94:571–572

Langer E (2001) Phylogeny of non-gilled and gilled basidiomycetes dna sequence inferrence, ultrastructure and comparative morphology. Dissertation, Tuebingen University

Langer E, Oberwinkler F (1993) Corticioid basidiomycetes. I. Morphology and Ultrastructure. Windahlia 20:1–28

Larsson KH (1992) The genus *Trechispora* (Corticiaceae, Basidiomycetes). Dissertation, University of Göteborg

Larsson KH (1994) Poroid species in Trechispora and use of calcium oxalate crystals for species identification. Mycol Res 98:1153–1172

Larsson KH (1996) New species and combinations in Trechispora (Corticiaceae, Basidiomycotina). Nordic J Bot 16:83–98

Larsson KH (2007) Re-thinking the classification of corticioid fungi. Mycol Res 111:1040–1063

Larsson E, Larsson KH (2003) Phylogenetic relationships of russuloid basidiomycetes with emphasis on aphyllophoralean taxa. Mycologia 95(6):1037–1065

Larsson K, Ryvarden L (2021) Corticioid fungi of Europe, vol 1. Fungiflora, Oslo

Larsson KH, Larsson E, Kõljalg U (2004) High phylogenetic diversity among corticioid homobasidiomycetes. Mycol Res 108:983–1002. https://doi.org/10.1017/s0953756204000851

Larsson KH, Parmasto E, Fischer M, Langer E, Nakasone KK, Redhead SA (2006) Hymenochaetales: a molecular phylogeny for the hymenochaetoid clade. Mycologia 98:926–936

Larsson KH, Læssøe T, Nourou S, Ryvarden L (2011) The phylogenetic position of Hydnodon and Scytinopogon. Inoculum 62(3):28

Larsson KH, Svantesson S, Miscevic D, Kõljalg U, Larsson E (2019) Reassessment of the generic limits for *Hydnellum* and *Sarcodon*(Thelephorales, Basidiomycota). MycoKeys 54:31–47. https://doi.org/10.3897/mycokeys.54.35386

Læssøe TH, Davey ML, Petersen JH (2016) A new species of *Maireina* on *Filipendula ulmaria*. Karstenia 56(1–2):39–46

Leal-Dutra CA, Neves MA, Griffith GW, Reck MA, Clasen LA, Dentinger BTM (2018) Reclassification of *Parapterulicium Corner* (Pterulaceae, Agaricales), contributions to Lachnocladiaceae and Peniophoraceae (Russulales) and introduction of *Baltazaria* gen. nov. MycoKeys 37:39–56. https://doi.org/10.3897/mycokeys.37.26303

Leal-Dutra CA, Griffith GW, Neves MA, McLaughlin DJ, McLaughlin EG, Clasen LA, Dentinger BT (2020) Reclassification of *Pterulaceae Corner* (Basidiomycota: Agaricales) introducing the ant-associated genus *Myrmecopterula* gen. nov., *Phaeopterula* Henn. and the corticioid Radulomycetaceae fam. nov. IMA fungus 11(1):1–24

Lebel T, Tonkin JE (2007) Australasian species of *Macowanites* are sequestrate species of *Russula* (Russulaceae, Basidiomycota). Aust Syst Bot 20:355–381

Lebel T, Davoodian N, Bloomfield M, Syme K, May T, Hosaka K, Castellano M (2022) A mixed bag of sequestrate fungi from five different families: Boletaceae, Russulaceae, Psathyrellaceae, Strophariaceae, and Hysterangiaceae. Swainsona 36:33–65

Lee IS, Nishikawa A (2003) *Polyozellus multiplex*, a Korean wild mushroom, as a potent chemopreventive agent against stomach cancer. Life Sci 73(25):3225–3234.https://doi.org/10.1016/j.lfs.2003.06.006

Lee KK, Tang KHD (2020) Agaricales (Gilled mushrooms) as biosorbents of synthetic dye. Mal J Med Health Sci 16(SUPP11):10–17

Lee SO, Kim HY, Choi GJ, Lee HB, Jang KS, Choi YH, Kim JC (2009) Mycofumigation with *Oxyporus latemarginatus* EF069 for control of postharvest apple decay and Rhizoctonia root rot on moth orchid. J Appl Microbiol 106:1213–1219. https://doi.org/10.1111/j.1365-2672.2008.04087.x

Legon N, Henrici A, Roberts PJ, Spooner BM, Watling R (2005) Checklist of the British and Irish Basidiomycota. Royal Botanic Gardens, Kew

Leppik EE (1953) Some viewpoints on the phylogeny of rust fungi. I. Coniferous rusts. Mycologia 45:46–74

Leppik EE (1965) Some viewpoints on the phylogeny of rust fungi. V. Evolution of biological specialization. Mycologia 57(6):22

Leppik EE (1967) Some viewpoints on the phylogeny of rust fungi. VI. Biogenic radiation. Mycologia 54:568–579

Leppik EE (1972) Evolutionary specialization of rust fungi (Uredinales) on the Leguminosae. Ann Bot Fenn 9:135–148

Li G-J (2014) Taxonomy of *Russula* from China. Dissertation. University of Chinese Academy of Sciences

Li H (2017) Extraction, purification, characterization and antioxidant activities of polysaccharides from *Ramaria botrytis* (Pers.). Ricken Chem Cent J 11:24.https://doi.org/10.1186/s13065-017-0252-x

Li G-J, Wen H-A (2009) Research of prospects on taxonomy of the *Russula* in China. Mycosystema 28(2):303–309

Li S-J, Dong C-H (2022) A new type of homokaryotic strain of *Wolfiporia hoelen* with indistinguishable phenotypes from the parent strains. Mycosystema 41(8):1279–1292. https://doi.org/10.13346/j.mycosystema.210504

Li M, Liang J, Li Y, Feng B, Yang ZL, James TY, Xu J (2010) Genetic diversity of Dahongjun, the commercially important “Big Red Mushroom” from southern China. PLoS ONE 5(5):e10684

Li C-T, Mao X-X, Xu B-J (2013a) Pulsed electric field extraction enhanced anti-coagulant effect of fungal polysaccharide from Jew’s Ear (*Auricularia auricula*). Phytochem Anal 24:36–40. https://doi.org/10.1002/pca.2376

Li G-J, Zhao Q, Zhao D, Yue S-F, Li S-F, Wen H-A, Liu X-Z (2013b) *Russula atroaeruginea* and *R. sichuanensis* spp. nov. from southwest China. Mycotaxon 124:173–188

Li G-J, Li S-F, Zhao D, Wen H-A (2015) Recent research progress of *Russula* (Russulales, Agaricomycetes): a review. Mycosystema 34(5):821–848

Li G-J, Zhao R-L, Zhang C-L, Lin F-C (2018) Hypogeous gasteroid *Lactarius sulphosmus* sp. nov. and agaricoid *Russula* *vinosobrunneola*sp. nov. (Russulaceae) from China. Mycosphere 9(4):838–858

Li Q, He X, Ren Y, Xiong C, Jin X, Peng L, Huang W (2020a) Comparative mitogenome analysis reveals mitochondrial genome differentiation in ectomycorrhizal and asymbiotic *Amanita* species. Front Microbiol 11:1382. https://doi.org/10.3389/fmicb.2020.01382

Li A-H, Yuan F-X, Groenewald M et al (2020b) Diversity and phylogeny of basidiomycetous yeasts from plant leaves and soil: proposal of two new orders, three new families, eight new genera and one hundred and seven new species. Stud Mycol 96:17–140. https://doi.org/10.1016/j.simyco.2020.01.002

Li G-J, Deng C-Y, Shi L-Y, Wang J, Meng Q-F, Li S-M (2020c) Three new species of *Russula* subsect. Lactarioideae from China. Mycosystema 39(4):618–636

Li T, Li T, Deng W, Song B, Deng C, Yang Z-L (2020d) *Phallus dongsun* and *P. lutescens*, two new species of Phallaceae (Basidiomycota) from China. Phytotaxa 443:19–37

Li G-J, Li S-M, Buyck B, Zhao S-Y, Xie X-J, Shi L-Y, Deng C-Y, Meng Q-F, Sun Q-B, Yan J-Q, Wang J, Li M (2021a) Three new *Russula* species in sect. *Ingratae* (Russulales, Basidiomycota) from southern China. MycoKeys 84:103–139

Li H, Tian Y, Menolli N, Ye L, Karunarathna SC et al (2021b) Reviewing the world's edible mushroom species: a new evidence-based classification system. Compr Rev Food Sci Food Saf 20:1982–2014

Li Y, Steenwyk JL, Chang Y, Wang Y et al (2021c) A genome-scale phylogeny of the kingdom Fungi. Curr Biol 31(8):1653–1665

Li Q, Bao Z, Tan K, Feng H, Tu W, Li L, Han Y, Cao M, Xhao C (2022a) First two mitocondrial genomes for the order Filobasidiales reveal novel gene rearrangements and intron dynamics of Tremellocyetes. IMA Fungus 13:7

Li Q, Li L, Zhang T et al (2022b) The first two mitochondrial genomes for the genus *Ramaria* reveal mitochondrial genome evolution of *Ramaria* and phylogeny of Basidiomycota. IMA Fungus 13:16. https://doi.org/10.1186/s43008-022-00100-7

Li Y-Y, Wang M-M, Groenewald M, Li A-H, Guo Y-T, Wu F, Zhang B-Q, Tanaka E, Wang Q-M, Bai F-Y, Begerow D (2022c) Proposal of two new combinations, twenty new species, four new genera, one new family, and one new order for the anamorphic basidiomycetous yeast species in Ustilaginomycotina. Front Microbiol 12:777338

Li G-J, Liu T-Z, Li S-M, Zhao S-Y, Niu C-Y, Liu Z-Z, Xie X-J, Zhang X, Shi L-Y, Guo Y-B, Wang K (2023a) Four new species of *Russula* subsection *Sardoninae* from China. J Fungi 9(2):199

Li Y, Wang P, Zhang Z, Liu Q (2023b) A novel lectin from mushroom *Phellodon melaleucus* displays hemagglutination activity, and antitumor activity in a B16 melanoma mouse model. Food Sci Human Wellness 12(5):1885–1892. https://doi.org/10.1016/j.fshw.2023.02.040

Li W-Y, Gao L, Wu F, Dou Z-P (2023c) Research progress of edible and medicinal mushroom domesticated and cultivated in China during the last 10 years. Mycosystema 42(10):2011–2024. https://doi.org/10.13346/j.mycosystema.230120

Li G-Q, Yu D-S, Zhu P-L, Zhao G-Y, Liu C-Y, Zhao H-Y (2023d) Three new cultivars of *Ganoderma sinense* and *Auricularia heimuer*-from southern Anhui. Mycosystema 42(5):1219–1222. https://doi.org/10.13346/j.mycosystema.220259

Lian Y-P, Tohtirjap A, Wu F (2022) Two New Species of *Dacrymyces* (Dacrymycetales, Basidiomycota) from Southwestern China. Diversity 14:379. https://doi.org/10.3390/d14050379

Liberta AE (1973) The genus *Trechispora* (Basidiomycetes, Corticiaceae). Can J Bot 51:1871–1892

Liimatainen K, Kim JT, Pokorny L, Kirk PM, Dentinger B, Niskanen T (2022) Taming the beast: a revised classification of Cortinariaceae based on genomic data. Fungal Divers 112(1):89–170

Lilleskov EA, Bruns TD (2005) Spore dispersal of a resupinate ectomycorrhizal fungus, *Tomentella sublilacina*, via soil food webs. Mycologia 97(4):762–769

Limber DP (1940) A new form genus of the Moniliaceae. Mycologia 32(1):23–30

Limon JJ, Tang J et al (2019) *Malassezia* is associated with Crohn's disease and exacerbates colitis in mouse models. Cell Host Microbe 25(3):377–388. https://doi.org/10.1016/j.chom.2019.01.007

Lin X, Heitman J (2006) The biology of the *Cryptococcus neoformans* species complex. Annu Rev Microbiol 60:69–105

Lin YY, Zhang MZ, Ling ZL, Cao B, Wu XP, Peng H, Wang ZR, Zhao RL (2022) Evolutionary relationship and a novel method of efficient identification of *Lentinula edodes* cultivars in China. Mycosphere 13(2):56–85

Lindeberg B (1959) *Ustilaginales* of Sweden (exclusive of the Cintractias on *Caricoideae*). Symb Bot Upsal 16(2):1–175

Linnaeus C (1753) Species Plantarum. Tomus II. Imprensis laurentii Salvii, Holmiæ

Linnakoski R, Jyske T, Eerikäinen R, Veteli P, Cortina-Escribano M, Magalhães F, Järvenpää E, Heikkilä L, Hutzler M, Gibson B (2023) Brewing potential of strains of the boreal wild yeast *Mrakia gelida*. Front Microbiol 14:1108961

Liro JI (1938) Die Ustilagineen Finnlands II. Ann Acad Sci Fenn Ser A 42(1):1–720

Liu K, Wang J, Zhao L et al (2013) Anticancer, antioxidant and antibiotic activities of mushroom *Ramaria flava*. Food Chem Toxicol 58:375–380. https://doi.org/10.1016/j.fct.2013.05.00

Liu X-Z, Wang Q-M, Theelen B, Groenewald M, Bai F-Y, Boekhout T (2015a) Phylogeny of tremellaceous yeasts and related dimorphic filamentous basidiomycetous reconstructed from multiple gene sequence analyses. Stud Mycol 81:1–26

Liu X-Z, Wang Q-M, Göker M, Groenewald M, Kachalkin AV, Lumbsch HT, Millanes AM, Wedin M, Yurkov AM, Boekhout T, Bai FY (2015b) Towards an integrated phylogenetic classification of the Tremellomycetes. Stud Mycol 81:85–147

Liu D, Goffinet B, Ertz D et al (2017a) Circumscription and phylogeny of the Lepidostromatales (lichenized Basidiomycota) following discovery of new species from China and Africa. Mycologia 109:730–748

Liu X-Z, Groenewald M, Boekhout T, Feng-Yan Bai F-Y (2017b) *Heitmania* gen. nov., a new yeast genus in Microbotryomycetes, and description of three novel species:*Heitmania litseae* sp. nov., *Heitmania castanopsis* sp. nov. and *Heitmania elacocarpi* sp. nov. Int J Syst Evol Microbiol 67:4534–4540

Liu S-L, Ma H-X, He S-H, Dai Y-C (2019a) Four new corticioid species in Trechisporales (Basidiomycota) from East Asia and notes on phylogeny of the order. MycoKeys 48:97–113

Liu D, Wang X-Y, Wang L-S, Maekawa N, Hur JS (2019b) *Sulzbacheromyces sinensis*, an Unexpected Basidiolichen, was Newly Discovered from Korean Peninsula and Philippines, with a Phylogenetic Reconstruction of Genus *Sulzbacheromyces*. Mycobiology 47(2):191–199. https://doi.org/10.1080/12298093.2019.1617825

Liu J-W, Ge Z-W, Horak E, Vizzini A, Halling RE, Pan C-L, Yang Z-L (2021) Squamanitaceae and three new species of *Squamanita* parasitic on *Amanita* basidiomes. IMA Fungus 12(1):1–24

Liu S-L, He S-H, Wang X-W, May TW, He G, Chen S-L, Zhou L-W (2022a) Trechisporales emended with a segregation of Sistotremastrales ord. nov. (Basidiomycota). Mycosphere 13(1):862–954

Liu S-L, Shen Z-Q, Li Q-Z, Liu X-Y, Zhou L-W (2022b) *Alloexidiopsis* gen. nov., a revision of generic delimitation in Auriculariales (Basidiomycota). Front Microbiol 13:894641. https://doi.org/10.3389/fmicb.2022.894641

Liu Z-B, Zhou M, Wu F, Yu J (2022c) Two new species of *Sidera* (Hymenochaetales, Basidiomycota) from Southwest China. J Fungi 8:385

Liu N-N, Zhao X, Tan J-C, Liu S, Li B-W, Xu W-X, Peng L, Gu P, Li W, Shapiro R, Zheng X (2022d) Mycobiome dysbiosis in women with intrauterine adhesions. Microbiol Spectrum 10(4):e01324-e1422

Liu Z-B, Wu Y-D, Zhao H, Lian Y-P, Wang Y-R, Wang C-G, Mao W-L, Yuan Y (2022e) Outline, divergence times, and phylogenetic analyses of Trechisporales (Agaricomycetes, Basidiomycota). Front Microbiol 13:818358. https://doi.org/10.3389/fmicb.2022.818358

Liu S, Chen Y-Y, Sun Y-F, He X-L, Song C-G, Si J, Liu D-M, Gates G, Cui B-K (2023a) Systematic classifcation and phylogenetic relationships of the brown-rot fungi within the Polyporales. Fungal Divers 118:1–94

Liu S, Zhou J-L, Song J, Sun Y-F, Dai Y-C, Cui B-K (2023b) Climacocystaceae fam. nov. and Gloeoporellaceae fam. nov., two new families of Polyporales (Basidiomycota). Front Microbiol 14:1115761

Liu S-L, Wei H-W, Zhou L-W (2023c) Xenasmatellales ord. nov. and Xenasmatellaceae fam. nov. for*Xenasmatella* (Agaricomycetes, Basidiomycota). Mycology 21:1–5

Lloyd CG (1908) Mycological notes: polyporoid issue, no. 1. Mycological Writings of C.G. Lloyd 3:1–16

Lodge DJ, Padamsee M, Matheny PB, Aime MC, Cantrell SA, Boertmann D, Kovalenko A, Vizzini A, Dentinger BT, Kirk PM, Ainsworth AM (2014) Molecular phylogeny, morphology, pigment chemistry and ecology in Hygrophoraceae (Agaricales). Fungal Divers 64:1–99

Locquin MV (1974) De Taxia Fungorum I. UAE Mondedition, Paris

Long W-H (1917) Notes on new or rare species of Gasteromycetes. Mycologia 9:271–274

Long W-H (1945) Studies in the Gasteromycetes XI. The Genera Trichaster and Terrostella. Mycologia 37:601–608

Long W-H, Stouffer DJ (1948) Studies in the Gasteromycetes XVI. The Geastraceae of the southwestern United States. Mycologia 40:547–585

Looney BP, Ryberg M, Hampe F, Sánchez-García M, Matheny PB (2016) Into and out of the tropics: global diversification patterns in a hyperdiverse clade of ectomycorrhizal fungi. Mol Ecol 25:630–647

Lorch JM, Palmer JM et al (2018) *Malassezia vespertilionis*sp. nov.: a new cold-tolerant species of yeast isolated from bats. Persoonia 41:56–70. https://doi.org/10.3767/persoonia.2018.41.04

Loron CC, François C, Rainbird RH et al (2019) Early fungi from the Proterozoic era in Arctic Canada. Nature 570(7760):232–235

Lotsy JP (1907) Vorträge über botanische Stammesgeschichte: 706. G. Fischer, Jena

Louzan R, Wilson AW, Binder M, Hibbett DS (2007) Phylogenetic placement of *Diplocystis wrightii* in the Sclerodermatineae (Boletales) based on nuclear ribosomal large subunit DNA sequences. Mycoscience 48:66–69

Lowy B (1971) Tremellales. Flora Neotropica Monograph 6:1–153

Lu X, Steffen K, Yuan H-S (2018) Morphological and molecular identification of three new species of *Tomentella* from Finland. Mycologia 110:677–691. https://doi.org/10.1080/00275514.2018.1474683

Luangharn T, Karunarathna SC, Dutta AK, Paloi S, Promputtha I, Hyde KD, Xu J, Mortimer PE (2021) *Ganoderma* (Ganodermataceae, Basidiomycota) species from the Greater Mekong Subregion. J Fungi 7(10):819

Lücking R, Aime MC, Robbertse B et al (2021) Fungal taxonomy and sequence-based nomenclature. Nat Microbiol 6(5):540–548

Luna-Flores CH, Wang A, von Hellens J, Speight RE (2022) Towards commercial levels of astaxanthin production in *Phaffia rhodozyma*. J Biotechnol 350:42–54

Lunde LF et al (2022) DNA metabarcoding reveals host-specific communities of arthropods residing in fungal fruit bodies. Proc R Soc B 289:20212622

Luo K-Y, Zhao C-L (2022) Molecular systematics and taxonomy research on *Trechispora* (Hydnodontaceae, Trechisporales): concentrating on three new*Trechispora* species from East Asia. J Fungi 2022:1020. https://doi.org/10.3390/jof8101020

Luo K-Y, Qu M-H, Zhao C-L (2021) Additions to the knowledge of corticioid *Xylodon* (Schizoporaceae, Hymenochaetales): introducing three new *Xylodon* species from Southern China. Diversity 13:581

Luo S-Z, Ji K-P, Cao Y, Ji G-Y (2022) A new *Phlebopus portentosus* cultivar 'YL1701-2.' Mycosystema 41(7):1140–1142. https://doi.org/10.13346/j.mycosystema.210442

Lutz M, Bauer R, Begerow D, Oberwinkler F, Triebel D (2004a) Tuberculina: rust relatives attack rusts. Mycologia 96(3):614–626

Lutz M, Bauer R, Begerow D, Oberwinkler F (2004b) Tuberculina—Thanatophytum/Rhizoctonia crocorum—Helicobasidium: a unique mycoparasitic-phytoparasitic life strategy. Mycol Res 108(3):227–238

Lutz M, Bauer R, Begerow D, Oberwinkler F (2004c) Tuberculina—Helicobasidium: host specificity of the Tuberculina—stage reveals unexpected diversity within the group. Mycologia 96(6):1316–1329

Lutz M, Vánky K, Bauer R (2012) *Melanoxa*, a new genus in the Urocystidales (Ustilaginomycotina). Mycol Prog 11:149–158

Lv J, Yao L, Li S, Dong J, Ye M et al (2022) New aniline derivatives from the volva of*Phallus rubrovolvatus* and their anti-inflammatory activity. Bioorg Chem 119:105577

Lv G-Y, Song T-T, Zhang Y-Y, Cai W-M, Zhang Z-F (2023) A comparative study on antioxidant activities of fermentation products of *Sanghuangporus sanghuang* and*S. vaninii* based on UPLC-triple-TOF-MS. Mycosystema 42(4):939–948.https://doi.org/10.13346/j.mycosystema.220125

Ma K, Han J-J, Bao L, Wei T-Z, Liu H-W (2014) Two Sarcoviolins with antioxidative and α-glucosidase inhibitory activity from the edible mushroom *Sarcodon leucopus* collected in Tibet. J Nat Prod 77:942–947. https://doi.org/10.1021/np401026b

Macbride TH (1911) A new genus of myxomycetes. Mycologia 3:39–40

Madhanraj R, Eyini M, Balaji P (2017) Antioxidant assay of gold and silver nanoparticles from edible Basidiomycetes mushroom fungi. Free Radic Antioxid 7:137–142

Maekawa N (1994) Taxonomic study of Japanese Corticiaceae (Aphyllophoraceae) II. Rep Tottori Mycol Inst 32:1–123

Maekawa N, Yokoi H, Sotome K et al (2020) *Athelia termitophila* sp. nov. is the teleomorph of the termite ball fungus *Fibularhizoctonia* sp. Mycoscience 61:323–330. https://doi.org/10.1016/j.myc.2020.08.002

Magallón-Puebla S, Cevallos-Ferriz SRS (1993) A fossil earthstar (Geasteraceae; Gasteromycetes) from the late Cenozoic of Puebla, Mexico. Am J Bot 80:1162–1167

Magnago AC, Alves-Silva G, Neves MA, Silveira RMB (2018) A new species of *Gyroporus* (Gyroporaceae, Boletales) from Atlantic forest in southern Brazil. Nova Hedwigia 107:291–301

Maier W, Khoza T, Harmse N, Wingfield BD, Wingfield MJ (2006) A disease epidemic on *Zizyphus mucronata* in the Kruger National Park caused by *Coniodictyum chevalieri*. Stud Mycol 55:279–288

Malençon G, Riousset L (1977) *Pyrenogaster pithyopilus* G. Malençon et L. Riousset, nouveau genre et nouvelle espèce de Gastéromycète (Geastraceae). Bulletin De La Société Mycologique De France 93:289–311

Malysheva V, Spirin V (2017) Taxonomy and phylogeny of the Auriculariales (Agaricomycetes, Basidiomycota) with stereoid basidiocarps. Fungal Biol 121:689–715. https://doi.org/10.1016/j.funbio.2017.05.001

Malysheva V, Spirin V, Miettinen O, Motato-Vásquez V, Hernawati Seelan J, Larsson KH (2018) Revision of *Protohydnum* (Auriculariales, Basidiomycota). Mycol Prog 17(7):805–814

Malysheva V, Spirin V, Miettinen O, Kout J, Savchenko A, Larsson KH (2019) On craterocolla and ditangium (Sebacinales, Basidiomycota). Mycol Prog 18:753–762. https://doi.org/10.1007/s11557-019-01485-3

Malysheva V, Spirin V, Schoutteten N et al (2020) New and noteworthy species of *Helicogloea* (Atractiellomycetes, Basidiomycota) from Europe. Ann Bot Fenn 57:1–7

Manohar CS, Boekhout T, Müller WH, Stoeck T (2014) *Tritirachium candoliensis* sp. nov., a novel basidiomycetous fungus isolated from the anoxic zone of the Arabian Sea. Fung Biol 118:353–366

Mapook A, Hyde KD, Hassan K et al (2022) Ten decadal advances in fungal biology leading towards human well-being. Fungal Divers 116(1):547–614

Marr CD, Stuntz DE (1973) *Ramaria* of western Washington. Bibl Mycol 38:1–232

Martin GW (1939) New or noteworthy fungi from Panama and Colombia. IV. Mycologia 31(5):507–518

Martin GW (1957) The tulasnelloid fungi and their bearing on basidial terminology. Brittonia 9:25–30

Martin JK, Gilbertson RL (1973) The mating system and some other cultural aspects of *Veluticeps berkeleyi*. Mycologia 65(3):548–557

Martin JK, Gilbertson R (1980) Synopsis of wood-rotting fungi on spruce in North America: III. Mycotaxon 10:479–501

Martín MP, Högberg N, Llistosella J (1999) *Macowanites messapicoides*, a hypogeous relative of *Russula messapica*. Mycol Res 103:203–208

Martin R, Gazis R, Skaltsas D, Chaverri P, Hibbett D (2015) Unexpected diversity of basidiomycetous endophytes in sapwood and leaves of Hevea. Mycologia 107(2):284–297. https://doi.org/10.3852/14-206

Marvanová L, Bandoni RJ (1987) *Naiadella fluitans* gen. et sp. Nov.: a conidial basidiomycete. Mycologia 79:578–586

Marvanová M, Suberkropp K (1990) *Camptobasidium hydrophyllum*and its anamorph *Crucella subtilis*: a new heterobasidiomycete from streams. Mycologia 82:208–217

Masumoto H, Degawa Y (2020) Bryoclavula phycophila gen. et sp. nov. belonging to a novel lichenized lineage in Cantharellales (Basidiomycota). Mycol Prog 19(7):705–714

Matheny PB, Curtis JM, Hofstetter V, Aime MC, Moncalvo JM, Ge ZW, Yang ZL, Slot JC, Ammirati JF, Baroni TL, Bougher NL, Hughes KW, Lodge DJ, Kerrigan RW, Seidl MT, Aanen DK, DeNitis M, Daniele GM, Desjardin DE, Kropp BR, Norvell LL, Parker A, Vellina EC, Vilgalys R, Hibbett DS (2006) Major clades of Agaricales: a multilocus phylogenetic overview. Mycologia 98:982–995. https://doi.org/10.3852/mycologia.98.6.982

Matheny PB, Aime MC, Bougher NL et al (2009) Out of the Palaeotropics? Historical biogeography and diversification of the cosmopolitan ectomycorrhizal mushroom family Inocybaceae. J Biogeogr 36(4):577–592. https://doi.org/10.1111/j.1365-2699.2008.02055.x

Matheny PB, Hobbs AM, Esteve-Raventós F (2020a) Genera of Inocybaceae: new skin for the old ceremony. Mycologia 112(1):83–120

Matheny PB, Hughes KW, Kalichman J, Lebeuf R (2020b) *Pulverulina*, a new genus of Agaricales for *Clitocybe ulmicola*. Southeast Nat 19:447–459

Matsumoto T, Yamamoto W, Hirane S (1932) Physiology and parasitology of the fungi generally referred to as *Hypochnus sasaki* Shirai. I. Differentiation of the strains by means of hyphal fusion and culture in differential media. J Soc Trop Agric 4:370–388

Matsuura K, Tanaka C, Nishida T (2000) Symbiosis of a termite and a sclerotium-forming fungus: sclerotia mimic termite eggs. Ecol Res 15:405–414

Matsuura K, Yashiro T, Shimizu K, Tatsumi S, Tamura T (2009a) Cuckoo fungus mimics termite eggs by producing the cellulose-digesting enzyme β-glucosidase. Curr Biol 19:30–36. https://doi.org/10.1016/j.cub.2008.11.030

Matsuura M, Saikawa Y, Inui K, Nakae K, Igarashi M, Hashimoto K, Nakata M (2009b) Identification of the toxic trigger in mushroom poisoning. Nat Chem Biol 7(7):465–467

Mattoo BB, Singh AP, Dhingra GS, Singh SK, Rana S, Maurya DK (2022) Molecular and morphological characterization of a new species of *Gloeophyllum* (Basidiomycota, Agaricomycetes) from India. Nova Hedwigia 114(3–4):461–471

Maurice S, Arnault G, Nordén J, Botnen SS, Miettinen O, Kauserud H (2021) Fungal sporocarps house diverse and host-specific communities of fungicolous fungi. ISME J 15:1445–1457. https://doi.org/10.1038/s41396-020-00862-1

McKendrick SL, Leake JR, Taylor DL, Read DJ (2002) Symbiotic germination and development of the myco-heterotrophic orchid Neottia nidus-avis in nature and its requirement for locally distributed *Sebacina* spp. New Phytol 154:233–247

McLaughlin DJ (1990) A new cytoplasmic structure in the basidiomycete Helicogloea: the microscala. Exp Mycol 14(4):331–338

McLaughlin DJ, Spatafora JW (2014) 7A systematics and evolution. Springer, Berlin

McNabb RFR (1964) Taxonomic studies in the Dacrymycetaceae I. Cerinomyces Martin. NZ J Bot 2:415–424

McNabb RFR (1965a) Some Auriculariaceous fungi from the British Isles. Trans Br Mycol Soc 48:187–192

McNabb RFR (1965b) Taxonomic studies in the Dacrymycetaceae: V. Heterotextus Lloyd. NZ J Bot 3:215–222

McNabb RFR (1965c) Taxonomic studies in the Dacrymycetaceae: III. Dacryopinax Martin. NZ J Bot 3:59–72

McNabb RFR (1965d) Taxonomic studies in the Dacrymycetaceae: II. Calocera (Fries) Fries. NZ J Bot 3:31–58

McNabb RFR (1965e) Taxonomic studies in the Dacrymycetaceae VI. Femsjonia Nees ex Fries. NZ J Bot 3:223–228

McNabb RFR (1965f) Taxonomic studies in the Dacrymycetaceae IV. Guepiniopsis Patouillard. NZ J Bot 3:159–169

McNabb RFR (1966) Taxonomic Studies in the Dacrymycetaceae: VII. Ditiola Fries. NZ J Bot 4:546–558

McNabb RFR (1973) Taxonomic studies in the Dacrymycetaceae VIII. Dacrymyces Nees ex Fries. NZ J Bot 11:461–524

McTaggart AR, Shivas RG, Geering ADW, Vánky K, Scharaschkin T (2012a) A review of the *Ustilago-Sporisorium-Macalpinomyces* complex. Persoonia 29:55–62

McTaggart AR, Shivas RG, Geering ADW, Callaghan B, Vánky K, Scharaschkin T (2012b) Soral synapomorphies are significant for the systematics of the *Ustilago-Sporisorium-Macalpinomyces* complex (*Ustilaginaceae*). Persoonia 29:63–77

McTaggart AR, Shivas RG, Geering ADW, Vánky K, Scharaschkin T (2012c) Taxonomic revision of*Ustilago*, *Sporisorium* and *Macalpinomyces*. Persoonia 29:116–132

McTaggart AR, Shivas RG, Boekhout T, Oberwinkler F, Vánky K, Pennycook S, Begerow D (2016) *Mycosarcoma* (Ustilaginaceae), a resurrected generic name for corn smut (*Ustilago maydis*) and its close relatives with hypertrophied, tubular sori. IMA Fungus 7:309–315

McTaggart AR, Prychid CJ, Bruhl JJ, Shivas RG (2020) The PhyloCode applied to Cintractiellales, a new order of smut fungi with unresolved phylogenetic relationships in the Ustilaginomycotina. Fungal Syst Evol 6:55–64

Mei Y, Liu C-Y, Li S-H, Guerin-Laguette A, Xiao Y-J, Tang P, Wan S-P, Bonito G, Wang Y (2021)*Phlebopus roseus*, a new edible bolete from China, is associated with insects and plants. Mycologia 113(1):33–42

Melanda GCS, Accioly T, Ferreira RJ, Rodrigues ACM, Cabral TS et al (2020) Diversity trapped in cages: Revision of *Blumenavia* Möller (Clathraceae, Basidiomycota) reveals three hidden species. PLoS ONE 15:e0232467

Melanda GCS, Silva-Filho AGS, Lenz AR, Menolli N Jr, Limma AA et al (2021) An overview of 24 years of molecular phylogenetic studies in Phallales (Basidiomycota) with notes on systematics, geographic distribution, lifestyle, and edibility. Front Microbiol 12:689374

Melhuish JH, Hacskaylo E (1980) Fatty acids of selected *Athelia* species. Mycologia 72:251–258. https://doi.org/10.1080/00275514.1980.12021178

Menaga D, Rajakumar S, Ayyasamy PM (2021) Spent mushroom substrate: a crucial biosorbent for the removal of ferrous iron from groundwater. SN Appl Sci 3:32

Mendes-Alvarenga RL, Gibertoni TB (2022) Dacrymyces flavobrunneus sp. nov. and two new combinations in Dacrymyces Nees based on morphological and phylogenetic data. Mycol Prog 21:96.https://doi.org/10.1007/s11557-022-01847-4

Meng F, Xu P, Wang X, Huang Y, Wu L et al (2017) Investigation on the immunomodulatory activities of *Sarcodon imbricatus* extracts in a cyclophosphamide (CTX)-induced immunosuppresanted mouse model. Saudi Pharm J 25:460–463. https://doi.org/10.1016/j.jsps.2017.04.006

Methany PB, Gossman JA, Zalar P, Arun Kumar TK, Hibbett DS (2006) Resolving the phylogenetic position of the Wallemiomycetes: an enigmatic major lineage of Basidiomycota. Can J Bot 84:1794–1805

Methven AS (1990) The genus *Clavariadelphus* in North America. J Cramer Berlin Stuttgart, Berlin

Metin B, Findley K, Heitman J (2010) The mating type locus (MAT) and sexual reproduction of*Cryptococcus heveanensis*: insights into the evolution of sex and sex-determining chromosomal regions in fungi. PLoS Genet 6(5):e1000961

Metzgar JS, Skog JE, Zimmer EA, Pryer KM (2008) The paraphyly of *Osmunda* is confirmed by phylogenetic analyses of seven plastid loci. Syst Bot 33:31–36

Metzler B, Oberwinkler F, Petzold H (1989) *Rhynchogastrema*gen. nov. and Rhynchogastremaceae fam. nov. (Tremellales). Syst Appl Microbiol 12:280–287

Micheli PA (1729) Nova plantarum genera. Typis Bernardi Paperinii, Florentiae

Miettinen O, Kõljalg U (2007) *Amaurodon sumatranus*(Thelephorales, Basidiomycota), a new species from Indonesia. Mycotaxon 100:51–59

Miettinen O, Larsson K-H (2006) *Trechispora elongata* species nova from North Europe. Mycotaxon 96:193–198

Miettinen O, Larsson E, Sjökvist E, Larsson KH (2011) Comprehensive taxon sampling reveals unaccounted diversity and morphological plasticity in a group of dimitic polypores (Polyporales, Basidiomycota). Cladistics 28:251–270

Millanes AM, Diederich P, Ekman S, Wedin M (2011) Phylogeny and character evolution in the jelly fungi (Tremellomycetes, Basidiomycota, Fungi). Mol Phylogenet Evol 61:12–28

Millanes AM, Diederich P, Wedin M (2016) *Cyphobasidium* gen. nov., a new lichen inhabiting lineage in the Cystobasidiomycetes (Pucciniomycotina, Basidiomycetes, Fungi). Fung Biol 120:1468–1477

Miller OK (1964) Monograph of *Chroogomphus* (Gomphidiaceae). Mycologia 56(4):526–549

Miller OK (2003) The Gomphidiaceae revisited: a worldwide perspective. Mycologia 95(1):176–183

Miller OK, Miller HH (1988) Gasteromycetes. Morphological and development features with keys to the orders, families and genera. Mad River Press, Eureka

Miller SL, McClean TM, Walker JF, Buyck B (2001) A molecular phylogeny of the Russulales including agaricoid, gasteroid and pleurotoid taxa. Mycologia 93(2):344–354

Miller SL, Larsson E, Larsson KH, Verbeken A, Nuytinck J (2006) Perspectives in the new Russulales. Mycologia 98(6):960–970

Millington S, Leach DN, Wyllie SG, Claridge AW (1998) Aroma profile of the Australian truffle-like fungus *Mesophellia glauca*. ACS Symp Ser 705:331–342

Mishra B, Choi YJ, Thines M (2018) Phylogenomics of *Bartheletia paradoxa* reveals its basal position in Agaricomycotina and that the early evolutionary history of basidiomycetes was rapid and probably not strictly bifurcating. Mycol Prog 17:333–341.https://doi.org/10.1007/s11557-017-1349-2

Mitaka Y, Mori N, Matsuura K (2019) A termite fungistatic compound, mellein, inhibits entomopathogenic fungi but not egg-mimicking termite ball fungi. Appl Entomol Zool 54:39–46

Mitchell TG, White TJ, Taylor JW (1992) Comparison of 5.8S ribosomal DNA sequences among the basidiomycetous yeast genera *Cystofilobasidium,Filobasidium* and *Filobasidiella*. Med Mycol 30:207–218

Mix AJ (1947) *Taphrina osmundae* Nishida and *Taphrina higginsii* sp. nov. Mycologia 39:71–76

Mix AJ (1949) A monograph of the genus *Taphrina*. Univ Kansas Sci Bull 33:3–167

Miyauchi S, Kiss E, Kuo A, Drula E, Kohler A, Sánchez-García M, Morin E, Andreopoulos B, Barry KW, Bonito G, Buée M (2020) Large-scale genome sequencing of mycorrhizal fungi provides insights into the early evolution of symbiotic traits. Nat Commun 11(1):5125

Mizuno T, Zhuang C (1995) Maitake, *Grifola frondosa*: pharmacological effects. Food Rev Int 111:135–149

Moliné M, Libkind D, del Diéguez MC, van Broock M (2009) Photoprotective role of carotenoids in yeasts: Response to UV-B of pigmented and naturally occurring albino strains. J Photochem Photobiol B 95(3):156–161

Moncalvo J-M, Lutzoni FM, Rehner SA, Johnson J, Vilgalys R (2000) Phylogenetic relationships of agaric fungi based on Nuclear Large Subunit Ribosomal DNA sequences. Syst Biol 49:278–305

Moncalvo J-M, Vilgalys R, Redhead SA, Johnson JE, James TY, Aime MC, Hofstetter V, Verduin SJW, Larsson E, Baroni TJ, Thorn RG, Jacobsson S, Clémençon H, MillerJr OK (2002) One hundred and seventeen clades of Euagarics. Mol Phylogenet Evol 23:357–400

Moncalvo J-M, Nilsson RH, Koster B et al (2006) The cantharelloid clade: dealing with incongruent gene trees and phylogenetic reconstruction methods. Mycologia 98:937–948

Money NP (2016) Fungal diversity. In: Watkinson SC, Boddy, Money NP (eds) The Fungi, 3rd edn. Academic Press, New York, pp 1–36. https://doi.org/10.1016/b978-0-12-382034-1.00001-3

Moore RT (1985) The challenge of the dolipore/parenthesome septum. In: Moore D, Casselton LA, Wood DA, Frankland J (eds) Developmental biology of higher fungi. Cambridge University Press, Cambridge, pp 175–212

Moore RT (1990) Order Platygloeales ord. nov. Mycotaxon 34:245–248

Moore RT (1996) The dolipore/parenthesome septum in modern taxonomy. In: Sneh B, Jabaji-Hare S, Neate S, Dijst G (eds) Rhizoctonia species: taxonomy, molecular biology, ecology, pathology and disease control. Springer, Dordrecht. https://doi.org/10.1007/978-94-017-2901-7_2

Morel S, Arnould S, Vitou M, Boudard F, Guzman C, Poucheret P, Fons F, Rapior S (2018) Antiproliferative and antioxidant activities of wild Boletales mushrooms from France. Int J Med Mushrooms 20(1):13–29

Moreno G, Prieto M, Esteve-Raventós F, Olariaga I (2017) Phylogenetic assessment of Chromocyphellaceae (Agaricineae, Basidiomycota) and a new lamellate species of *Chromocyphella*. Mycologia 109(4):578–587

Moreno-Fuentes A, Cifuentes J, Bye R, Valenzuela R (1996) Kutémo'kó-a: un hongo comestible de los indios Rarámuri de México. Scient Fung 12:31–39

Morgenstern I, Klopman S, Hibbett DS (2008) Molecular evolution and diversity of lignin degrading heme peroxidases in the Agaricomycetes. J Mol Evol 66:243–257

Mou G-F, Bau T (2021) Asproinocybaceae fam. nov.(Agaricales, Agaricomycetes) for accommodating the genera *Asproinocybe* and *Tricholosporum*, and description of *Asproinocybe sinensis* and *Tricholosporum guangxiense* sp. nov. J Fungi 7(12):1086

Moyersoen B, Beever RE, Martin F (2003) Genetic diversity of *Pisolithus* in New Zealand indicates multiple long-distance dispersal from Australia. New Phytol 160(3):569–579

Mu Y-H, Yu J-R, Cao T, Wang X-H, Yuan H-S (2021) Multi-gene phylogeny and taxonomy of *Hydnellum* (Bankeraceae, Basidiomycota) from China. J Fungi (basel) 7(10):818.https://doi.org/10.3390/jof7100818

Mueller GM, Cunha KM, May TW, Allen JL, Westrip JRS et al (2022) What do the first 597 global Fungal Red List assessments tell us about the threat status of Fungi? Diversity 14:736

Mühlmann O, Göbl F (2006) Mycorrhiza of the host-specific Lactarius deterrimus on the roots of*Picea abies* and *Arctostaphylos uva-ursi*. Mycorrhiza 16(4):245–250

Mujic AB, Hosaka K, Spatafora JW (2014) *Rhizopogon togasawariana* sp. nov., the first report of *Rhizopogon* associated with an Asian species of *Pseudotsuga*. Mycologia 106(1):105–112

Muller WH, Stalpers JA, van Aelst AC, de Jong MDM, van der Krift TP, Boekhout T (2000) The taxonomic position of *Asterodon*, *Asterostroma* and *Coltricia* inferred from the septal pore cap ultrastructure. Mycol Res 104(12):1485–1491

Murrill WA (1904) The Polyporaceae of North America. VII. The genera *Hexagona*, *Grifola*, *Romellia*, *Coltricia* and *Coltriciella*. Bull Torrey Bot Club 31:325–348

Murrill WA (1907) Polyporaceae. N Am Flora 9:1–72

Naeem MY, Ugur S, Rani S (2020) Emerging role of edible mushrooms in food industry and its nutritional and medicinal consequences. Eur J Food Sci Technol 4:6–23

Nagasawa E (2001) Taxonomic studies of Japanese boletes. I. The genera Boletinellus, Gyrodon and Gyroporus. Rep Tottori Mycol Inst 39:1–27

Nagy LG, Szöllősi G (2017) Fungal phylogeny in the age of genomics: insights into phylogenetic inference from genome-scale datasets. Adv Genet 100:49–72

Nagy LG, Riley R, Tritt A, Adam C, Daum C, Floudas D, Sun H, Yadav JS, Pangilinan J, Larsson KH, Matsuura K, Barry K, Labutti K, Kuo R, Ohm RA, Bhattacharya SS, Shirouzu T, Yoshinaga Y, Martin FM, Grigoriev IV, Hibbett DS (2016) Comparative genomics of early-diverging mushroom-forming fungi provides insights into the origins of lignocellulose decay capabilities. Mol Biol Evol 33:959–970

Nagy LG, Riley R, Bergmann PJ et al (2017) Genetic bases of fungal white rot wood decay predicted by phylogenomic analysis of correlated gene-phenotype evolution. Mol Biol Evol 34:35–44

Nair A, Ahirwar A, Singh S, Lodhi R, Lodhi A, Rai A, Jadhav DA, Harish VS, Singh G, Marchand J, Schoefs B, Vinayak V (2023) Astaxanthin as a king of ketocarotenoids: structure, synthesis, accumulation, bioavailability and antioxidant properties. Mar Drugs 21(3):176

Nakasone KK (1990) Cultural studies and identification of wood-inhabiting Corticiaceae and selected Hymenomycetes from North America. J. Cramer, Berlin

Nannenga-Bremekamp NE (1967) Notes on Myxomycetes XII. A revision of the Stemonitales. Proc Van De Koninklijke Nederlandse Akademie Van Wetenschappen Sect C 70:201–216

Nannfeldt JA (1981) *Exobasidium*, a taxonomic reassessment applied to the European species. Symb Bot Upsal 23(2):1–72

Nannfeldt JA, Eriksson J (1953) On the Hymenomycetous genus *Jaapia* Bres. and its taxonomical position. Sven Bot Tidskr 47:177–189

Naranjo-Ortiz MA, Gabaldón T (2019) Fungal evolution: diversity, taxonomy and phylogeny of the fungi. Biol Rev Camb Philos Soc 94(6):2101–2137. https://doi.org/10.1111/brv.12550

Nasr S, Soudi MR, Fazeli SAS, Nguyen HDT, Lutz M, Piątek M (2014a) Expanding evolutionary diversity in the Ustilaginomycotina: Fereydouniaceae fam. nov. and *Fereydounia* gen. nov., the first urocystidalean yeast lineage. Mycol Progr 13:1217–1226

Nasr S, Soudi MR, Nasrabadi SMZ, Nikou MM, Salmanian AH, Nguyen HDT (2014b) *Basidioascus persicus* sp. nov., a yeast-like species of the order Geminibasidiales isolated from soil. Int J Syst Evol Microbiol 64:3046–3052

Nasr S, Mohammadimehr M, Geranpayeh Vaghei M, Amoozegar MA, Shahzadeh Fazeli SA, Yurkov A (2017) *Jaminaea pallidilutea* sp. nov. (Microstromatales), a basidiomycetous yeast isolated from plant material of mangrove forests in Iran. Int J Syst Evol Microbiol 67:4405–4408

Nasr S, Lutz M, Amoozegar MA, Eparvier V, Stien D, Fazeli SAS, Yurkov A (2019) *Graphiola fimbriata*: the first species of Graphiolaceae (Exobasidiales, Basidiomycota) described only based on its yeast stage. Mycol Progr 18:359–368

Natori S, Inouye Y, Nishikawa H. (1967) The structures of mompain and deoxyhelicobasidin and the biosynthesis of helicobasidin, quinonoid metabolites of *Helicobasidium mompa* Tanaka. Chemical Pharma Bulletin 15(4):380-390

Nees von Esenbeck CGD (1817) Das system der pilze und schwämme, 2nd edn. In der Stahelschen Buchhandlung, Würzburg

Neuhoff W (1924) Zytologie und systematische Stellung der Auriculariaceen und Tremellaceen. Bot Arch 8:250–297

Ng KK, MacDonald L, Punja ZK (1997) Biological control of rose powdery mildew with the antagonist yeast *Tilletiopsis pallescens*. HortScience 32:262–266

Nguyen HDT, Nickerson NL, Seifert KA (2013) *Basidioascus* and*Geminibasidium*: a new lineage of heat-resistant and xerotolerant basidiomycetes. Mycologia 105(5):1231–1250

Nguyen HDT, Tanney JB, Chabot D, Nickerson NL, Seifert KA (2014) *Paratritirachium curvibasidium*, a new heat resistant basidiomycete from flare pit spils in Alberta. Mycol Progr 13:575–587

Nguyen HDT, Chabot D, Hirooka Y, Roberson RW, Seifert KA (2015) *Basidioascus undulatus*: genome, origins, and sexuality. IMA Fungus 6(1):215–231

Nguyen NH, Vellinga EC, Bruns TD, Kennedy PG (2016) Phylogenetic assessment of global Suillus ITS sequences supports morphologically defined species and reveals synonymous and undescribed taxa. Mycologia 108:1216–1228

Niego AGT, Lambert C, Mortimer P et al (2023) The contribution of fungi to the global economy. Fungal Divers 121:95–137. https://doi.org/10.1007/s13225-023-00520-9

Niessl G (1861) Bemerkungen über den Pilz *Fusisporium pallidum* Niessl. Oesterr Bot Z 11:250–253

Niku-Paavola ML, Karhunen E, Salola P, Raunio V (1988) Ligninolytic enzymes of the white-rot fungus *Phlebia radiata*. Biochem J 254(3):877–883

Nilsson RH, Larsson KH, Taylor AFS, Bengtsson-Palme J, Jeppesen TS et al (2018) The UNITE database for molecular identification of fungi: handling dark taxa and parallel taxonomic classifications. Nuc Acids Res 47(D1):D259–D264. https://doi.org/10.1093/nar/gky1022

Nishida T (1911) A contribution to the monograph of the parasitic Exoascaceae of Japan (in Japanese with English summary). In:

Takahashi Y (ed) Collection of botanical papers presented to Prof. Dr. Kingo Miyabe on the occasion of the twenty-fi fth anniversary of his academic service by his friends and pupils [the title is abbreviated as 'Miyabe Festschrift']. Rokumeikan, Tokyo, pp 157–212, pls 15–19

Nishida H, Sugiyama J (1993) Phylogenetic relationships among *Taphrina*, *Saitoella*, and other higher fungi. Mol Biol Evol 10:431–436

Nishida H, Sugiyama J (1994) Phylogeny and molecular evolution among higher fungi. Nippon Nougeikagaku Kaishi 68:54–57

Nishida H, Ando K, Ando Y, Hirata A, Sugiyama J (1995) *Mixia osmundae*: transfer from the Ascomycota to the Basidiomycota based on evidence from molecules and morphology. Can J Bot 73(Supplement 1):S660–S666

Nishida H, Nagatsuka Y, Sugiyama J (2011a) Draft genome sequencing of the enigmatic basidiomycete *Mixia osmundae*. J Gen Appl Microbiol 57:63–67

Nishida H, Robert V, Sugiyama J (2011b) Mixia C. L. Kramer emend. H. Nishida, K. Ando, Y. Ando, Hirata & Sugiyama (1995). In: Kurtzman CP, Fell JW, Boekhout T (eds) The yeasts, a taxonomic study, 5th edn. Elsevier, Amsterdam, pp 1499–1502

Niskanen T, Lücking R, Dahlberg A et al (2023) Pushing the frontiers of biodiversity research: unveiling the global diversity, distribution, and conservation of fungi. Annu Rev Environ Resour 48.https://doi.org/10.1146/annurev-environ-112621-090937

Nitare J (2014) *Tremellodendropsis helvetica* (Schild) Nitare comb. et stat. nov. found on the island of Öland, SE Sweden (in Swedish with English abstract). Svensk Mykologisk Tidskrift 35(2):24–31

Nitare J (2019) Skyddsvärd skog—naturvårdsarter och andra kriterier för naturvärdesbedömning. Skogsstyrelsen, Jönköping

Nitare J, Hallingbäck T (2000) Signalarter indikatorer på skyddsvärd skog: flora över kryptogamer. Skogsstyrelsen, Jönköping

Norikura T, Fujiwara K, Narita T, Yamaguchi S, Morinaga Y, Iwai K, Matsue H (2011) Anticancer activities of thelephantin O and vialinin A isolated from *Thelephora aurantiotincta*. J Agric Food Chem 59(13):6974–6979. https://doi.org/10.1021/jf200461j

Norstedt G, Bader P, Ericson L (2001) *Polypores* as indicators of conservation value in Corsican pine forests. Biol Conserv 99(3):347–354

Norvell L (2011) Report of the Nomenclature Committee for Fungi: 16. Taxon 60:223–226

Nouhra ER, Domínguez de Toledo LS (1994) Interaccion entre Phallales (Basidiomycotina) e insectos (Coleopteros y Dipteros). Boletín De La Sociedad Argentina De Botánica 30(1–2):21–24

Novaes MRCG, Novaes LCG, Taveira VC (2007) Natural products from Agaricales medicinal mushrooms: biology, nutritional properties, and pharmacological effects on cancer. Rev Bras Cancerol 53:411–420

Ntana F, Bhat WW, Johnson SR, Jørgensen HJ, Collinge DB, Jensen B, Hamberger B (2021) A sesquiterpene synthase from the endophytic fungus *Serendipita indica*catalyzes formation of viridiflorol. Biomolecules 11(6):898

Nuhn ME, Binder M, Taylor AF, Halling RE, Hibbett DS (2013) Phylogenetic overview of the Boletineae. Fungal Biol 117:479–511

Nuñez M, Ryvarden L (1994) A note on the genus *Beenakia*. Sydowia 46(2):321–328

Nuske SJ, Vernes K, May TW, Claridge AW, Congdon BC, Krockenberger A, Abell SE (2017) Data on the fungal species consumed by mammal species in Australia. Data Brief 12:251–260

Nutarat P, Boontham W, Khunnamwong P (2022) A novel yeast genus and two novel species isolated from Pineapple leaves in Thailand: *Savitreella phatthalungensis* gen. nov., sp. nov. and *Goffeauzyma siamensis* sp. nov. J Fungi 8:118

Nyland G (1950) The genus *Tilletiopsis*. Mycologia 42:487–496

Obara Y, Nakahata N, Kita T, Takaya Y, Kobayashi H, Hosoi S et al (1999) Stimulation of neurotrophic factor secretion from 1321N1 human astrocytoma cells by novel diterpenoids, scabronines A and G. Eur J Pharmacol 370:79–84. https://doi.org/10.1016/s0014-2999(99)00077-1

Oberwinkler F (1966) Primitive Basidiomyceten. Revision einiger Formenkreise von Basidienpilzen mit plastischer Basidie. Sydowia 19(1–3):1–72

Oberwinkler F (1970) Die Gattungen der Basidiolichenen. Vortr Gesamtgeb Bot 4:139–169

Oberwinkler F (1976) Eine agaricoide Gattung der Thelephorales. Sydowia 28(1–6):359–362

Oberwinkler F (1977) Das neue System der Basidiomyceten. In: Frey W, Hurka H, Oberwinkler F (eds) Beiträge zur Biologie der niederen Pflanzen. Gustav Fischer Verlag, Stuttgart

Oberwinkler F (1984) Fungus-alga interactions in Basidiolichens. Beih Nova Hedwigia 79:739–774

Oberwinkler F (1990) New genera of auricularioid heterobasidiomycetes. Rep Tottori Mycol Inst 28:113–127

Oberwinkler F (2012) Basidiolichens. In: Hock B (ed) The Mycota, vol IX. Fungal associations. Springer, New York, pp 341–362

Oberwinkler F (2017) Yeasts in Pucciniomycotina. Mycol Progr 16:831–856

Oberwinkler F, Bandoni RJ (1981) *Tetragoniomyces* gen. nov. and Tetragoniomycetaceae fam. nov. (Tremellales). Can J Bot 59(6):1034–1040

Oberwinkler F, Bandoni RJ (1982) A taxonomic survey of the gasteroid, auricularioid Heterobasidiomycetes. Can J Bot 60:1726–1750

Oberwinkler F, Bandoni RJ (1984) *Herpobasidium* and allied genera. Trans Br Mycol Soc 83(4):639–658

Oberwinkler F, Bauer R (1989) The systematics of gasteroid, auricularioid Heterobasidiomycetes. Sydowia 41:224–256

Oberwinkler F, Bauer R (1990a) *Cryptomycocola*x: a new mycoparasitic heterobasidiomycete. Mycologia 82:671–692

Oberwinkler F, Bauer R (1990b) Heterogastridiales: a new order of Basidiomycetes. Mycologia 82(1):48–58

Oberwinkler F, Bandoni RJ, Blanz P, Deml G, Kisimova-Horovitz L (1982) Graphiolales: Basidiomycetes parasitic on palms. Plant Syst Evol 140:251–277

Oberwinkler F, Bauer R, Bandoni RJ (1990) *Colacogloea*—a new genus in the auricularioid Heterobasidiomycetes. Can J Bot 68:2531–2536. https://doi.org/10.1139/b90-318

Oberwinkler F, Bauer R, Tschen J (1999) The mycoparasitism of *Platygloea bispora*. Kew Bull 54:763–769. https://doi.org/10.2307/4110873

Oberwinkler F, Kirschner R, Arenal F, Villarreal M, Rubio V, Begerow D, Bauer R (2006) Two new members of the Atractiellale: *Basidiopycnis hyalina* and *Proceropycnis pinicola*. Mycologia 98(4):637–649

Oberwinkler F, Riess K, Bauer R, Garnica S (2014) Morphology and molecules: the Sebacinales, a case study. Mycol Prog 13:445–470

Oberwinkler F, Riess K, Bauer R, Selosse M-A, Weiss M, Garnica S, Zuccaro A (2013a) Enigmatic Sebacinales. Mycol Prog 12:1–27

Oberwinkler F, Riess K, Bauer R, Kirschner R, Garnica S (2013b) Taxonomic re-evaluation of the ceratobasidium-rhizoctonia complex and rhizoctonia butinii, a new species attacking spruce. Mycol Prog 12:763–776

Ochoa C, Moreno G (2006) Hongos gasteroides y secotioides de Baja California, México. Boletín De La Sociedad Micológica De Madrid 30:121–166

Ogura-Tsujita Y, Gebauer G, Xu H, Fukasawa Y, Umata H, Tetsuka K, Kubota M, Schweiger JM, Yamashita S, Maekawa N, Maki M (2018) The giant mycoheterotrophic orchid *Erythrorchis altissima* is associated mainly with a divergent set of wood-decaying fungi. Mol Ecol 27(5):1324–1337

Okayama M, Yamato M, Yagame T, Iwase K (2012) Mycorrhizal diversity and specificity in*Lecanorchis* (Orchidaceae). Mycorrhiza 22:545–553

Oja J, Bahram M, Tedersoo L, Kull T, Kõljalg U (2015) Temporal patterns of orchid mycorrhizal fungi in meadows and forests as revealed by 454 pyrosequencing. New Phytol 205:1608–1618

Olariaga I (2021) Cantharellales Gaüm. In: Zaragoza O, Casadevall A (eds) Encyclopedia of mycology, 1st edn. Elsevier, pp 320–328

Olariaga I, Huhtinen S, Læssøe T, Petersen JH, Hansen K (2020) Phylogenetic origins and family classification of typhuloid fungi, with emphasis on Ceratellopsis, *Macrotyphula* and *Typhula* (Basidiomycota). Stud Mycol 96:155–184

Olive LS (1952) A new species of *Cystobasidium* from New Jersey. Mycologia 44(4):564–569

Olive LS (1968) An unusual heterobasidiomycete with *Tilletia*-like basidia. J Elisha Mitchell Sci Soc 84:261–266

Oliveira JJ, Vargas-Isla R, Cabral TS, Rodrigues DP, Ishikawa NK (2019) Progress on the phylogeny of the Omphalotaceae: *Gymnopus* s. str., *Marasmiellus* s. str., *Paragymnopus* gen. nov. and *Pusillomyces* gen. nov. Mycol Prog 18:713–739

Olufunmilola OM, Shian AJ, Dooshima IB (2019) Effects of plasticizer concentration and mushroom (*Pleurotus pulmonarius*) flour inclusion on the sensory, mechanical and barrier properties of cassava starch based edible films. Eur J Food Sci Technol 7:47–62

Ordynets A, Larsson K-H, Langer E (2015) Two new Trechispora species from La Réunion Island. Mycol Prog 14:113

Ordynets A, Scherf D, Pansegrau F, Denecke J, Lysenko L, Larsson K-H, Langer E (2018) Short-spored Subulicystidium (Trechisporales, Basidiomycota): high morphological diversity and only partly clear species boundaries. MycoKeys 35:41–99

Orihara T, Smith ME (2017) Unique phylogenetic position of the African truffle-like fungus,*Octaviania ivoryan*a (Boletaceae, Boletales), and the proposal of a new genus, Afrocastellanoa. Mycologia 109(2):323–332

Orihara T, Healy R, Corrales A, Smith ME (2021) Multilocus phylogenies reveal three new truffle-like taxa and the traces of interspecific hybridization in *Octaviania* (Boletaceae, Boletales). IMA Fungus 12:1–22

Ortiz-Santana B, Lindner DL, Miettinen O, Justo A, Hibbett DS (2013) A phylogenetic overview of the antrodia clade (Basidiomycota, Polyporales). Mycologia 105(6):1391–1411

Otero JT, Flanagan NS, Alomia YA, Mosquera Espinosa AT (2017) Seed Viability and Symbiotic Seed Germination in *Vanilla* spp. (Orchidaceae). Res J Seed Sci 10:43–52

Overholts LO (1915) Comparative studies in the Polyporaceae. Ann Missouri Bot Garden 2(4):667–724+726–730

Overholts LO (1953) The Polyporaceae of the United States, Alaska, and Canada. The University of Michigan Press, Ann Arbor

Owaid MN, Ibraheem IJ (2017) Mycosynthesis of nanoparticles using edible and medicinal mushrooms. Eur J Nanomed 9:5–23

Owaid MN, Barish A, Ali Shariati M (2017) Cultivation of *Agaricus bisporus* (button mushroom) and its usages in the biosynthesis of nanoparticles. Open Agric 2:537–543. https://doi.org/10.1515/opag-2017-0056

Oyetayo VO, Oyetayo FL (2007) Hematological parameters of rats fed mushroom, *Pleurotus sajor-caju* diets and orogastrically dosed with probiotic *Lactobacillus fermentum* Ovl. Int J Probiotics Prebiotics 2:39–42

Pacquiao MR, de Luna MDG, Thongsai N, Kladsomboon S, Paoprasert P (2018) Highly fluorescent carbon dots from Enokitake mushroom as multi-faceted optical nanomaterials for Cr^{6+} and VOC detection and imaging applications. Appl Surf Sci 453:192–203

Palfner G (2006) *Austrobasidium*, a new gall-forming genus of Exobasidiaceae (Exobasidiales, Basidiomycota) on *Hydrangea serratifolia*from Chile. Austral Syst Bot 19:431–436

Palfner G, Galleguillos F, Arnold N, Casanova-Katny A, Horak E (2020) Sequestrate syndrome in*Bondarzewia guaitecasensis* (Fungi, Basidiomycota)? The case of *Hybogaster giganteus* revisited. Phytotaxa 474(3):272–282

Pandey K, Ghosh SK (2022) Biodiversity of *Astraeus asiaticus*, a wild indigenous edible mushroom, in the forests of Bankura district, west Bengal and its antioxidant property. Acta Mycol 57:575

Parmasto E (1968) Conspectus Systematis Corticiacearum. Institutum Zoologicum et Botanicum Academiae Scientiarum RPSS Estonicae, Tartu

Parmasto E, Parmasto I (1979) The xanthocroic reaction in Aphyllophorales. Mycotaxon 8:201–232

Patouillard NT (1885) Note sur un genre nouveau d'Hyménomycètes (Helicobasidium). Bulletin De La Société Botanique De France 32:171–172

Patouillard NT (1889) Le genre *Ganoderma*. Bull Soc Mycol Fr 5:64–80

Patouillard NT (1892) *Septobasidium*, Nouveau genre d'Hyménomycètes hétérobasidiés. Journal De Botanique 6(4):61–64

Patouillard NT (1900) Essai taxonomique sur les familles et les genres des Hyménomycètes. Dissertation, University of Paris

Peay KG, Kennedy PG, Talbot JM (2016) Dimensions of biodiversity in the Earth mycobiome. Nat Rev Microbiol 14(7):434–447

Pegg GS, Carnegie AJ, Wingfield MJ, Drenth A (2009) *Quambalaria* species: increasing threat to eucalypt plantations in Australia. South for 71:111–114

Pegler DN, Young TWK (1979) The gasteroid Russulales. Trans Br Mycol Soc 72(3):353–388

Pérez-Moreno J, Guerin-Laguette A, Rinaldi AC et al (2021) Edible mycorrhizal fungi of the world: What is their role in forest sustainability, food security, biocultural conservation and climate change? Plants People Planet 3(5):471–490. https://doi.org/10.1002/ppp3.10199

Perini L, Andrejašič K, Gostinčar C, Gunde-Cimerman N, Zalar P (2021) Greenland and Svalbard glaciers host unknown basidiomycetes: the yeast *Camptobasidium arcticum*sp. nov. and the dimorphic *Psychromyces glacialis* gen. and sp. nov. Int J Syst Evolut Microbiol 71(2):004655

Persoon CH (1794a) Dispositio methodica fungorum. Neues Magazin Für Die Botanik 1:81–128

Persoon CH (1794b) Neuer Versuch einer systematischen Einteilung der Schwämme. Neues Mag Bot 1:63–128

Persoon CH (1796) Observationes mycologicae. Apud Petrum Phillippum Wolf, Leipzig

Persoon CH (1797) Tentamen Dsipositionis Methodicae Fungorum in Classes, Ordinis, Genera et Familias cum Supplemento Adjecto i-iv, 1–76, 4 plates,. PP Wolf, Leipzig

Persoon CH (1801) Synopsis Methodica Fungorum, vol 1. Henricum Dieterich, Gottingae

Persoon CH (1825) Mycologia. Europaea 2:1–214

Petcharat V (2008) Edible *Astraeus* (Basidiomycota) from Thailand. Nord J Bot 23:499–503

Peter M, Ayer F, Cudlín P, Egli S (2008) Belowground ectomycorrhizal communities in three Norway spruce stands with different degrees of decline in the Czech Republic. Mycorrhiza 18:157–169

Petersen RH (1967) Notes on clavarioid fungi. VII. Redefinition of the *Clavaria vernalis-C. mucida* complex. Am Midland Nat 77:205–221

Petersen RH (1971) Interfamilial relationships in the clavaroid and cantharelloid fungi. In: Petersen RH (ed) Evolution in the higher Basidiomycetes. University of Knoxville Press, Knoxville, pp 345–374

Petersen RH (1985) Type studies in the clavarioid fungi-IX. Miscellaneous taxa, with a section on Tremellodendropsis. Persoonia 12:401–413

Petersen RH (1987) Notes on clavarioid fungi. XXI. New Zealand Taxa of Tremellodendropsis. Mycotaxon 29:45–65

Petersen RH (2008a) Scanning electron microscope images of basidiospores of *Xerula* (Physalacriaceae, Agaricales). Mycoscience 49:19–34

Petersen RH (2008b) Species of *Xerula* from sub-Saharan Africa. Fungal Divers 30:121–147

Petersen RH (2008c) The genus *Xerula* (Agaricales; Fungi) in Australia and New Zealand. Nova Hedwigia 87:1–67

Petersen RH, Hughes KW (2010) The *xerula*/*Oudemansiella* complex. Beiheft Zur Nova Hedwigia 137:1–625

Petersen RH, Hughes KW (2020) Two new genera of gymnopoid/marasmioid euagarics. Mycotaxon 135(1):1–95

Petersen RH, Hughes KW (2021) *Collybiopsis* and its type species, *Co. Ramealis*. Mycotaxon 136:263–349

Petersen RH, Nagasawa E (2005) The genus *Xerula* in temperate east Asia. Rep Tottori Mycol Inst 43:1–49

Phookamsak R, Hyde KD, Jeewon R et al (2019) Fungal diversity notes 929–1035: taxonomic and phylogenetic contributions on genera and species of fungi. Fungal Divers 95:1–273. https://doi.org/10.1007/s13225-019-00421-w

Phosri C, Martín MP, Sihanonth P, Whalley AJ, Watling R (2007) Molecular study of the genus*Astraeus*. Mycol Res 111(3):275–286

Piątek M (2005) A note on the genus *Xenasmatella* (Fungi, Basidiomycetes). Pol Bot J 50(1):11–13

Piątek M, Riess K, Karasiński D et al (2016) Integrative analysis of the West African *Ceraceosorus africanus* sp. nov. provides insights into the diversity, biogeography, and evolution of the enigmatic Ceraceosorales (Fungi: Ustilaginomycotina). Org Divers Evol 16:743–760

Piepenbring M (2000) The species of *Cintractia* s. lat. (Ustilaginales, Basidiomycota). Nova Hedwigia 70:289–372

Piepenbring M (2001) *Cintractiella diplasiae*—a second species of *Cintractiella* (Ustilaginales) with sori in adventitious spikelets on Hypolytreae (Cyperaceae). Perspect Pl Ecol Evol Syst 4(2):116–120

Piepenbring M, Bauer R (1997) *Erratomyces*, a new genus of Tilletiales with species on Leguminosae. Mycologia 89:924–936

Piepenbring M, Vánky K, Oberwinkler F (1996) *Aurantiosporium,* a new genus for *Ustilago subnitens* (Ustilaginales). PI Syst Evol 199:53–64

Piepenbring M, Begerow D, Oberwinkler F (1999) Molecular sequence data assess the value of morphological characteristics for a phylogenetic classification of species of *Cintractia*. Mycologia 91:485–498

Piepenbring M, Nold F, Trampe T, Kirschner R (2012) Revision of the genus *Graphiola* (Exobasidiales, Basidiomycota). Nova Hedwigia 94:67–93

Piepenbring M, Hartmann M, Hofmann TA, Lutz M (2020) Two new species in a new genus and a critical revision of Brachybasidiaceae (Exobasidiales, Basidiomycota) in honor of Franz Oberwinkler. Mycol Prog 19:351–365

Pilát A (1958) Phallales. In: Cejp K, Moravec Z, Pilát A, Pouzar Z, Staněk VJ, Surček M, Šebek S, Smarda F (eds) Gasteromycetes. Flora. ČSR Nakladatelstvi Československé Akademie Věd, Prague, pp 704–715

Pilz D, Norvell L, Danell E, Molina R (2003) Ecology and Management of Commercially Harvested Chanterelle Mushrooms (General Technical Report). Pacific Northwest Research Station, Portland

Pine EM, Hibbett DS, Donoghue MJ (1999) Phylogenetic relationships of cantharelloid and clavarioid homobasidiomycetes based on mitochondrial and nuclear rDNA sequences. Mycologia 91:944–963

Pino-Bodas R, Laakso I, Stenroos S (2017) Genetic variation and factors affecting the generic structure of the lichenicolous fungus *Heterocephalacria bachamannii*(Filobasidiales, Basidiomycota). PLoS ONE 12:e0189603

Plumier C (1705) Traité des fougeres de l'Amerique. L'Imprimerie Royale, Paris

Põlme S, Abarenkov K, Henrik Nilsson R et al (2020) FungalTraits: a user-friendly traits database of fungi and fungus-like stramenopiles. Fungal Divers 105:1–16

Ponce de León P (1968) A revision of the family Geastraceae. Fieldiana Bot 31:302–349

Pontes A, Röhl O, Maldonado C, Yurkov AM, Sampaio JP (2017) *Cryptotrichosporon argae* sp. nov., *Cryptotrichosporon brontae* sp. nov. and *Cryptotrichosporon steropae* sp. nov., isolated from forest soils. Int J Syst Evolut Microbiol 67(9):3610–3614

Pontes A, Ruethi J, Frey B, Aires A, Thomas A, Overy D, Halti B, Kerr R, Sampaio JP (2020) *Cryolevonia* gen. nov. and *Cryolevonia schafbergensis* sp. nov., a cryophilic yeast from ancient permafrost and melted sea ice. Int J Syst Evolut Microbiol 70(4):2334–2338

Pouzar Z (1958) Nova Genera Macromycetum II. Česká Mykologie 12:31–36

Poverenov E, Arnon-Rips H, Zaitsev Y, Bar V, Danay O, Horev B, Rodov V (2018) Potential of chitosan from mushroom waste to enhance quality and storability of fresh-cut melons. Food Chem 268:233–241

Pratt JE, Niemi M, Sierota ZH (2000) Comparison of three products based on *Phlebiopsis gigantea* for the control of *Heterobasidion annosum* in Europe. Biocontrol Sci Tech 10:467–477. https://doi.org/10.1080/09583150050115052

Prencipe S, Spadaro D, Fruk G, Jemric T (2016) First report of *Tilletiopsis pallescens* causing white haze on apple in Croatia. Plant Dis 100:225.https://doi.org/10.1094/PDIS-05-15-0505-PDN

Preußing M, Nebel M, Oberwinkler F, Weiss M (2010) Diverging diversity patterns in the*Tulasnella* (Basidiomycota, Tulasnellales) mycobionts of *Aneura pinguis* (Marchantiophyta, Metzgeriales) from Europe and Ecuador. Mycorrhiza 20:147–159

Qiao M, Li W, Huang Y, Xu J, Zhang L, Yu Z (2018) *Classicula sinensis*, a new species of basidiomycetous aquatic hyphomycetes from Southwest china. Mycokeys 40:1–12

Qu J, Zang T, Gu H, Li K, Hu Y, Ren G, Xu X, Jin Y (2015) Biosorption of copper ions from aqueous solution by *Flammulina velutipes* spent substrate. BioResources 10:8058–8075

Quélet L (1886) Enchiridion fungorum in Europa media et praesertim in Gallia vigentum. O Doin, Lutetiae

Quintero-Cabello KP, Lugo-Flores MA, Rivera-Palafox P, Silva-Espinoza BA, González-Aguilar GA, Esqueda M, Gaitán-Hernández R, Ayala-Zavala JF (2021) Antioxidant properties and industrial uses of edible polyporales. J Fungi 7(3):196. https://doi.org/10.3390/jof7030196

Raciborski M (1909) Parasitische und epiphytische Pilze Java's. Bulletin International De L'academie Des Sciences De Cracovie. Classe Des Sciences Mathematiques Et Naturelles 3:346–394

Raghoonundon B, Raspé O, Thongklang N, Hyde KD (2021) *Phlebopus* (Boletales, Boletinellaceae), a peculiar bolete genus with widely consumed edible species and potential for economic development in tropical countries. Food Biosci 41:100962

Rahi DK, Malik D (2016) Diversity of mushrooms and their metabolites of nutraceutical and therapeutic significance. J Mycol 2016:1–18. https://doi.org/10.1155/2016/7654123

Raidl S, Scattolin L, Agerer R (2006) *Gyroporus castaneus*(Bull.: Fr.) Quél. + *Quercus robur* L. Descr Ectomycorrhizae 9:39–44

Raj KA, Latha KD, Leelavathy KM, Manimohan P (2019) *Anupama*: a new genus of Biannulariaceae (Agaricales) from tropical India. Mycol Prog 18:659–669

Raj K, Wati L, Kumar A (2021) Fungal diversity and its role in sustainable agriculture. In: Jogaiah S (ed) Biocontrol Agents and Secondary Metabolites: Applications and Immunization for Plant Growth and Protection. Woodhead Publishing, pp 519–535. https://doi.org/10.1016/b978-0-12-822919-4.00023-5

Rajchenberg M, Robledo G (2013) Pathogenic polypores in Argentina. For Path 43(3):171–184.https://doi.org/10.1111/efp.12032

Ramírez-López I, Villegas-Ríos M, Salas-Lizana R (2015) *Thelephora versatilis* and *Thelephora pseudoversatilis*: two new cryptic species with polymorphic basidiomes inhabiting tropical deciduous and sub-perennial forests of the Mexican Pacific coast. Mycologia 107:346–358. https://doi.org/10.3852/14-151

Rapior S, Fons F, Bessière JM (2000) The fenugreek odor of Lactarius helvus. Mycologia 92:305–308

Rea C (1922) British Basidiomycetae: a handbook to the larger British Fungi. University Press, Cambridge

Redberg GL, Rodriguez R, Ammirati J, Hibbett DS (2003) Phylogenetic relationships of *Bridgeoporus nobilissimus* inferred from rDNA sequences. Mycologia 95(5):685–687

Reddy MS, Kramer CL (1975) A taxonomic revision of the Protomycetales. Mycotaxon 3:1–50

Redhead SA, Ginns JH (1985) A reappraisal of agaric genera associated with brown rots of wood. Trans Mycol Soc Japan 26:349–381

Redhead SA, Moncalvo JM, Rytas V, Lutzoni F (2002) Phylogeny of agarics: partial systematics solutions for bryophilous omphalinoid agarics outside of the Agaricales (euagarics). Mycotaxon 82:151–168

Redhead SA, Vizzini A, Drehmel DC, Contu M (2015) *Saproamanita*, a new name for both *Lepidella* E.-J. Gilbert and *Aspidella* E.-J. Gilbert (Amanitae, Amanitaceae). IMA Fungus 7:119–129

Reid DA (1956) New or Interesting Records of Australasian Basidiomycetes: II. Kew Bull 11(3):535–540

Reid DA (1963) New or interesting records of Australasian Basidiomycetes: V. Kew Bull 17:267–308

Reid DA, Manimohan P (1985) *Auriculoscypha*, a new genus of Auriculariales (Basidiomycetes) from India. Trans Br Mycol Soc 85:532–535

Retnowati A, Kusumawaty A, Apandi I, Haryadi A (2020) Short communication: two newly recorded species of Agaricales (Basidiomycota) from Banggai Kepulauan, Sulawesi, Indonesia. Biodiversitas 21:5615–5621. https://doi.org/10.13057/biodiv/d211217

Reynolds HT, Vijayakumar V, Gluck-Thaler E, Korotkin HB, Matheny PB, Slot JC (2018) Horizontal gene cluster transfer increased hallucinogenic mushroom diversity. Evol Lett 2:88–101. https://doi.org/10.1002/evl3.42

Rhimi W, Theelen B et al (2020) *Malassezia* spp. Yeasts of emerging concern in fungemia. Front Cell Infect Microbiol 10:370. https://doi.org/10.3389/fcimb.2020.00370

Richard F, Millot S, Gardes M, Selosse MA (2005) Diversity and specificity of ectomycorrhizal fungi retrieved from an old-growth Mediterranean forest dominated by Quercus ilex. New Phytol 166(3):1011–1023

Richter C, Yurkov AM, Boekhout T, Stadler M (2019) Diversity of *Tilletiopsis*-like fungi in Exobasidiomycetes (Ustilaginomycotina) and description of six novel species. Front Microbiol 10:2544

Riess K, Oberwinkler F, Bauer R, Garnica S (2013) High genetic diversity at the regional scale and possible speciation in *Sebacina epigaea* and *S. incrustans*. BMC Evolut Biol 13:102

Riess K, Oberwinkler F, Bauer R, Garnica S (2014) Communities of endophytic Sebacinales associated with roots of herbaceous plants in agricultural and grassland ecosystems are dominated by*Serendipita herbamans* sp. nov. PLoS ONE 17:e94676

Riess K, Schön ME, Lutz M, Butin H, Oberwinkler F, Garnica S (2016) On the evolutionary history of *Uleiella chilensis*, a smut fungus parasite of *Araucaria araucana* in South America: Uleiellales ord. nov. in Ustilaginomycetes. PLoS ONE 11:e0147107

Riley R, Salamov AA, Brown DW et al (2014) Extensive sampling of basidiomycete genomes demonstrates inadequacy of the whiterot/brown-rot paradigm for wood decay fungi. Proc Natl Acad Sci USA 111:9923–9928

Rincón YA, Siless GE, D'Jonsiles F et al (2023) Antifungal γ-pyrone and isoprenylated cyclohexanoids from the fungus *Beenakia informis*. Chem Biodivers 20:e202300021. https://doi.org/10.1002/cbdv.202300021

Ringel M, Dimos N, Himpich S, Haack M, Huber C, Eisenreich W, Schenk G, Loll B, Brück T (2022) Biotechnological potential and initial characterization of two novel sesquiterpene synthases from Basidiomycota Coniophora puteana for heterologous production of δ-cadinol. Microb Cell Fact 21(1):64

Rivas-Ferreiro M, Otero A, Morán P (2023) It's what's inside that counts: DNA-barcoding of porcini (*Boletus* sp., Basidiomycota) commercial products reveals product mislabelling. Food Control 144:109346

Rivera OA, Albarracin W, Lares M (2017) Bioactive components of Shiitake (*Lentinula edodes* Berk. Pegler) and its impact on health. Arch Venez Farmacol Ter 36:67–71

Roberts P (1996) Heterobasidiomycetes from Majorca & Cabrera (Nalearic islands). Mycotaxon 60:111–123

Roberts P (1997) New heterobasidiomycetes from Great Britain. Mycotaxon 63:195–216

Roberts P (1999) Rhizoctonia-forming Fungi. Royal Botanic Gardens, Kew

Robledo G, Urcelay C (2017) *Kavinia chacoserrana* sp. nov. (Gomphales, Basidiomycota): a new species from South America based on morphological and molecular data. Mycosphere 8(6):1028–1034. https://doi.org/10.5943/mycosphere/8/6/3

Robledo GL, Palacio M, Urcelay C, Vasco-Palacios AM, Crespo E, Popoff O, Põldmaa K, Ryvarden L, Costa-Rezende DH (2020) Mystery unveiled: *Diacanthodes* Singer—a lineage within the core polyporoid clade. Syst Biodivers 18(6):538–556

Rogers DP (1932) A cytological study of *Tulasnella*. Bot Gaz 94:86–105

Rogers DP (1935) Notes on the lower basidiomycetes. Univ Iowa Stud Nat Hist 17:3–43

Rogers DP (1943) The genus *Pellicularia* (Thelephoraceae). Farlowia 1:95–118

Rogers R (2011) The fungal pharmacy, The complete guide to medinal mushrooms & lichens of North America. Published by North Atlantics Books, Berkeley

Rosa CA, Jindamorakot S, Limtong S, Nakase T, Lachance MA (2008) Synonymy of the yeast genera*Moniliella* and *Sporotrichonoides* and proposal of *Moniliella fonsecae* sp. nov. and five new species combinations. Int J Syst Evol Microbiol 59:425–429

Rosenthal LM, Larsson K-H, Branco S et al (2017) Survey of corticioid fungi in North American pinaceous forests reveals hyperdiversity, underpopulated sequence databases, and species that are potentially ectomycorrhizal. Mycologia 109:115–127

Roskov Y, Ower G, Orrell T, Nicolson D, Bailly N, Kirk PM, Bourgoin T, DeWalt RE, Decock W, Nieukerken E. van, Zarucchi J, Penev L (2023) Species 2000 & ITIS Catalogue of Life, 25th March 2019. Digital resource at www.catalogueoflife.org/col. Species 2000. Naturalis, Leiden

Roy D, Fahim A (2019) The effect of different level of mushroom (*Agaricus bisporus*) and probiotics (*Saccharomyces cerevisiae*) on sensory evaluation of broiler meat. J Entomol Zool Stud 7:347–349

Roy M, Watthana S, Stier A, Richard F, Vessabutr S, Selosse MA (2009) Two mycoheterotrophic orchids from Thailand tropical dipterocarpacean forests associate with a broad diversity of ectomycorrhizal fungi. BMC Biol 7(1):51

Royse DJ (2014) A global perspective on the high five: *Agaricus*, *Pleurotus, Lentinula, Auricularia* & *Flammulina*. Proceedings of the 8th International Conference on Mushroom Biology and Mushroom Products (ICMBMP8), vol 1. New Delhi, India

Royse DJ, Baars J, Tan Q (2017) Current overview of mushroom production in the world. In: Diego CZ, Pardo-Giménez A (eds) Edible and medicinal mushrooms: technology and applications. Wiley, Hoboken, pp 5–13

Ruiz-Dueñas FJ, Barrasa JM, Sánchez-García M, Camarero S, Miyauchi S, Serrano A, Linde D, Babiker R, Drula E, Ayuso-Fernández I, Pacheco R, Padilla G, Ferreira P, Barriuso J, Kellner H, Castanera R, Alfaro M, Ramírez L, Pisabarro AG, Riley R, Kuo A, Andreopoulos W, LaButti K, Pangilinan J, Tritt A, Lipzen A, He G, Yan M, Ng V, Grigoriev IV, Cullen D, Martin F, Rosso MN, Henrissat B, Hibbett D, Martínez AT (2020) Genomic analysis enlightens Agaricales Lifestyle Evolution and increasing peroxidase diversity. Mol Biol Evol 38:1428–1446. https://doi.org/10.1093/molbev/msaa301

Runnel K, Miettinen O, Lõhmus A (2021) Polypore fungi as a flagship group to indicate changes in biodiversity—a test case from Estonia. IMA Fungus 12:2. https://doi.org/10.1186/s43008-020-00050-y

Rush TA, Aime MC (2013) The genus *Meira*: phylogenetic placement and description of a new species. Antonie Van Leeuwenhoek 103:1097–1106

Russ L, Lombaers-van der Plas C, Castillo-Russi JD, Zijlstra C, Köhl J (2021) Deciphering the modes of action of *Golubevia sp*., an antagonist against the causal agent of powdery mildew in wheat, using an mRNA-based systems approach. Biol Control 152:104446

Ryberg M, Larsson E, Molau U (2009) Ectomycorrhizal diversity on *Dryas octopetala* and *Salix reticulata* in an alpine cliff ecosystem. Arct Antarct Alp Res 41(4):506–514. https://doi.org/10.1657/1938-4246-41.4.506

Ryvarden L (1991) Genera of Polypores, Nomenclature and Taxonomy. Synopsis fungorum 5. Fungiflora, Oslo

Ryvarden L (2002) A note on the genus Hydnodon Banker. Syn Fung 15:31–33

Ryvarden L (2005) Genera of polypores. Nomclature and Taxonomy Syn Fung 5:1–363

Ryvarden L, Gilbertson RL (1994) European polypores, vol 2. Synopsis Fungorum 6. Fungiflora, Oslo

Ryvarden L, Johansen I (1980) A preliminary polypore flora of East Africa. Fungiflora, Oslo

Sa'diyah W, Hashimoto A, Okada G, Ohkuma M (2021) Notes on some interesting sporocarp-inhabiting fungi isolated from xylarialean fungi in Japan. Diversity 13:574

Saar I, Thorn RG, Nagasawa E, Henkel TW, Cooper JA (2022) A phylogenetic overview of *Squamanita*, with descriptions of nine new species and four new combinations. Mycologia 114(4):769–797

Saccardo PA (1880a) Conspectus generum fungorum Italiae inferiorum nempe ad Sphaeropsideas, Melanconieas et Hyphomyceteas pertinentium systemate sporologico dispositorum. Michelia 2(6):1–38

Saccardo PA (1880b) Fungi gallici lecti a cl. viris P. Brunaud, Abb. Letendre, A. Malbranche, J. Therry vel editi in Mycotheca gallica C. Rumeguèri. Series II. Michelia 2(6):39–135

Saccardo PA, Traverso JB (1910) Sylloge Fungorum, vol 19. sumptibus auctoris, Patavii

Saheb Kashaf S, Proctor DM et al (2022) Integrating cultivation and metagenomics for a multi-kingdom view of skin microbiome diversity and functions. Nat Microbiol 7(1):169–179. https://doi.org/10.1038/s41564-021-01011-w

Sampaio JP (2011a) Rhodosporidium Banno (1967). In: Kurtzman CP, Fell JW, Boekhout T (eds) The yeasts, a taxonomic study, 5th edn. Elsevier, Amsterdam, pp 1523–1539

Sampaio JP (2011b) Sporidiobolus Nyland (1949). In: Kurtzman CP, Fell JW, Boekhout T (eds) The yeasts, a taxonomic study, 5th edn. Elsevier, Amsterdam, pp 1549–1561

Sampaio JP (2011c) Rhodotorula Harrison (1928). In: Kurtzman CP, Fell JW, Boekhout T (eds) The yeasts, a taxonomic study, 5th edn. Elsevier, Amsterdam, pp 1873–1927

Sampaio JP (2011d) Leucosporidium Fell, Statzell, I.L. Hunter & Phaff (1969). In: Kurtzman CP, Fell JW, Boekhout T (eds) The yeasts, a taxonomic study, 5th edn. Elsevier, Amsterdam, pp 1485–1494

Sampaio JP (2011e) Papiliotrema Sampaio, Weiss & Bauer (2002). In: Kurtzman CP, Fell JW, Boekhout T (eds) The yeasts, a taxonomic study, 5th edn. Elsevier, Amsterdam, pp 1519–1521

Sampaio JP, Chen C-J (2011) Naohidea Oberwinkler (1990). In: Kurtzman CP, Fell JW, Boekhout T (eds) The yeasts, a taxonomic study, 5th edn. Elsevier, Amsterdam, pp 1511–1513

Sampaio JP, Oberwinkler F (2011a) Cystobasidium (Lagerheim) Neuhoff (1924). In: Kurtzman CP, Fell JW, Boekhout T (eds) The yeasts, a taxonomic study, 5th edn. Elsevier, Amsterdam, pp 1419–1422

Sampaio JP, Oberwinkler F (2011b) Kriegeria Bresadola 1891. In: Kurtzman CP, Fell JW, Boekhout T (eds) The yeasts, a taxonomic study, 5th edn. Elsevier, Amsterdam, pp 1477–1479

Sampaio JP, Bauer R, Begerow D, Oberwinkler F (1999a) *Occultifur externus* sp. nov., a new species of simple-pored auricularioid heterobasidiomycete from plant litter in Portugal. Mycologia 91(6):1094–1101

Sampaio J, Fell JW, Gadanho M, Bauer R (1999b) *Kurtzmanomyces insolitus* sp. nov. a new anamorphic heterobasidiomycetous yeast species. Syst Appl Microbiol 22:619–625

Sampaio JP, Weiβ M, Gadanho M et al (2002) New taxa in the Tremellales: *Bulleribasidium oberjochense* gen. et sp. nov., *Papiliotrema bandonii* gen. et sp. nov. and *Fibulobasidium murrhardtense* sp. nov. Mycologia 94:873–887

Sampaio JP, Gadanho M, Bauer R, Weiss M (2003) Taxonomic studies in the Microbotryomycetidae:*Leucosporidium golubevii* sp. nov., *Leucosporidiella* gen. nov. and the new orders Leucosporidiales and Sporidiobolales. Mycol Prog 2(1):53–68

Sampaio JP, Inacio J, Fonseca A et al (2004) *Auriculibuller fuscus* gen. nov., sp. nov. and *Bullera japonica* sp. nov., novel taxa in the Tremellales. Int J Syst Evol Microbiol 54:987–993

Sánchez-García M, Matheny PB (2017) Is the switch to an ectomycorrhizal state an evolutionary key innovation in mushroom-forming fungi? A case study in the Tricholomatineae (Agaricales). Evolution 71(1):51–65

Sánchez-García M, Henkel TW, Aime MC, Smith ME, Matheny PB (2016) *Guyanagarika*, a new ectomycorrhizal genus of Agaricales from the Neotropics. Fungal Biol 120(12):1540–1553

Sánchez-García M, Ryberg M, Khan FK, Varga T, Nagy LG, Hibbett DS (2020) Fruiting body form, not nutritional mode, is the major driver of diversification in mushroom-forming fungi. Proc Natl Acad Sci USA 117(51):32528–32534

Sánchez-Ruiz MI, Ayuso-Fernández I, Rencoret J, González-Ramírez AM, Linde D, Davó-Siguero I, Romero A, Gutiérrez A, Martínez AT, Ruiz-Dueñas FJ (2021) Agaricales mushroom lignin peroxidase: from structure-function to degradative capabilities. Antioxidants 10:1446

Sandargo B, Chepkirui C, Cheng T et al (2019) Biological and chemical diversity go hand in hand: Basidiomycota as source of new pharmaceuticals and agrochemicals. Biotechnol Adv 37:107344

Sanderson MJ (2003) r8s: inferring absolute rates of molecular evolution and divergence times in the absence of a molecular clock. Bioinformatics 19:301–302. https://doi.org/10.1093/bioinformatics/19.2.301

Sandoval P, Calle A, Robledo G (2022) *Kavinia altoandina*(Basidiomycota, Gomphales), a new species from the Andean Mountains of northern Chile. Lilloa 59:77–88.https://doi.org/10.30550/j.lil/2022.59.S/2022.08.17

Sato H, Toju H (2019) Timing of evolutionary innovation: scenarios of evolutionary diversification in a species-rich fungal clade. Boletales New Phytol 222(4):1924–1935

Saunte DML, Gaitanis G, Hay RJ (2020) *Malassezia*-associated skin diseases, the use of diagnostics and treatment. Front Cell Infect Microbiol 10:112. https://doi.org/10.3389/fcimb.2020.00112

Savchenko A (2023) Taxonomic studies in Dacrymycetes: Cerinomyces and allied taxa. Dissertation, University of Tartu

Savchenko KG, Carris LM, Castlebury LA, Heluta VP, Wasser SP, Nevo E (2016) [‘2015’]. *Entyloma scandicis*, a new smut fungus on *Scandix verna* from Mediterranean forests of Israel. Mycotaxon 130:1061–1071

Savchenko A, Zamora JC, Shirouzu T et al (2021) Revision of Cerinomyces (Dacrymycetes, Basidiomycota) with notes on morphologically and historically related taxa. Stud Mycol 99:100117.https://doi.org/10.1016/j.simyco.2021.100117

Savchenko A, Zamora JC, Alvarenga R et al (2022) Additions to Dendrodacrys and outline of taxa with branched hyphidia in Dacrymycetes (Basidiomycota). Fungal Syst Evol 10:103–126. https://doi.org/10.3114/fuse.2022.10.04

Savile DBO (1947) A study of the species of *Entyloma* on North American composites. Can J Res Sect C 25:105–120

Savile DBO (1955) A phylogeny of the Basidiomycetes. Can J Bot 33:60–104

Savile DBO (1959) Notes on *Exobasidium*. Can J Bot 37:641–656

Savile DBO (1968) Possible interrelationships between fungal groups. In: Ainsworth GC, Sussman AS (eds) The fungi, an advance treatise, vol 3. The fungal population. Academic Press, New York, pp 649–675

Savile DBO (1974) *Orphanomyces*, a new genus of cypericolous smuts. Can J Bot 52:341–343

Savile DBO, Parmelee JA (1964) Parasitic fungi of the Queen Elisabeth Islands. Can J Bot 42:699–722

Sawada K (1929) Fungi from Taiwan (no. 27). Transactions of the Natural History Society of Formosa 19(100):31–39

Sawada K (1931) Reports on Formosan fungi. Part 5. Rep Cent Inst Formosan Gov No 51:11–12

Sawada K (1952) Researches of fungi in the Tōhoku district of Japan (II) [in Japanese]. Ascomycetes and Protomycetes. Bull Gov for Exp Stn 53:153–193

Sawada K (1959) Descriptive catalogue of Taiwan (Formosan) fungi. National Taiwan University, Taiwan

Sawada A, Sato H, Inoue E, Otani Y, Hanya G (2013) Mycophagy among Japanese macaques in Yakushima: fungal species diversity and behavioral patterns. Primates 55(2):249–257

Schell WA, Lee A, Aime MC (2011) A new lineage in Pucciniomyctina: class Tritirachiomycetes, order Tritirachiales, family Tritirachiaceaa. Mycologia 103:1331–1340

Scheuer C, Bauer R, Lutz M, Stabentheiner E, Grube M (2008) *Bartheletia paradoxa* is a living fossil on Ginkgo leaf litter with a unique septal structure in the Basidiomycota. Mycol Res 112(11):1265–1279. https://doi.org/10.1016/j.mycres.2008.06.008

Schild E (1971) *Tremellodendropsis tuberosa* (Grev.) Crawford var. helvetica var. nov. Westfälische Pilzbriefe 8(8):191–194

Schmidt O (2006) Wood and tree fungi: biology, damage, protection, and use. Springer, Berlin

Schmitt CL, Tatum ML (2008) The Malheur National Forest: Location of the World’s largest living organism [The humongous fungus]. Agriculture Forest Service, Pacific Northwest Region. https://www.fs.usda.gov/Internet/FSE_DOCUMENTS/fsbdev3_033146.pdf

Schoutteten N, Roberts P, Van De Put K, Verbeken A (2018) New species in *Helicogloea* and *Spiculogloea*, including a type study of *H. graminicola* (Bres.) GE Baker (Basidiomycota, Pucciniomycotina). Cryptogamie Mycologie 39(3):311–323

Schoutteten N, Yurkov A, Leroux O, Haelewaters D, Van Der Straeten D, Miettinen O, Boekhout T, Begerow D, Verbeken A (2023) Diversity of colacosome-interacting mycoparasites expands the understanding of the evolution and ecology of Microbotryomycetes. Stud Mycol 106:41–94. https://doi.org/10.3114/sim.2022.106.02

Schroeder WA, Johnson EA (1995) Singlet oxygen and peroxyl radicals regulate carotenoid biosynthesis in Phaffia rhodozyma. J Biol Chem 270(31):18374–18379

Schröter J (1887) Ustilaginei. In: Cohn F (ed) Kryptogamen-Flora von Schlesien, J.U. Kern’s Verlag, Breslau, vol 3(1), pp 261–291

Schröter J (1889) Die Pilze Schlesiens. In: Cohn FJ (ed) Kryptogamen Flora von Schlesien 3. JU Kern’s Verlag, Breslau

Schröter J (1892) Südamerikanische Pilze. Bot Centralbl 50:39–42

Schröter J (1894) *Uleiella* gen. nov. In Pazschke, Sammlungen. Hedwigia Beibl 33:64–66

Scorzetti G, Fell JW, Fonseca A, Statzell-Tallman A (2002) Systematics of basidiomycetous yeasts: a comparison of large sub-unit D1/D2 and internal transcribed spacer rDNA regions. FEMS Yeast Res 2:495–517

Seifert KA, Bandoni RJ (2001) Revisiones generum obscurorum hyphomycetum: *Phacellula* Sydow and *Cladosterigma* Pat. Sydowia 53:156–166

Seifert KA, Oberwinkler F, Bandoni R (1992) Notes on *Stilbum vulgare* and *Fibulostilbum phylacicola* gen. et sp. nov. Atractiellales. Boletín De La Sociedad Argentina De Botánica 28:213–217

Seifert K, Mogan-Jones G, Gams W, Kendrick B (2011) The genera of *hyphomycetes*. CBS-KNAW Fungal Biodiversity Centre, Utrecht

Sekan AS, Myronycheva OS, Karlsson O, Gryganskyi AP, Blume Y (2019) Green potential of*Pleurotus* spp. in biotechnology. PeerJ 7:e6664

Selosse M-A, Setaro S, Glatard F, Richard F, Urcelay C, Weiss M (2007) Sebacinales are common mycorrhizal associates of Ericaceae. New Phytol 174:864–878

Selvam K, Shanmuga Priya M, Arungandhi K (2011) Pretreatment of wood chips and pulps with*Thelephora* sp. to reduce chemical consumption in paper industries. Int J Chemtech Res 3(1):471–476

Sesli E, Vizzini A, Ercole E, Contu M (2016) *Clitolyophyllum akcaabatense* gen. nov., sp. nov.(Agaricales, Tricholomatineae); a new fan-shaped clitocyboid agaric from Turkey. Botany 94(2):73–80

Setchell WA (1892) An examination of the species of the genus *Doassansia* Cornu. Ann Bot (Oxford) 6:1–48 + 2 Pls

Sfetcu N (2006) Health & drugs: disease, prescription & medication. MultiMedia Publishing

Sha T, Xu J, Palanichamy MG, Zhang HB, Li T et al (2008) Genetic diversity of the endemic gourmet mushroom *Thelephora ganbajun* from south-western China. Microbiology 154:3460–3468. https://doi.org/10.1099/mic.0.2008/020495-0

Shankar A, Sharma KK (2022) Fungal secondary metabolites in food and pharmaceuticals in the era of multi-omics. Appl Microbiol Biotechnol 106:3465–3488. https://doi.org/10.1007/s00253-022-11945-8

Sharma R, Xia X, Riess K et al (2015) Comparative genomics including the early-diverging smut fungus *Ceraceosorus bombacis* reveals signatures of parallel evolution within plant and animal pathogens of fungi and oomycetes. Genome Biol Evol 7:2781–2798

Sharon M, Kuninaga S, Hyakumachi M, Naito S (2008) Classification of *Rhizoctonia* spp. using rDNA-ITS sequence analysis supports the genetic basis of the classical anastomosis grouping. Mycoscience 49:93–114

Shen LL, Wang M, Zhou JL, Xing JH, Cui BK, Dai YC (2019) Taxonomy and phylogeny of *Postia*. Multi-gene phylogeny and taxonomy of the brown-rot fungi: *Postia* (Polyporales, Basidiomycota) and related genera. Persoonia 42:101–126.https://doi.org/10.3767/persoonia.2019.42.05

Shirouzu T, Hirose D, Oberwinkler F et al (2013) Combined molecular and morphological data for improving phylogenetic hypothesis in Dacrymycetes. Mycologia 105:1110–1125. https://doi.org/10.3852/12-147

Shirouzu T, Matsuoka S, Doi H et al (2020) Complementary molecular methods reveal comprehensive phylogenetic diversity integrating inconspicuous lineages of early-diverged wood-decaying mushrooms. Sci Rep 10:1–12. https://doi.org/10.1038/s41598-020-59620-0

Si J, Cui B-K, Dai Y-C (2013) Decolorization of chemically different dyes by white-rot fungi in submerged cultures. Ann Microbiol 63:1099–1108. https://doi.org/10.1016/j.bse.2012.11.011

Silva-Filho AG, Mombert A, Nascimento CC, Nóbrega BB, Soares DM, Martins AG, Domingos AH, Santos I, Della-Torre OH, Perry BA, Desjardin DE (2023) *Eoscyphella luciurceolata* gen. and sp. nov. (Agaricomycetes) Shed Light on Cyphellopsidaceae with a New Lineage of Bioluminescent Fungi. J Fungi 9(10):1004

Simão FA, Waterhouse RM, Ioannidis P et al (2015) BUSCO: assessing genome assembly and annotation completeness with single-copy orthologs. Bioinformatics 31:3210–3212. https://doi.org/10.1093/bioinformatics/btv351

Sing A (1998) Epidemiology of Karnal bunt of wheat. In: Malik VS, Mathre DE (eds) Bunts and smuts of wheat: International Symposium, Raleigh, North Carolina, August 17–20, 1997. North American Plant Protection Organization, Ottawa, pp 149–162

Singer R (1944) Notes on taxonomy and nomenclature of the Polypores. Mycologia 36:65–69

Singer R (1948) New and interesting species of Basidiomycetes. II. Pap Mich Acad Sci 32:103–150

Singer R (1951) The Agaricales (mushrooms) in modern taxonomy. Lilloa 22:5–832

Singer R (1962) The Agaricales in modern taxonomy, 2nd edn. J Cramer, Weinheim

Singer R (1964) Oudemansiellineae, Macrocystidiinae, Oseudohiatulinae in South America. Darwiniana 13:145–190

Singer R (1975) The Agaricales in modern taxonomy. 3rd ed. J Cramer, Vaduz

Singer R (1986) The agaricales in modern taxonomy, 4th edn. Koeltz Scientific Books, Koegnistein

Singer R, Smith AH (1960) Studies on Secotiaceous Fungi. IX.The Astrogastraceous series. Mem Torrey Bot Club 21:1–112

Singh RA, Pavgi MS (1973) Morphology, cytology and development of *Melanotaenium brachiariae*. Cytologia 38:455–466

Sitta N, Floriani M (2008) Nationalization and globalization trends in the wild mushroom commerce of Italy with emphasis on porcini (*Boletus edulis* and allied species). Econ Bot 62:307–322

Sjamsuridzal W, Tajiri Y, Nishida H, Thuan TB et al (1997) Evolutionary relationships of members of the genera *Taphrina*, *Protomyces*, *Schizosaccharomyces*, and related taxa within the archiascomycetes: Integrated analysis of genotypic and phenotypec characters. Mycoscience 38:267–280

Sjamsuridzal W, Nishida H, Ogawa H, Kakishima M, Sugiyama J (1999) Phylogenetic positions of rust fungi parasitic on ferns: evidence from 18S rDNA sequence analysis. Mycoscience 40:21–27

Sjamsuridzal W, Nishida H, Yokota A (2002) Phylogenetic position of *Mixia osmundae* inferred from 28S rDNA comparison. J Gen Appl Microbiol 48:121–123

Sjökvist E, Larsson E, Eberhardt U, Ryvarden L, Larsson KH (2012) Stipitate stereoid basidiocarps have evolved multiple times. Mycologia 104:1046–1055

Sjökvist E, Pfeil BE, Larsson E, Larsson K-H (2014) Stereopsidales—a new order of mushroom-forming fungi. PLoS ONE 9(4):e95227

Skrede I, Engh IB, Binder M, Carlsen T, Kauserud H, Bendiksby M (2011) Evolutionary history of Serpulaceae (Basidiomycota): molecular phylogeny, historical biogeography and evidence for a single transition of nutritional mode. BMC Evol Biol 11:1–13

Smith AH, Zeller SM. (1966) A preliminary account of the North American species of Rhizopogon. Memoirs of the New York Botanical Garden 14:1–178

Smith SE, Read DJ (2002) Mycorrhizas in managed environments: forest production, interactions with other microorganisms and pollutants. In: Smith SE, Read DJ (eds) Mycorrhizal Symbiosis (second Edition). Academic Press, Amsterdam, pp 470–489. https://doi.org/10.1016/B978-012652840-4/50018-8

Smith SE, Read D (2008) Mycorrhizal Symbiosis, 3rd edn. Academic Press, Amsterdam

Smith AH, Thiers HD (1964) A Contribution Toward a Monograph of North American Species of*Suillus*. Privately published, Ann Arbor

Smith ME, Henkel TW, Rollins JA (2015) How many fungi make sclerotia? Fungal Ecol 13:211–220

Somrithipol S, Jones EG, Sommai S, Suetrong S, Mongkolsamrith S, Nathalang A, Pinruan U (2018)*Laurobasidiaceae* fam. nov. (Exobasidiales, Basidiomycota), a new family for fungi causing galls with aerial root-like outgrowths, with a new record from Thailand of *Laurobasidium hachijoense* on a new host. Cinnamomum Subavenium Phytotaxa 347:150–164

Song J-L, Lu N, Yan J, Cheng J-W, Zhou Z-F, Lin J-Y, Wang W-K, Yuan W-D (2023) Effects of mulberry sawdust on the content of main active components and antioxidant activities in *Sanghuangporus vaninii*. Mycosystema 42(4):949–960

Sotome K, MaekawaN NakagiriA, Lee SS, Hattori T (2014) Taxonomic study of Asian species of poroid Auriculariales. Mycol Prog 13:987–997. https://doi.org/10.1007/s11557-014-0984-0

Sousa JO, Suz LM, García MA, Alfredo DS, Conrado LM, Marinho P, Ainsworth AM, Baseia IG, Martín MP (2017) More than one fungus in the pepper pot: Integrative taxonomy unmasks hidden species within*Myriostoma coliforme* (Geastraceae, Basidiomycota). PLoS ONE 12:e0177873

Sousa JO, Baseia IG, Martín MP (2019) Strengthening *Myriostoma* (Geastraceae, Basidiomycota) diversity: *Myriostoma australianum* sp. nov. Mycoscience 60:25–30

Southam H, Stafl N, Guichon S, Simard S (2022) Characterizing the ectomycorrhizal fungal community of whitebark pine in Interior British Columbia: mature trees, natural regeneration and planted seedlings. Front for Glob Chang 4:225

Spatafora JW, Aime MC, Grigoriev IV, Martin F, Stajich JE (2017) The fungal tree of life: from molecular systematics to genome-scale phylogenies. Microbiol Spectr. https://doi.org/10.1128/microbiolspec.FUNK-0053-2016

Spatafora JW, Aime MC, Grigoriev IV, Martin F et al (2018) The fungal tree of life: from molecular systematics to genome-scale phylogenies. In: Heitman J, Howlett BJ, Crous PW et al (eds) The fungal kingdom. American Society for Microbiology, Wahingdon, pp 1–32

Spatz M, Richard ML (2020) Overview of the potential role of *Malassezia* in gut health and disease. Front Cell Infect Microbiol 10:201. https://doi.org/10.3389/fcimb.2020.00201

Spirin V, Malysheva V, Larsson KH (2018a) On some forgotten of *Exidia* and *Myxarium* (Auriculariales, Basidiomycota). Nord J Bot 36:e01601. https://doi.org/10.1111/njb.01601

Spirin V, Malysheva V, Trichies G et al (2018b) A preliminary overview of the corticioid Atractiellomycetes (Pucciniomycotina, Basidiomycetes). Fungal Syst Evol 2(1):311–340

Spirin V, Malysheva V, Roberts P, Trichies G, Savchenko A, Larsson KH (2019a) A convolute diversity of the Auriculariales (Agaricomycetes, Basidiomycota) with sphaeropedunculate basidia. Nordic J Bot 37:e02394. https://doi.org/10.1111/njb.02394

Spirin V, Malysheva V, Haelewaters D, Larsson KH (2019b) Studies in the *Stypella vermiformis* group (Auriculariales, Basidiomycota). Antonie Van Leeuwenhoek 112:753–764. https://doi.org/10.1007/s10482-018-01209-9

Spirin V, Volobuev S, Viner I, Miettinen O, Vlasák J, Schoutteten N, Motato-Vásquez V, Kotiranta H, Larsson K-H (2021) On Sistotremastrum and similar-looking taxa (Trechisporales, Basidiomycota). Mycol Prog 20(4):453–476

Spooner B, Læssøe T (1994) The folklore of "Gasteromycetes." Mycologist 8(3):119–123

Spribille T, Tuovinen V, Resl P, Vanderpool D, Wolinski H, Aime MC, Schneider K, Stabentheiner E, Toome-Heller M, Thor G, Mayrhofer H (2016) Basidiomycete yeasts in the cortex of ascomycete macrolichens. Science 353(6298):488–491

Spribille T, Tagirdzhanova S, Goyette V et al (2020) 3D biofilms: in search of the polysaccharides holding together lichen symbioses. FEMS Microbiol Lett 367:fnaa023

Sriramulu M, Shanmugam S, Ponnusamy VK (2020) *Agaricus bisporus* mediated biosynthesis of copper nanoparticles and its biological effects: an in-vitro study. Colloid Interface Sci Commun 35:100254

Sriswasdi S, Takashima M, Manabe RI, Ohkuma M, Iwasaki W (2019) Genome and transcriptome evolve separately in recently hybridized Trichosporon fungi. Commun Biol 2:263

Stadler M, Anke T, Dasenbrock J, Steglich W (1993) Phellodonic acid, a new biologically active hirsutane derivative from *Phellodon melaleucus* (Thelephoraceae, Basidiomycetes). Z Naturforsch C J Biosci 48(7–8):545–549. https://doi.org/10.1515/znc-1993-7-803

Stafleu FA, Cowan RS (1976) Taxonomic literature : a selective guide to botanical publications and collections with dates, commentaries and types, 2d ed. vol 1. Bohn, Scheltema & Holkema, Utrecht

Stafleu FA, Cowan RS (1985) Taxonomic literature : a selective guide to botanical publications and collections with dates, commentaries and types, 2d ed. vol 5. Bohn, Scheltema & Holkema, Utrecht

Stalhberger T, Simenel C et al (2014) Chemical organization of the cell wall polysaccharide core of *Malassezia restricta*. J Biol Chem 289(18):12647–12656.https://doi.org/10.1074/jbc.M113.547034

Stalpers JA (1993) The aphyllophoraceous fungi I. Keys to the species of the Thelephorales. Stud Mycol 35:1–168

Stanke M, Waack S (2003) Gene prediction with a hidden Markov model and a new intron submodel. Bioinformatics 19:215–225. https://doi.org/10.1093/bioinformatics/btg1080

Steyaert RL (1972) Species of Ganoderma and related genera mainly of the Bogor and Leiden Herbaria. Persoonia 7:55–118

Stolk AC, Dakin JC (1966) *Moniliella*, a new genus of Moniellales. Antonie Van Leeuwenhoek 32:399–409

Stosiek N, Terebieniec A, Ząbek A, Młynarz P, Cieśliński H, Klimek-Ochab M (2019) N-phosphonomethylglycine utilization by the psychrotolerant yeast *Solicoccozyma terricola* M 3.1.4. Bioorg Chem 93:102866

Stoytchev I, Homolka L, Nerud F (2001) *Geastrum pouzarii*stanek in agar culture. Antonie Van Leeuwenhoek 79:363–436

Sugita T (2011) Trichosporon Behrend (1890). In: Kurtzman CP, Fell JW, Boekhout T (eds) The yeasts, a taxonomic study, 5th edn. Elsevier, Amsterdam, pp 2015–2061

Sugiyama J (1998) Relatedness, phylogeny, and evolution of the fungi. Mycoscience 39:487–511

Sugiyama J, Katumoto K (2008a) Identity of the plasmodial slime mold *Phytoceratiomyxa osmundae* and the lectotypification of *Taphrina osmundae*, the basionym of Mixia osmundae. Mycoscience 49:192–198

Sugiyama J, Katumoto K (2008b) Proposal to conserve the name *Mixia* against *Phytoceratiomyxa* (Basidiomycota). Taxon 57:991–992

Sugiyama J, Nishida H (1995) The higher fungi: their evolutionary relationships and implications for fungal systematics. In: Arai R, Kato M, Doi Y (eds) Biodiversity and evolution. National Science Museum Foundation, Tokyo, pp 177–195

Sugiyama J, Nagahama T, Nishida H (1996) Fungal diversity and phylogeny with emphasis on 18S ribosomal DNA sequence divergence. In: Colwell RR, Simidu I, Ohwada K (eds) Microbial diversity in time and space. Plenum Press, New York, pp 41–51

Sugiyama J, Nishida H, Hosoya KM (2018) The enigmatic *Mixia osmundae* revisited: a systematic review including new distributional data and recent advances in its phylogeny and phylogenomics. Mycologia 110:179–191

Suh S-O, Sugiyama J (1994) Phylogenetic placement of the basidiomycetous yeasts *Kondoa malvinella* and *Rhodosporidium dacryoidum*, and the anamorphic yeast *Sympodiomycopsis paphipedili* by means of 18S rDNA gene sequence analysis. Mycoscience 35:367–375

Suh S-O, Maslov DA, Molestina RE, Zhou JJ (2012) *Microbotryozyma collariae* gen. nov., sp. nov., a basidiomycetous yeast isolated from a plant bug *Collaria oleosa* (Miridae). Antonie Van Leeuwenhoek 102:99–104

Sulistyo BP, Larsson KH, Haelewaters D, Ryberg M (2021) Multigene phylogeny and taxonomic revision of Atheliales sl: reinstatement of three families and one new family, Lobuliciaceae fam. Nov. Fung Biol 125(3):239–255

Sulzbacher MA, Baseia IG, Lücking R, Parnmen S, Moncada B (2012) Unexpected discovery of a novel basidiolichen in the threatened Caatinga biome of northeastern Brazil. Bryologist 115:601–609.https://doi.org/10.1639/0007-2745-115.4.601

Sulzbacher MA, Grebenc T, Cabral TS, Giachini AJ, Goto BT et al (2016a) *Restingomyces*, a new sequestrate genus from the Brazilian Atlantic rainforest that is phylogenetically related to early-diverging taxa in Trappeaceae (Phallales). Mycologia 108:954–966

Sulzbacher MA, Sousa JO, Cortez VG, Giachini AJ, Baseia IG (2016b) *Sclerogaster araripensis*, a new hypogeous fungus from the upland wet forest enclaves of northeast Brazil. Sydowia 68:107–111

Sulzbacher MA, Wartchow F, Ovrebo CL et al (2016c) *Sulzbacheromyces caatingae*: notes on its systematics, morphology and distribution based on ITS barcoding sequences. Lichenologist 48:61–70. https://doi.org/10.1017/S0024282915000420

Sun Y-F, Costa-Rezende DH, Xing J-H, Zhou J-L, Zhang B, Gibertoni TB, Gates G, Glen M, Dai Y-C, Cui B-K (2020) Multi-gene phylogeny and taxonomy of Amauroderma s. lat. (Ganodermataceae). Persoonia 44:206–239

Sun Y-F, Xing J-H, He X-L, Wu D-M, Song C-G, Liu S, Vlasák J, Gates G, Gibertoni TB, Cui B-K (2022) Species diversity, systematic revision and molecular phylogeny of Ganodermataceae (Polyporales, Basidiomycota) with an emphasis on Chinese collections. Stud Mycol 101(1):287–415

Sun Y, Zhang Y-J, Cao X-Y, Zhou J-S, Jiang J-H (2023) Characteristics related to sexual reproduction and mating type locus of *Inonotus obliquus*. Mycosystema 42(2):520–529. https://doi.org/10.13346/j.mycosystema.220210

Sunhede S (1989) Geastraceae (Basidiomycotina). Morphology, ecology and systematics with special emphasis on the North European species. Synopsis Fungorum 1:1–534

Svantesson S (2020) Taxonomy and systematics of Thelephorales—glimpses into its hidden hyperdiversity. Dissertation, University of Gothenburg. https://gupea.ub.gu.se/handle/2077/66642

Svantesson S, Larsson K-H, Kõljalg U, May TW, Cangren P, Nilsson RH, Larsson E (2019) Solving the taxonomic identity of *Pseudotomentella tristis* s.l. (Thelephorales, Basidiomycota)—a multi-gene phylogeny and taxonomic review, integrating ecological and geographical data. MycoKeys 50:1–77. https://doi.org/10.3897/mycokeys.50.32432

Svantesson S, Kõljalg U, Wurzbacher C, Saar I, Larsson K-H, Larsson E (2021a) *Polyozellus* vs *Pseudotomentella*: generic delimitation with a multi-gene dataset. FUSE 8(1):143–154. https://doi.org/10.3114/fuse.2021.08.11

Svantesson S, Larsson K-H, Larsson E (2021b) *Polyozellus badjelanndana*, *Polyozellus sorjusensis* and *Tomentella viridibasidia*—three new corticioid Thelephorales species from the Scandes Mountains. Phytotaxa 497(2):61–78. https://doi.org/10.11646/phytotaxa.497.2.1

Svantesson S, Syme K, Douch JD, Robinson RM, May TW (2021c) "The Mouldy Marshmallow" *Amaurodon caeruleocaseus* (Thelephorales, Basidiomycota)—the first stipitate species in the genus *Amaurodon*. Sydowia 74:181–192. https://doi.org/10.12905/0380.sydowia74-2021-0181

Swann EC, Taylor JW (1993) Higher taxa of Basidiomycetes: an 18S rRNA gene perspective. Mycologia 85:923–936. https://doi.org/10.2307/3760675

Swann EC, Frieders EM, McLaughlin DJ (2001) Urediniomycetes. In: McLaughlin DJ, McLughlin EG, Lemke PA (eds) The Mycota VII, Part b, systematics and evolution. Springer, Berlin, pp 37–56

Tagirdzhanova G, Saary P, Tingley JP, Díaz-Escandón D, Abbott DW, Finn RD, Spribille T (2021) Predicted input of uncultured fungal symbionts to a lichen symbiosis from metagenome-assembled genomes. Genome Biol Evol 13(4):evab047

Tai F-L (1979) Sylloge fungorum Sinicorum. Science Press, Beijing

Takahashi A, Agatsuma T, Matsuda M, Ohta T, Nunozawa T, Endo T, Nozoe S (1992) Russuphelin A, a new cytotoxic substance from the mushroom Russula subnigricans Hongo. Chem Pharm Bull 40(12):3185–3188

Takashima M, Manabe R-I, Nishimura Y, Endoh R, Ohkuma M, Sriswasdi S, Sugita T, Iwasaki W (2019) Recognition and delineation of yeast genera based on genomic data: lessons from Trichosporonales. Fungal Genet Biol 130:31–42

Tan Y-P, Marney TS, Shivas RG (2021) Nomenclatural novelties. Index Fungorum 495:1–6

Tanaka E, Shimizu K, Imanishi Y, Yasuda F, Tanaka C (2008) Isolation of basidiomycetous anamorphic yeast like fungus *Meira argovae* found on Japanese bamboo. Mycoscience 49:329–333

Taofiq O, Heleno SA, Calhelha RC, Alves MJ, Barros L, Barreiro MF, González-Paramás AM, Ferreira ICFR (2016) Development of mushroom-based cosmeceutical formulations with anti-inflammatory, anti-tyrosinase, antioxidant, and antibacterial properties. Molecules 21:1372

Taofiq O, Heleno SA, Calhelha RC, Fernandes IP, Alves MJ, Barros L, González-Paramás AM, Ferreira ICFR (2018) Mushroom-based cosmeceutical ingredients: Microencapsulation and in vitro release profile. Ind Crops Prod 124:44–52

Taş M, Küçükaydın S, Tel-Çayan G, Duru ME, Öztürk M, Türk M (2021) Chemical constituents and their bioactivities from truffle *Hysterangium inflatum*. J Food Meas Charact 15(5):4181–4189

Taylor DL, Bruns TD (1999) Community structure of ectomycorrhizal fungi in a *Pinus muricata* forest: minimal overlap between the mature forest and resistant propagule communities. Mol Ecol 8:1837–1850

Taylor DL, Bruns TD, Szaro TM, Hodges SA (2003) Divergence in mycorrhizal specialization within*Hexalectris spicata* (Orchidaceae), a nonphotosynthetic desert orchid. Am J Bot 90:1168–1179

Taylor DL, Bruns TD, Hodges SA (2004) Evidence for mycorrhizal races in a cheating orchid. Proc R Soc B 271(1534):35–43

Taylor TN, Taylor EL, Krings M (2009) Paleobotany: the biology and evolution of fossil plants, 2nd edn. Academic Press, New York

Tedersoo L, Nara K (2010) General latitudinal gradient of biodiversity is reversed in ectomycorrhizal fungi. New Phytol 185(2):351–354

Tedersoo L, Põlme S (2012) Infrageneric variation in partner specificity: multiple ectomycorrhizal symbionts associate with *Gnetum gnemon* (Gnetophyta) in Papua New Guinea. Mycorrhiza 22(8):663–668

Tedersoo L, Smith ME (2013) Lineages of ectomycorrhizal fungi revisited: foraging strategies and novel lineages revealed by sequences from belowground. Fungal Biol Rev 27:83–99

Tedersoo L, Sadam A, Zambrano M, Valencia R, Bahram M (2009) Low diversity and high host preference of ectomycorrhizal fungi in Western Amazonia, a neotropical biodiversity hotspot. ISME J 4(4):465–471

Tedersoo L, May TW, Smith ME (2010) Ectomycorrhizal lifestyle in fungi: global diversity, distribution, and evolution of phylogenetic lineages. Mycorrhiza 20:217–263. https://doi.org/10.1007/s00572-009-0274-x

Tedersoo L, Bahram M, Põlme S, Kõljalg U, Yorou NS, Wijesundera R et al (2014a) Fungal biogeography. Global diversity and geography of soil fungi. Science 346(6213):1256688. https://doi.org/10.1126/science.1256688

Tedersoo L, Bahram M, Ryberg M, Otsing E, Koljalg U, Abarenkov K (2014b) Global biogeography of the ectomycorrhizal/sebacina lineage (Fungi, Sebacinales) as revealed from comparative phylogenetics analyses. Mol Ecol 23:4168–4183

Tedersoo L, Harend H, Buegger F, Pritsch K, Saar I et al (2014c) Stable isotope analysis, field observations and synthesis experiments suggest that *Odontia* is a non-mycorrhizal sister genus of *Tomentella* and *Thelephora*. Fungal Ecol 11:80–90. https://doi.org/10.1016/j.funeco.2014.04.006

Tedersoo L, Sánchez- Ramírez S, Kõljalg U, Bahram M et al (2018) High-level classification of the Fungi and a tool for evolutionary ecological analyses. Fungal Divers 90:135–159

Tedersoo L, Mikryukov V, Anslan S et al (2021) The Global Soil Mycobiome consortium dataset for boosting fungal diversity research. Fungal Divers 111:573–588

Telleria MT, Melo I, Dueñas M (1997) An annotated list of the aphyllophorales of the Balearic Islands. Mycotaxon 65:353–377

Telleria MT, Melo I, Dueñas M, Larsson KH, Paz Martín MP (2013) Molecular analyses confirm Brevicellicium in Trechisporales. IMA Fungus 4:21–28

Telleria MT, Dueñas M, Melo I, Salcedo I, Martín MP (2015) Spelling out *Jaapia* species. Mycol Prog 14:57

Teng S-C (1963) Fungi of China. Science Press, Beijing

Thakur MP (2020) Advances in mushroom production: key to food, nutritional and employment security: a review. Indian Phytopathol 73:377–395

Theelen B, Cafarchia C et al (2018) *Malassezia* ecology, pathophysiology, and treatment. Med Mycol 56:S10-25. https://doi.org/10.1093/mmy/myx134

Theelen B, Mixão V et al (2022) Multiple hybridization events punctuate the evolutionary trajectory of *Malassezia furfur*. mBio 13(2):e0385321

Thongbai B, Rapior S, Hyde KD, Wittstein K, Stadler M (2015) *Hericium erinaceus*, an amazing medicinal mushroom. Mycol Prog 14:91

Thorn RG, Moncalvo JM, Reddy CA, Vilgalys R (2000) Phylogenetic analyses and the distribution of nematophagy support a monophyletic Pleurotaceae within the polyphyletic pleurotoid-lentinoid fungi. Mycologia 92(2):241–252

Tian E-J, Matheny PB (2021) A phylogenetic assessment of Pholiota and the new genus Pyrrhulomyces. Mycologia 113(1):146–167

Tiffney BH (1981) Re-evaluation of *Geaster florissantensis*(Oligocene, North America). Trans Br Mycol Soc 76:493–495

Tode HJ (1790) Fungi Mecklenburgenses Selecti. Fasciculus–I, Nova Fungorum Genera Complectens, Luneburgi

Tohtirjap A, Hou SX, Rivoire B, Gates G, Wu F, Dai YC (2023) Two new species of *Exidia* sensu lato (Auriculariales, Basidiomycota) based on morphology and DNA sequences. Front Microbiol 13:1080290. https://doi.org/10.3389/fmicb.2022.1080290

Toome M, Aime MC (2014) *Pycnopulvinus aurantiacus* gen. et sp. nov., a new sporocoapr-forming member of Pucciniomycotina. MycoKeys 8:43–50

Toome M, Roberson RW, Aime MC (2013) *Meredithblackwellia eburnea* gen. et spec. nov., Kriegeriaceae fam. nov. and Kriegeriales ord. nov.—toward resolving higher-level classification in Microbotryomycetes. Mycologia 105(2):486–495

Toome M, Ohm RA, Riley RW, James TY et al (2014) Genome sequencing provides insight into the reproductive biology, nutritional mode and ploidy of the fern pathogen *Mixia osmundae*. New Phytol 202:554–564

Trichies G (2006) Hétérobasidiomycètes inusuels ou nouveaux découverts en France. Bull Soc Mycol Fr 122(1):29–60

Trichiès G, Schultheis B (2002) *Trechispora antipus* sp. nov., une seconde espèce bisporique du genre *Trechispora* (Basidiomycota, Stereales). Mycotaxon 82:453–458

Trierveiler-Pereira L, Loguercio-Leite C, Calonge FD, Baseia IG (2009) An emendation of*Phallus glutinolens*. Mycol Prog 8:377–380

Trierveiler-Pereira L, Meijer AA, Hosaka K, Silveira RMB (2014a) Updates on *Protubera* (Protophallaceae, Phallales) and additional notes on P. maracuja. Mycoscience 55(1):35–42

Trierveiler-Pereira L, Silveira RMB, Hosaka K (2014b) Multigene phylogeny of the Phallales (Phallomycetidae, Agaricomycetes) focusing on some previously unrepresented genera. Mycologia 106(5):904–911

Trierveiler-Pereira L, Silva HCS, Funez LA, Baltazar JM (2016) Mycophagy by small mammals: new and interesting observations from Brazil. Mycosphere 7(3):297–304

Trierveiler-Pereira L, Meijer AAR, Silveira RMB (2019) Phallales (Agaricomycetes, Fungi) from Southern Brazil. Stud Fungi 4(1):162–184

Truong C, Mujic AB, Healy R, Kuhar F, Furci G, Torres D, Niskanen T, Sandoval-Leiva PA, Fernández N, Escobar JM, Moretto A, Palfner G, Pfister D, Nouhra E, Swenie R, Sánchez-García M, Matheny PB, Smith ME (2017) How to know the fungi: combining field inventories and DNA-barcoding to document fungal diversity. New Phytol 214(3):913–919

Tsukamoto S, Macabalang AD, Abe T, Hirota H, Ohta T (2002) Thelephorin A: a new radical scavenger from the mushroom *Thelephora vialis*. Tetrahedron 58:1103–1105.https://doi.org/10.1016/S0040-4020(01)01214-5

Tsukiboshi T, Yoshida S, Shinohara H, Tsushima S (2007) Index of dried plant specimen of microbes stocked in NIAES Herbarium Japan. Miscellaneous Publ Natl Inst Agro-Environ Sci 30:86

Tsutsumi C, Yatabe-Kakugawa Y, Hirayama Y, Chiou W-L et al (2021) Molecular analyses of the disjunctly distributed *Osmunda regalis* and *O. japonica* (Osmundaceae), with particular reference to introgression and hybridization. Plant Syst Evol 307(35):1–13. https://doi.org/10.1007/s00606-021-01751-6

Tulasne L-R, Tulasne C (1847) Mémoire sur les Ustilaginées comparées aux Urédinées. Ann Sci Nat Bot Sér 3 7:12–127 + Pls 2–7

Tulloss RE, Kuyper TW, Vellinga EC, Yang ZL, Halling RE, Geml J, Sánchez-Ramírez S, Gonçalves SC, Hess J, Pringle A (2016) The genus *Amanita* should not be split. Amanitaceae J 1:1–16

Turchetti B, Thomas Hall SR, Connell LB, Branda E, Buzzini P, Theelen B, Müller WH, Boekhout T (2011) Psychrophilic yeasts from Antarctica and European glaciers: description of *Glaciozyma* gen. nov., *Glaciozyma martinii* sp. nov. and*Glaciozyma watsonii* sp. nov. Extremophiles 15:573–586

Turland NJ, Wiersema JH, Barrie FR, Greuter W, Hawksworth DL, Herendeen PS, Knapp S, Kusber W-H, Li D-Z, Marhold K, May TW, McNeill J, Monro AM, Prado J, Price MJ, Smith GF (2018) International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code). Regnum Vegetabile 159. Koeltz Botanical Books, Glashütten

Udagawa S, Kinjo N, Kobayashi T, Suzuki A et al (2006) A brief history of mycology in Japan. The Mycological Society of Japan, Nara, pp 24–25

Uehling JK, Henkel TW, Aime MC, Smith ME (2012) New species of *Clavulina* (Cantharellales, Basidiomycota) with resupinate and effused basidiomata from the Guiana Shield. Mycologia 104(2):547–556

Ulloa M, Hanlin RT (2012) Illustrated dictionary of mycology. The American Phytopathological Society, Minnesota

Underwood LM (1899) Moulds, mildews, and mushrooms; a guide to the systematic study of the Fungi and Mycetozoa and their literature. Henry Holt and Company, New York

United States Forest Service (1994) Record of decision for amendments to Forest Service and Bureau of Land Management planning documents within the range of the Northern Spotted Owl, and, standards and guidelines for management of habitat for latesuccessional and old-growth forest related species within the range of the Northern Spotted Owl. https://www.fs.usda.gov/r6/reo/library/

Urquhart E, Menzies J, Punja Z (1994) Growth and biological control activity of *Tilletiopsis* species against powdery mildew (*Sphaerotheca fuliginea*) on greenhouse cucumber. Phytopathology 84:341–351

Ushijima S, Maekawa N, Sotome K (2019) A new species of the genus *Tubulicium* collected from living Pieris japonica. Mycoscience 60:137–140

Valenzuela R, Raymundo T, Cifuentes J, Esqueda M, Amalfi M, Decock C (2012) *Coltriciella sonorensis* sp. nov. (Basidiomycota, Hymenochaetales) from Mexico: evidence from morphology and DNA sequence data. Mycol Prog 11:181–189

Van Doan H, Doolgindachbaporn S, Suksri A (2016) Effects of Eryngii mushroom (*Pleurotus eryngii*) and *Lactobacillus plantarumon* growth performance, immunity and disease resistance of Pangasius catfish (*Pangasius bocourti*, Sauvage 1880). Fish Physiol Biochem 42:1427–1440

van Driel KGA, Humbel BM, Verkleij AJ, Stalpers J, Müller WH, Boekhout T (2009) Septal pore complex morphology in the Agaricomycotina (Basidiomycota) with emphasis on the Cantharellales and Hymenochaetales. Mycol Res 113:559–576

van de Peppel LJ, Aime MC, Læssøe T, Pedersen OS, Coimbra VR, Kuyper TW, Stubbe D, Aanen DK, Baroni TJ (2022) Four new genera and six new species of lyophylloid agarics (Agaricales, Basidiomycota) from three different continents. Mycol Prog 21(10):85

Vanegas-León ML, Sulzbacher MA, Rinaldi AC et al (2019) Are Trechisporales ectomycorrhizal or non-mycorrhizal root endophytes? Mycol Prog 18:1231–1240. https://doi.org/10.1007/s11557-019-01519-w

Vánky K (1981) Two new genera of Ustilaginales: *Nannfeldtiomyces* and *Pseudodoassansia*, and a survey of allied genera. Sydowia 34:167–178

Vánky K (1994) European smut fungi. Gustav Fischer Verlag, Stuttgart

Vánky K (1996) *Mycosyrinx* and other pair-spored Ustilaginales. Mycoscience 37:173–185

Vánky K (2001) The emended *Ustilaginaceae* of the modern classificatory system for smut fimgi. Fungal Divers 6:131–147

Vánky K (2003) Cintractiellaceae fam. nov. (Ustilaginomycetes). Fungal Divers 13:167–173

Vánky K (2004) *Pilocintractia* gen. nov. (Ustilaginomycetes). Mycol Balcan 1:169–174

Vánky K (2005) The smut fungi (Ustilaginomycetes) of Eriocaulaceae. II. *Eriocaulago* and *Eriosporium* new genera. Mycol Balcan 2:113–118

Vánky K (2008) Taxonomic studies on Ustilaginomycetes—28. Mycotaxon 106:133–178

Vánky K (2011) [‘2012’] Smut fungi of the world. American Phytopathological Society Press, Minnesota

Vánky K (2013) Illustrated genera of smut fungi, 3rd edn. American Phytopathological Society Press, Minnesota

Vánky K, Bauer R (1992) *Conidiosporomyces*, a new genus of Ustilaginales. Mycotaxon 43:427–436

Vánky K, Bauer R (1995) *Oberwinkleria*, a new genus of Ustilaginales. Mycotaxon 53:361–368

Vánky K, Bauer R (1996) *Ingoldiomyces*, a new genus of Ustilaginales. Mycotaxon 59:277–287

Vánky K, Bauer R, Begerow D (1998) *Doassinga*, a new genus of Doassansiales. Mycologia 90:964–970

Vánky K, Lutz M, Bauer R (2008a) About the genus *Thecaphora*(Glomosporiaceae) and its new synonyms. Mycol Prog 7:31–39

Vánky K, Lutz M, Bauer R (2008b) *Floromyces*, a new genus of Ustilaginomycotina. Mycotaxon 104:171–184

Varga T, Krizsán K, Földi C, Dima B, Sánchez-García M, Sánchez-Ramírez S, Szöllősi GJ, Szarkándi JG, Papp V, Albert L, Andreopoulos W, Angelini C, Antonín V, Barry KW, Bougher NL, Buchanan P, Buyck B, Bense V, Catcheside P, Chovatia M, Cooper J, Dämon W, Desjardin D, Finy P, Geml J, Haridas S, Hughes K, Justo A, Karasiński D, Kautmanova I, Kiss B, Kocsubé S, Kotiranta H, LaButti KM, Lechner BE, Liimatainen K, Lipzen A, Lukács Z, Mihaltcheva S, Morgado LN, Niskanen T, Noordeloos ME, Ohm RA, Ortiz-Santana B, Ovrebo C, Rácz N, Riley R, Savchenko A, Shiryaev A, Soop K, Spirin V, Szebenyi C, Tomšovský M, Tulloss RE, Uehling J, Grigoriev IV, Vágvölgyi C, Papp T, Martin FM, Miettinen O, Hibbett DS, Nagy LG (2019) Megaphylogeny resolves global patterns of mushroom evolution. Nat Ecol Evol 3:668–678

Varga T, Földi C, Bense V, Nagy LG (2022) Radiation of mushroom-forming fungi correlates with novel modes of protecting sexual fruiting bodies. Fungal Biol 126(9):556–565

Veldre V, Abarenkov K, Bahram M et al (2013) Evolution of nutritional modes of Ceratobasidiaceae (Cantharellales, Basidiomycota) as revealed from publicly available ITS sequences. Fungal Ecol 6:256–268

Venneman J, Vandermeersch L, Walgraeve C, Audenaert K, Ameye M, Verwaeren J, Steppe K, Van Langenhove H, Haesaert G, Vereecke D (2020) Respiratory CO2 combined with a blend of volatiles emitted by endophytic *Serendipita* strains strongly stimulate growth of *Arabidopsis* implicating auxin and cytokinin signaling. Front Plant Sci 11:544435

Verbeken A, Stubbe D, van de Putte K, Eberhardt U, Nuytinck J (2014) Tales of the unexpected: angiocarpous representatives of the Russulaceae in tropical South East Asia. Persoonia 32:13–24

Verma S, Varma A, Rexer K-H, Hassel A, Kost G, Sarbhoy A, Bisen P, Bütehorn B, Franken P (1998)*Piriformospora indica*, gen. et sp. Nov., a new root-colonizing fungus. Mycologia 90:896–903

Vidari G, Vita-Finzi P (1995) Sesquiterpenes and other secondary metabolites of genus *Lactarius* (Basidiomycetes): chemistry and biological activity. Stud Nat Prod Chem 17:153–206

Vijaya Chandra SH, Srinivas R et al (2020) Cutaneous *Malassezia*: commensal, pathogen, or protector? Front Cell Infect Microbiol 10:614446. https://doi.org/10.3389/fcimb.2020.614446

Vilgalys R, Cubeta MA (1994) Molecular systematics and population biology of *Rhizoctonia*. Annu Rev Phytopathol 32:135–155

Villegas M, De Luna E, Cifuentes J et al (1999) Phylogenetic studies in Gomphaceae sensu lato (Basidiomycetes). Mycotaxon 70:127–147

Virágh M, Merényi Z, Csernetics Á, Földi C, Sahu N, Liu XB, Hibbett DS, Nagy LG (2021) Evolutionary morphogenesis of sexual fruiting bodies in Basidiomycota: toward a new evo-devo synthesis. Microbiol Mol Biol Rev 86(1):e0001921

Vishniac HS (2006) A multivariate analysis of soil yeast isolated from a latitudinal gradient. Microb Ecol 52:90–103

Vizzini A (2014) Nomenclatural novelties. Tremellodendropsidales. Index Fungorum 152:1

Vizzini A, Ercole E (2012) *Paralepistopsis* gen. nov. and*Paralepista* (Basidiomycota, Agaricales). Mycotaxon 120(1):253–267

Vizzini A, Contu M, Ercole E (2011) *Musumecia* gen. nov. in the Tricholomatoid clade (Basidiomycota, Agaricales) related to *Pseudoclitocybe*. Nordic J Bot 29(6):734–740

Vizzini A, Contu M, Ercole E, Voyron S (2012a) Rivalutazione e delimitazione del genere*Aspidella* (Agaricales, Amanitaceae) nuovamente separato da *Amanita*. Micol Veget Medit 27:75–90

Vizzini A, Ercole E, Contu M (2012b) A contribution to the ITS-LSU phylogeny of the genus*Leucopaxillus* (Tricholomatoid clade, Agaricales), with three new genera and notes on Porpoloma. Mycosphere 3:79–90

Vizzini A, Para R, Fontenla R, Ghignone S, Ercole E (2012c) A preliminary ITS phylogeny of*Melanoleuca* (Agaricales), with special reference to European taxa. Mycotaxon 118(1):361–381

Vizzini A, Angelini C, Ercole E (2014) Le sezioni Velatae e Aporus di Agrocybe sottogenere Aporus: rivalutazione del genere Cyclocybe Velen. ed una nuova specie. RMR 92:21–38

Vizzini A, Angelini C, Los C, Ercole E (2016) *Thelephora dominicana* (Basidiomycota, Thelephorales), a new species from the Dominican Republic, and preliminary noteson thelephoroid genera. Phytotaxa 265(1):27–38. https://doi.org/10.11646/phytotaxa.265.1.2

Vizzini A, Consiglio G, Marchetti M (2019) Mythicomycetaceae fam. nov. (Agaricineae, Agaricales) for Accommodating the Genera Mythicomyces and Stagnicola, and Simocybe parvispora reconsidered. Fungal Syst Evol 3(1):41–56

Vizzini A, Consiglio G, Marchetti M, Alvarado P (2020a) Insights into the Tricholomatineae (Agaricales, Agaricomycetes): a new arrangement of Biannulariaceae and Callistosporium, Callistosporiaceae fam. nov., Xerophorus stat. nov., and Pleurocollybia incorporated into Callistosporium. Fungal Divers 101(1):211–259

Vizzini A, Picillo B, Perrone L, Dovana F (2020b) *Chrysomycena perplexa* gen. et sp. nov. (*Agaricales*, *Porotheleaceae*), a new entity from the lazio region. Rivista Micologica Romana Bolletino Amer 107(35):96–107

Vizzini A, Consiglio G, Marchetti M (2020c) Index Fungorum 462:1

Vizzini A, Consiglio G, Marchetti M, Borovička J, Campo E, Cooper J, Lebeuf R, Ševčíková H (2022) New data in Porotheleaceae and Cyphellaceae: epitypification of *Prunulus scabripes* Murrill, the status of *Mycopan* Redhead, Moncalvo & Vilgalys and a new combination in *Pleurella* Horak emend. Mycol Prog 21:44

Vlasenko VA, Vlasenko AV, Zmitrovich IV (2017) First record of *Neolentinus lepideus* f. *ceratoides* (Gloeophyllales, Basidiomycota) in Novosibirsk Region. Curr Res Environ Appl 7(3):187–192

Voitk A, Saar I, Trudell S, Spirin V, Beug M et al (2017) *Polyozellus multiplex* (Thelephorales) is a species complex containing four new species. Mycologia 109(6):975–992. https://doi.org/10.1080/00275514.2017.1416246

von Höhnel F (1912) Fragmente zur Mykologie 14. Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften. Mathematisch-naturwissenschaftliche Classe 121:339–424

Vondrák J, Svoboda S, Zíbarová L et al (2023) Alcobiosis, an algal-fungal association on the threshold of lichenisation. Sci Rep 13:1–13. https://doi.org/10.1038/s41598-023-29384-4

Wächter D, Melzer A (2020) Proposal for a subdivision of the family Psathyrellaceae based on a taxon-rich phylogenetic analysis with iterative multigene guide tree. Mycol Prog 19(11):1151–1265

Wagner T, Fischer M (2002) Proceedings towards a natural classification of the worldwide taxa*Phellinus* s.l. and *Inonotus* s.l., and phylogenetic relationships of allied gen*era*. Mycologia 94(6):998–1016

Walker LB (1927) Development and mechanism of discharge in *Sphaerobolus iowensis* and *S. stellatus* Tode. J Elisha Mitchell Sci Soc 42:151–178

Walker J (2001) *Yelsemia arthropodii* gen. et sp. nov. (Tilletiales) on *Arthropodium* in Australia. Mycol Res 105:225–232

Wang X-H (2008) The genus *Lactarius* in southwestern China: taxonomy, ontogeny, and floristic biogeography. Dissertation, University of Chinese Academy of Sciences

Wang X-H (2020) Taxonomic comments on edible species of Russulaceae. Mycosystema 39:1617–1639

Wang Y, Zhang H (2021) Advances in the extraction, purification, structural-property relationships and bioactive molecular mechanism of *Flammulina velutipes*polysaccharides: a review. Int J Biol Macromol 167:528–538

Wang X-N, Wang F, Du J-C, Ge H-M, Tan R-X, Liu J-K (2005) A new marasmane sesquiterpene from the Basidiomycete Russula foetens. Z Naturforsch 60:1065–1067

Wang X-H, Yang Z-L, Li Y-C, Knudsen H, Liu P-G (2009) *Russula griseocarnosa* sp. nov. (Russulaceae, Russulales), a commercially important edible mushroom in tropical China: mycorrhiza, phylogenetic position, and taxonomy. Nova Hedwigia 88(1–2):269–282

Wang G-Q, Wei K, Zhang L, Li Z-H, Wang Q-A, Liu J-K (2014a) Three new vibralactone-related compounds from cultures of Basidiomycete *Boreostereum vibrans*. J Asian Nat Prod Res 16(5):447–452

Wang Q-M, Theelen B, Groenewald M, Bai F-Y, Boekhout T (2014b) Moniliellomycetes and Malasseziomycetes, two new classes in Ustilaginomycotina. Persoonia 33:41–47

Wang Q-M, Groenewald M, Takashima M, Theelen B, Han P-J, Liu X-Z, Boekhut T, Bai F-Y (2015a) Phylogeny of yeasts and related fungi within Pucciniomycotina determined from multigene sequence analyses. Stud Mycol 81:27–53

Wang Q-M, Yurkov AM, Göker M, Lumbsch HT, Leavitt SD, Groenewald M, Theelen B, Liu X-Z, Boekhout T, Bai F-Y (2015b) Phylogenetic classification of yeasts and related taxa within Pucciniomycotina. Stud Mycol 81:149–189

Wang K, Chen B-S, Bao L, Ma K, Han J-J, Wang Q, Guo S-X, Liu H-W (2015c) A review of research on the active secondary metabolites of *Hericium* species. Mycosystema 34(4):553–568

Wang Q-M, Begerow D, Groenewald M, Liu XZ, Theelen B, Bai FY, Boekhout T (2015d) Multigene phylogeny and taxonomic revision of yeasts and related fungi in the Ustilaginomycotina. Stud Mycol 81:55–83

Wang P-M, Liu X-B, Dai Y-C, Horak E, Steffen K, Yang Z-L (2018) Phylogeny and species delimitation of *Flammulina*: taxonomic status of winter mushroom in East Asia and a new European species identified using an integrated approach. Mycol Prog 17:1013–1030

Wang X-W, May TW, Liu S-L, Zhou L-W (2021a) Towards a natural classification of *Hyphodontia* Sensu Lato and the trait evolution of Basidiocarps within Hymenochaetales (Basidiomycota). J Fungi 7(6):478. https://doi.org/10.3390/jof7060478

Wang Y-R, Wu Y-D, Vlasák J, Yuan Y, Dai Y-C (2021b) Phylogenetic analysis demonstrating four new species in *Megasporoporia* sensu lato (Polyporales, Basidiomycota). Mycosphere 12(1):1012–1037. https://doi.org/10.5943/mycosphere/12/1/11

Wang X-W, Jiang J-H, Liu S-L, Gafforov Y, Zhou L-H (2022a) Species diversification of the coniferous pathogenic fungal genus *Coniferiporia* (Hymenochaetales, Basidiomycota) in association with its biogeography and host plants. Phytopathology 112:404–413

Wang S-N, Fan Y-G, Yan J-Q (2022) *Iugisporipsathyra reticulopilea* gen. et sp. nov. (Agaricales, Psathyrellaceae) from tropical China produces unique ridge-ornamented spores with an obvious suprahilar plage. MycoKeys 90:147–162. https://doi.org/10.3897/mycokeys.90.85690

Wang X-W, Liu S-L, Zhou L-W (2023a) An updated taxonomic framework of Hymenochaetales (Agaricomycetes, Basidiomycota). Mycosphere 14(1):452–496

Wang H, Ma J-X, Wu D-M, Gao N, Si J, Cui B-K (2023b) Identifying bioactive ingredients and antioxidant activities of wild *Sanghuangporus* species of medicinal fungi. J Fungi 9(2):242

Wang G-S, Cai Q, Hao Y-J, Bau T, Chen Z-H, Li M-X, David N, Kraisitudomsook N, Yang Z-L (2023c) Phylogenetic and taxonomic updates of Agaricales, with an emphasis on Tricholomopsis. Mycology.https://doi.org/10.1080/21501203.2023.2263031

Warcup JH, Talbot PHB (1967) Perfect states of Rhizoctonias associated with orchids. New Phytol 66:631–641

Wartchow F (2019) The discovery of *Neolentinus cirrhosus*(Gloeophyllales, Basidiomycota) in the Neotropics. Plant Fungal Syst 64(1):111–114

Wartchow F, Coimbra V, Sá M (2022) *Gloeocantharellus corneri*(Gomphales, Basidiomycota) from the Brazilian Amazonia. Lilloa 59(2):227–234. https://doi.org/10.30550/j.lil/2022.59.2/2022.10.24

Watling R (1997) The business of fructification. Nature 385:299–300

Watling R, de Meijer AAR (1997) Macromicetos do Estado do Paraná, Brasil, 5. Boletos poróides e lamelares. Edinb J Bot 54(2):231–251

Weber RWS, Zabel D (2011) White Haze and Scarf Skin, two little-known cosmetic defects of apples in Northern Germany, Europ. J Hort Sci 76:45–50

Wei Y-L, Dai Y-C (2008) Notes on *Elmerina* and *Protomerulius* (Basidiomycota). Mycotaxon 105:349–354

Wei Q, Han R, Yan J, Huang J, Zhang W-R, Liu S-R, Xie B-G, Jiang Y-J (2022) Extraction and antioxidant activities of polysaccharides from the mycelia of *Laetiporus cremeiporus*. Mycosystema 41(12):2036–2047

Weiss M, Oberwinkler F (2001) Phylogenetic relationships in Auriculariales and related groups—hypotheses derived from nuclear ribosomal DNA sequences. Mycol Res 105:103–415. https://doi.org/10.1017/S095375620100363X

Weiss M, Bauer R, Begerow D (2004a) Spotlights on heterobasidiomycetes. In: Agerer R, Piepenbring M, Blanz P (eds) Frontiers in basidiomycote mycology. IHW-Verlag, Germany, pp 7–48

Weiss M, Selosse MA, Rexer KH, Urban A, Oberwinkler F (2004b) Sebacinales: a hitherto overlooked cosm of heterobasidiomycetes with a broad mycorrhizal potential. Mycol Res 108(9):1003–1010

Weiss M, Bauer R, Sampaio JP, Oberwinkler F (2014) Tremellomycetes and related groups. In: McLaughlin DJ, Spatafora JW (eds) The Mycota, vol 7, Part A, Systematics and evolution, 2nd edn. Springer, Berlin, pp 331–335

Weiss M, Waller F, Zuccaro A, Selosse M-A (2016) Sebacinales—one thousand and one interactions with land plants. New Phytol 211:20–40

Wells K (1994) Jelly fungi, then and now! Mycologia 86:18–48

Wells K, Bandoni RJ (2001) Heterobasidiomycetes. In: McLaughlin PDDJ, McLaughlin PDEG, Lemke PDPA (eds) Systematics and evolution. Springer, Berlin, pp 85–120

Wells K, Bandoni RJ, Lim SR, Berbee ML (2004) Observations on some species of *Myxarium* and reconsideration of the Auriculariaceae and Hyaloriaceae (Auriculariales). In: Blanz P, Agerer R, Piepenbring M (eds) Frontiers in basidiomycote mycology. IHW-Verlag, Eching, pp 237–248

Wen Q, Zhao H-Y, Shao Y-H, Hu Y-R, Qi Y-C, Wang F-Q, Shen J-W (2023) Content determination and factors influencing production of γ-aminobutyric acid content in fruiting bodies of main edible fungi in China. Mycosystema 42(1):231–243. https://doi.org/10.13346/j.mycosystema.220453

Wenneker M, Pham KTK, Lemmers MEC (2017) *Fibulorhizoctonia psychrophila* is the causal agent of lenticel spot on apple and pear fruit in the Netherlands. Eur J Plant Pathol 148:213–217

Widhelm TJ, Grewe F, Huang JP, Mercado-Díaz JA, Goffinet B, Lücking R, Moncada B, Mason-Gamer R, Lumbsch HT (2019) Multiple historical processes obscure phylogenetic relationships in a taxonomically difficult group (Lobariaceae, Ascomycota). Sci Rep 9(1):8968

Widhelm TJ, Grewe F, Goffinet B, Wedin M, Goward T, Coca LF, Distefano I, Košuthová A, Lumbsch HT (2021) Phylogenomic reconstruction addressing the Peltigeralean backbone (Lecanoromycetes, Ascomycota). Fungal Divers 110(1):59–73

Wiersema JH, McNeill J, Turland N, Barrie FR et al (2015) International Code of Nomenclature for algae, fungi, and plants (Melbourne Code), adopted by the Eighteenth International Botanical Congress Melbourne, Australia, July 2011: Appendix III (Conserved and Rejected Names of Genera and Subdivisions of Genera). Koeltz Scientific Books, Königstein

Wiest R (2022) *Hertzogia*, un nouveau genre clitocyboïde. Bull Soc Mycol Strasbourg 121:29–35

Wijayawardene NN, Hyde KD, Al-Ani LKT, Tedersoo L, Haelewaters D, Rajeshkumar KC, Zhao RL, Aptroot A, Leontyev DV, Saxena RK, Tokarev YS, Dai DQ, Letcher PM, Stephenson SL, Ertz D, Lumbsch HT, Kukwa M, Issi IV, Madrid H, Phillips AJL, Selbmann L, Pfliegler WP, Horváth E, Bensch K, Kirk PM, Kolaříková K, Raja HA, Radek R, Papp V, Dima B, Ma J, Malosso E, Takamatsu S, Rambold G, Gannibal PB, Triebel D, Gautam AK, Avasthi S, Suetrong S, Timdal E, Fryar SC, Delgado G, Réblová M, Doilom M, Dolatabadi S, Pawłowska J, Humber RA, Kodsueb R, Sánchez-Castro I, Goto BT, Silva DKA, de Souza FA, Oehl F, da Silva GA, Silva IR, Błaszkowski J, Jobim K, Maia LC, Barbosa FR, Fiuza PO, Divakar PK, Shenoy BD, Castañeda-Ruiz RF, Somrithipol S, Lateef AA, Karunarathna SC, Tibpromma S, Mortimer PE, Wanasinghe DN, Phookamsak R, Xu J, Wang Y, Tian F, Alvarado P, Li DW, Kušan I, Matočec N, Maharachchikumbura SSN, Papizadeh M, Heredia G, Wartchow F, Bakhshi M, Boehm E, Youssef N, Hustad VP, Lawrey JD, Santiago ALCMA, Bezerra JDP, Souza-Motta CM, Firmino AL, Tian Q, Houbraken J, Hongsanan S, Tanaka K, Dissanayake AJ, Monteiro JS, Grossart HP, Suija A, Weerakoon G, Etayo J, Tsurykau A, Vázquez V, Mungai P, Damm U, Li QR, Zhang H, Boonmee S, Lu YZ, Becerra AG, Kendrick B, Brearley FQ, Motiejūnaitė J, Sharma B, Khare R, Gaikwad S, Wijesundara DSA, Tang LZ, He MQ, Flakus A, Rodriguez-Flakus P, Zhurbenko MP, McKenzie EHC, Stadler M, Bhat DJ, Liu JK, Raza M, Jeewon R, Nassonova ES, Prieto M, Jayalal RGU, Erdoğdu M, Yurkov A, Schnittler M, Shchepin ON, Novozhilov YK, Silva-Filho AGS, Liu P, Cavender JC, Kang Y, Mohammad S, Zhang LF, Xu RF, Li YM, Dayarathne MC, Ekanayaka AH, Wen TC, Deng CY, Pereira OL, Navathe S, Hawksworth DL, Fan XL, Dissanayake LS, Kuhnert E, Grossart HP, Thines M (2020) Outline of Fungi and fungus-like taxa. Mycosphere 11(1):1060–1456

Wijayawardene NN, Hyde KD, Dai DQ, Sánchez-García M, Goto BT, Saxena RK, Erdoğdu M, Selçuk F, Rajeshkumar KC, Aptroot A, Błaszkowski J, Boonyuen N, da Silva GA, de Souza FA, Dong W, Ertz D, Haelewaters D, Jones EBG, Karunarathna SC, Kirk PM, Kukwa M, Kumla J, Leontyev DV, Lumbsch HT, Maharachchikumbura SSN, Marguno F, Martínez-Rodríguez P, Mešić A, Monteiro JS, Oehl F, Pawłowska J, Pem D, Pfliegler WP, Phillips AJL, Pošta A, He MQ, Li JX, Raza M, Sruthi OP, Suetrong S, Suwannarach N, Tedersoo L, Thiyagaraja V, Tibpromma S, Tkalčec Z, Tokarev YS, Wanasinghe DN, Wijesundara DSA, Wimalaseana SDMK, Madrid H, Zhang GQ, Gao Y, Sánchez-Castro I, Tang LZ, Stadler M, Yurkov A, Thines M (2022a) Outline of Fungi and fungus-like taxa—2021. Mycosphere 13(1):53–453

Wijayawardene NN, Phillips AJL, Pereira DS, Dai DQ et al (2022b) Forecasting the number of species of asexually reproducing fungi (Ascomycota and Basidiomycota). Fungal Diversity 114:463–490

Wille N (1903) Algologische Notizen. IX-XIV. Nytt Mag Naturvidenskapene 41:97–187

Willis KJ (2018) State of the world's fungi 2018. Royal Botanic Gardens, Kew

Wilson AW, Hobbie EA, Hibbett DS (2007) The ectomycorrhizal status of *Calostoma cinnabarinum* determined using isotopic, molecular, and morphological methods. Botany 85(4):385–393

Wilson AW, Binder M, Hibbett DS (2011) eEffects of gasteroid fruiting body morphology on diversification rates in three independent clades of fungi estimated using binary state speciation and extinction analysis. Evolution 65(5):1305–1322

Wilson AW, Binder M, Hibbett DS (2012) Diversity and evolution of ectomycorrhizal host associations in the Sclerodermatineae (Boletales, Basidiomycota). New Phytol 194(4):1079–1095

Wilson AW, Hosaka K, Mueller GM (2017) Evolution of ectomycorrhizas as a driver of diversification and biogeographic patterns in the model mycorrhizal mushroom genus *Laccaria*. New Phytol 213(4):1862–1873

Witfeld F, Guerreiro MA, Nitsche F, Wang QM, Nguyen HD, Begerow D (2023) Peribolosporomycetes class. nov.: description of a new heat resistant and osmotolerant basidiomycete lineage, represented by*Peribolospora* gen. nov., *P. kevripleyi*sp. nov., and *P. baueri* sp. nov. Mycol Prog 22(4):30

Wojewoda W (1981) Basidiomycetes (Podstawczaki), Tremellales (Trzesakowe), Auriculariales (Uszakowe), Septobasidiales (Czerwcogrzybowe). Mała Flora Grzybów 2 PWN, Warsaw

Wolfe BE, Kuo M, Pringle A (2011) *Amanita thiersii* is saprotrophic fungus expanding its range in the United States. Mycologia 104:22–33

Wolfe BE, Tulloss RE, Pringle A (2012) The Irreversible loss of a decomposition pathway marks the single origin of an ectomycorrhizal symbiosis. PLoS ONE 7:e39597. https://doi.org/10.1371/journal.pone.0039597

Wood WF, Brandes JA, Foy BD, Morgan CG, Mann TD, DeShazer DA (2012) The maple syrup odour of the "candy cap" mushroom, *Lactarius fragilis* var. rubidus. Biochem Syst Ecol 43:51–53

Worrall JJ, Anagnost SE, Zabel RA (1997) Comparison of wood decay among diverse lignicolous fungi. Mycologia 89:199–219

Wossa SW, Beekman AM, Ma P, Kevo O, Barrow RA (2013) Identification of boletopsin 11 and 12, antibiotics from the traditionally used fungus *Boletopsis* sp. Asian J Org Chem 2(7):565–567. https://doi.org/10.1002/ajoc.201300081

Wrzosek M, Dubiel G, Gorczak M, Pawłowska J, Tischer M, Bałazy S (2016) New insights on the phylogeny and biology of the fungal ant pathogen *Aegeritella*. J Inv Pathol 133:1–7

Wu F, Yuan Y, Malysheva VF, Du P, Dai Y-C (2014a) Species clarification of the most important and cultivated *Auricularia* mushroom "Heimuer": evidence from morphological and molecular data. Phytotaxa 186:241–253. https://doi.org/10.11646/phytotaxa.186.5.1

Wu G, Feng B, Xu J, Zhu X-T, Li Y-C, Zeng N-K, Hosen MI, Yang Z-L (2014b) Molecular phylogenetic analyses redefine seven major clades and reveal 22 new generic clades in the fungal family Boletaceae. Fungal Divers 69:93–115

Wu F, Yuan Y, He S-H, Bandara AR, Hyde KD, Malysheva VF, Dai Y-C (2015a) Global diversity and taxonomy of the *Auricularia auricula-judae* complex (Auriculariales, Basidiomycota). Mycol Prog 14:95. https://doi.org/10.1007/s11557-015-1113-4

Wu F, Yuan Y, Rivoire B, Dai Y-C (2015b) Phylogeny and diversity of the *Auricularia mesenterica* (Auriculariales, Basidiomycota) complex. Mycol Prog 14:42. https://doi.org/10.1007/s11557-015-1065-8

Wu F, Yuan Y, Dai Y-C (2015c) *Porpomyces submucidus*(Hydnodontaceae, Basidiomycota), a new species from tropical China based on morphological and molecular evidence. Phytotaxa 230(1):61–68

Wu G, Zhao H et al (2015d) Genus-wide comparative genomics of *Malassezia* delineates its phylogeny, physiology, and niche adaptation on human skin. PLoS Genet 11(11):e1005614. https://doi.org/10.1371/journal.pgen.1005614

Wu B, Hussain M, Zhang W (2019a) Current insights into fungal species diversity and perspective on naming the environmental DNA sequences of fungi. Mycology 10(3):127–140

Wu F, Zhou L-W, Yang Z-L, Bau T, Li T-H, Dai Y-C (2019b) Resource diversity of Chinese macrofungi: edible, medicinal and poisonous species. Fungal Divers 98:1–76. https://doi.org/10.1007/s13225-019-00432-7

Wu F, Yuan Y, Chen J, Cui B-K, Zhou M, Dai Y-C (2020a) Terrestriporiaceae fam. nov., a new family of Russulales (Basidiomycota). Mycosphere 11(1):2755–2766

Wu F, Zhao Q, Yang Z-L, Ye SY, Rivoire B, Dai Y-C (2020b) *Exidia yadongensis*, a new edible species from East Asia. Mycosystema 39(7):1203–1214

Wu G, Wu K, Qi L-L, Morozova OV, Alexandrova AV, Gorbunova IA, Li Y, Liu J-W, Yang Z-L (2020c) *Psiloboletinus* is an independent genus sister to *Suillus*. Mycologia 112:185–196

Wu F, Tohtirjap A, Fan L-F, Zhou L-W, Alvarenga RLM, Gibertoni TB, Dai Y-C (2021) Global diversity and updated phylogeny of *Auricularia* (Auriculariales, Basidiomycota). J Fungi 7:933. https://doi.org/10.3390/jof7110933

Wu F, Man X-W, Tohtirjap A, Dai Y-C (2022a) A comparison of polypore funga and species composition in forest ecosystems of China, North America, and Europe. For Ecosyst 9:100051. https://doi.org/10.1016/j.fecs.2022

Wu F, Zhou L-W, Vlasák J et al (2022b) Global diversity and systematics of Hymenochaetaceae with poroid hymenophore. Fungal Divers 113:1–192. https://doi.org/10.1007/s13225-021-00496-4

Wuczkowski M, Passoth V, Turchetti B, Andersson A-C, Olstorpe M, Laitila A, Theelen B, van broock M, Buzzini P, Prillinger H, Sterflinger K (2011) Description of *Holtermanniella* gen. nov., including *Holtermanniella takashimae* sp. nov. and four new combinations, and proposal of the order Holtermanniales to accommodate tremellaceous yeasts of the *Holtermannia* clade. Int J Syst Evol Microbiol 61:680–689

Xiao P, Kondo R (2019) Biodegradation and bioconversion of endrin by white rot fungi, *Phlebia acanthocystis* and *Phlebia brevispora*. Mycoscience 60:255–261. https://doi.org/10.1016/j.myc.2019.04.004

Xu J (2020) Fungal species concepts in the genomics era. Genome 63(9):459–468

Xu J, Saunders CW, Hu P, Grant RA, Boekhout T, Kuramae EE, Kronstad JW, Deangelis YM, Reeder NL, Johnstone KR, Leland M, Fieno AM, Begley WM, Sun Y, Lacey MP, Chaudhary T, Keough T, Chu L, Sears R, Yuan B, Dawson TL (2007) Dandruff-associated Malassezia genomes reveal convergent and divergent virulence traits shared with plant and human fungal pathogens. Proc Natl Acad Sci USA 104(47):18730–18735

Xu J-L, Zhao J, Wang L-F, Sun H-Y, Song C-L, Chi Z-M (2012) Enhanced β-galactosidase production from whey powder by a mutant of the psychrotolerant yeast Guehomyces pullulans 17–1 for hydrolysis of lactose. Appl Biochem Biotechnol 166(3):599–611

Xu D-P, Jie Z, Yue Z, Li Y, Li S et al (2016) Extraction of natural antioxidants from the*Thelephora ganbajun* mushroom by an ultrasound-assisted extraction technique and evaluation of antiproliferative activity of the extract against human cancer cells. Int J Mol Sci 17(10):1664. https://doi.org/10.3390/ijms17101664

Xu T-M, Chen Y-H, Zhao C-L (2019a) *Trechispora yunnanensis*sp. nov. (Hydnodontaceae, Basidiomycota) from China. Phytotaxa 424(4):253–261

Xu W-J, Qiao P, Wan S-P, Gong H-D, Yu F-Q (2019b) New record of *Macowanites* in China. J West China for Sci 48(3):137–140

Yang E-J, Song K-S (2015) Polyozellin, a key constituent of the edible mushroom *Polyozellus multiplex*, attenuates glutamate-induced mouse hippocampal neuronal HT22 cell death. Food Funct 6(12):3678–3686. https://doi.org/10.1039/c5fo00636h

Yang Z-L, Zhang L-F, Mueller GM, Kost GW, Rexer KH (2009) A new systematic arrangement of the genus *Oudemansiella* s. str. (Physalacriaceae, Agaricales). Mycosystema 28:1–13

Yang R-H, Li Y, Tang L-H et al (2017) Genome-wide comparison of lignocellulose degradation enzymes in Agaricales. Mycosystema 36:705–717

Yang K, Li Y, Zheng H, Luan X, Li H, Wang Y, Du Q, Sui K, Li H, Xia Y (2020) Adsorption of Congo red with hydrothermal treated shiitake mushroom. Mater Res Express 7:015103

Yao C-X, Tian G-T, Wang H, Yao Y, Sun Y-M (2022) A new *Auricularia heimuer* cultivar 'Gaoyuanyuner 3.' Mycosystema 41(2):318–320. https://doi.org/10.13346/j.mycosystema.210230

Yatabe Y, Nishida H, Murakami N (1999) Phylogeny of Osmundaceae inferred from rbcL nucleotide sequences and comparison to the fossil evidences. J Plant Res 112:397–404

Ye SY, Zhang YB, Wu F, Liu HX (2020) Multi-locus phylogeny reveals two new species of *Exidia* (Auriculariales, Basidiomycota) from China. Mycol Prog 19:859–868.https://doi.org/10.1007/s11557-020-01601-8

Yuan H-S, Lu X, Decock C (2018) Molecular and morphological evidence reveal a new genus and species in Auriculariales from tropical China. MycoKeys 35:27–39

Yuan Y, Chen J-J, Korhonen K, Martin F, Dai Y-C (2021) An updated global species diversity and phylogeny in the forest pathogenic genus *Heterobasidion* (Basidiomycota, Russulales). Front Microbiol 11:596393

Yuan Y, Wu Y-D, Wang Y-R, Zhou M, Qiu J-Z, Li D-W, Vlasák J, Liu H-G, Dai Y-C (2022) Two new forest pathogens in *Phaeolus* (Polyporales, Basidiomycota) on Chinese coniferous trees were confirmed by molecular phylogeny. Front Microbiol 13:942603. https://doi.org/10.3389/fmicb.2022.942603

Yuan Y, Bian L-S, Wu Y-D, Chen J-J, Wu F, Liu H-G, Zeng G-Y, Dai Y-C (2023) Species diversity of pathogenic wood-rotting fungi (Agaricomycetes, Basidiomycota) in China. Mycology 14:204–226.https://doi.org/10.1080/21501203.2023.2238779

Yurchenko E, Olubkov V (2003) The morphology, biology, and geography of a necrotrophic basidiomycete *Athelia arachnoidea* in Belarus. Mycol Prog 2:275–284

Yurchenko E, Wu S-H (2012) *Fibrodontia alba* sp. nov. (Basidiomycota) from Taiwan. Mycoscience 55:336–343

Yurkov AM (2018) Yeast of the soil-obscure but precious. Yeast 35:369–378

Yurkov AM, Vustin MM, Tyaglov BV et al (2008) Pigmented basidiomycetous yeasts are a promising source of carotenoids and ubiquinone Q 10. Microbiology 77:1–6

Yurkov AM, Kachalkin AV, Daniel HM, Groenewald M, Libkind D, de Garcia V, Zalar P, Gouliamova DE, Boekhout T, Begerow D (2015) Two yeast species *Cystobasidium psychroaquaticum* f.a. sp. nov. and *Cystobasidium rietchieii* f.a. sp. nov. isolated from natural environments, and the transfer of *Rhodotorula minuta* clade members to the genus *Cystobasidium*. Antonie Van Leeuwenhoek 107:173–185

Yurkov AM, Wehde T, Federici J et al (2016) Yeast diversity and species recovery rates from beech forest soils. Mycol Prog 15:845–859

Yurkov AM, Sannino C, Turchetti B (2020) *Mrakia fibulata* sp. nov., a psychrotolerant yeast from temperate and cold habitats. Antonie Van Leeuwenhoek 113:499–510

Zajc J, Liu Y, Dai W, Yang Z, Hu J, Gostinčar C, Gunde-Cimerman N (2013) Genome and transcriptome sequencing of the halophilic fungus *Wallemia ichtyophaga*: haloadaptations present and absent. BMC Genomics 14:617

Zalar P, de Hoog GS, Schoers F-J, Frank JM, Gunde-Cimerman N (2005) Taxonomy and physiology of the xerophilic genus *Wallemia* (Wallemiomycetes and Wallemiales, cl. et ord. nov.). Antonie Van Leeuwenhoek 87:311–328

Zambettakis C (1970) Les formes imparfaites des Ustilaginées. Rev Mycol 35:158–175

Zamora JC, Ekman S (2020) Phylogeny and character evolution in the Dacrymycetes, and systematics of Unilacrymaceae and Dacryonaemataceae fam. nov. Persoonia 44:161–205. https://doi.org/10.3767/persoonia.2020.44.07

Zamora JC, Calonge FD, Martín MP (2013) New sources of taxonomic information for earthstars (*Geastrum*, Geastraceae, Basidiomycota): phenoloxidases and rhizomorph crystals. Phytotaxa 132:1–20

Zamora JC, Calonge FD, Hosaka K, Martín MP (2014a) Systematics of the genus *Geastrum* (Fungi: Basidiomycota) revisited. Taxon 63:477–497

Zamora JC, Kuhar F, Castiglia V, Papinutti L (2014b) On *Geastrum argentinum*: a forgotten species. Mycoscience 55:177–182

Zamora JC, Calonge FD, Martín MP (2015) Integrative taxonomyreveals an unexpected diversity in*Geastrum* section Geastrum (Geastrales, Basidiomycota). Persoonia 34:130–165

Zamora JC, Savchenko A, González-Cruz Á et al (2022) *Dendrodacrys*: a new genus for species with branched hyphidia in Dacrymyces s.l., with the description of four new species. Fungal Syst Evol 9:27–42. https://doi.org/10.3114/fuse.2022.09.04

Zeller SM (1939) New and noteworthy Gasteromycetes. Mycologia 31(1):1–32

Zeller SM (1948) Notes on certain Gasteromycetes, including two new orders. Mycologia 40:639–668

Zeller SM (1949) Keys to the orders, families and genera of the Gasteromycetes. Mycologia 41:36–58

Zeller SM, Dodge CW (1919) *Arcangeliella*, *Gymnomyces*, and *Macowanites* in North America. Ann Mo Bot Gard 6(1):49–59

Zhang W, Wendel JF, Clark LG (1997) Bamboozled again! Inadvertent isolation of fungal DNA sequences from bamboos (Poaceae: Bambusoideae). Mol Phologenet Evol 8:205–217

Zhang M, Li T, Song B (2018) *Heliocybe villosa* sp. nov., a new member to the genus *Heliocybe* (Gloeophyllales). Phytotaxa 349(2):173–178

Zhang K, Wang W, Zhao K, Ma Y, Cheng S, Zhou J, Wu Z (2020) Producing a novel edible film from mushrooms (*L. edodes* and *F. velutipes*) by-products with a two-stage treatment namely grinding and bleaching. J Food Eng 275:109862

Zhang Q-H, Liu J-L, Li J-H, Chen L-D, Kong X-Q, Sun S-J (2022a) A new *Tremella fuciformis* cultivar 'Xiuyin 1.' Mycosystema 41(1):163–165. https://doi.org/10.13346/j.mycosystema.210293

Zhang Q-Y, Liu H-G, Papp V, Zhou M, Wu F, Dai Y-C (2022b) Taxonomy and multi-gene phylogeny of poroid *Panellus* (Mycenaceae, Agaricales) with description of five new species from China. Front Microbiol 13:928941. https://doi.org/10.3389/fmicb.2022.928941

Zhang B, Ye L, Zhou J, Tan W, Li X-L (2022c) A new *Auricularia cornea* cultivar 'Haoyanghuangbei 2.' Mycosystema 41(1):160–162. https://doi.org/10.13346/j.mycosystema.210198

Zhang J, Hou Y-H, Du J-F, Zhou Q-S, Li N (2023a) A comparative study on immunomodulatory effects of water extracts of *Inonotus hispidus*, *Sanghuangporus sanghuang* and *S. vaninii*. Mycosystema 42(4):907–915. https://doi.org/10.13346/j.mycosystema.220074

Zhang Q-Y, Liu H-G, Papp V, Zhou M, Dai Y-C, Yuan Y (2023b) New insights into the classification and evolution of *Favolaschia* (Agaricales, Basidiomycota) and its potential distribution, with descriptions of eight new species. Mycosphere 14:777–814. https://doi.org/10.5943/mycosphere/14/1/10

Zhao R-L, Desjardin DE, Soytong K, Hyde KD (2008) Advances in the phylogenesis of Agaricales and its higher ranks and strategies for establishing phylogenetic hypotheses. J Zhejiang Univ Sci B 9:779–786. https://doi.org/10.1631/jzus.B0860012

Zhao R-L, Zhou J-L, Chen J et al (2016a) Towards standardizing taxonomic ranks using divergence times—a case study for reconstruction of the Agaricus taxonomic system. Fungal Divers 78:239–292

Zhao S, Liu J, Tu H, Li F, Li X, Yang J, Liao J, Yang Y, Liu N, Sun Q (2016b) Characteristics of uranium biosorption from aqueous solutions on fungus *Pleurotus ostreatus*. Environ Sci Pollut Res 23:24846–24856

Zhao R-L, Li G-J, Sánchez-Ramírez S et al (2017) A six-gene phylogenetic overview of Basidiomycota and allied phyla with estimated divergence times of higher taxa and a phyloproteomics perspective. Fungal Divers 84:43–74. https://doi.org/10.1007/s132255-017-0381-5

Zhao P, Zhang Z-F, Hu D-M, Tsui KM, Qi X-H, Phurbu D, Gafforov Y, Cai L (2021) Contribution to rust flora in China I, tremendous diversity from natural reserves and parks. Fungal Divers 110(1):1–58

Zheng H-D, Liu P-G (2008) Additions to our knowledge of the genus Albatrellus (Basidiomycota) in China. Fungal Divers 32:157–170

Zheng C-J, Sohn MJ, Kim WG (2006) Atromentin and leucomelone, the first inhibitors specific to enoyl-ACP reductase (FabK) of *Streptococcus pneumoniae*. J Antibiot 59(12):808–812. https://doi.org/10.1038/ja.2006.108

Zhou L-W, Dai Y-C (2013) Phylogeny and taxonomy of poroid and lamellate genera in the Auriculariales (Basidiomycota). Mycologia 105:1219–1230. https://doi.org/10.3852/12-212

Zhou L-W, Kõljalg U (2013) A new species of *Lenzitopsis*: emphasizing its phylogenetic position and potential loss of ectomycorrhizal function. Mycol Prog 54(1):87–92. https://doi.org/10.1016/j.myc.2012.06.002

Zhou L-W, Ji X-H, Vlasák J, Dai Y-C (2018a) Taxonomy and phylogeny of *Pyrrhoderma*: a redefinition, the segregation of *Fulvoderma*, gen. nov., and identifying four new species. Mycologia 110(5):872–889

Zhou L-W, Wang X-W, Vlasák J, Ren G-J (2018b) Resolution of phylogenetic position of Nigrofomitaceae within Hymenochaetales (Basidiomycota) and *Nigrofomes sinomelanoporus* sp. nov. (Nigrofomitaceae) from China. MycoKeys 29:1–13

Zhou M, Liu Z-B, Lim Y-W, Cho Y, Yang R-H, Bao D-P, Zhao C-L, Li D-W, Vlasák J, Dai Y-C (2022a) Two new species of *Fistulina* (Agaricales, Basidiomycota) from the Northern Hemisphere. Front Microbiol 13:1063038. https://doi.org/10.3389/fmicb.2022.1063038

Zhou M, Vlasák J, Ghobad-Nejhad M, Lim YW, Dai Y-C (2022b) Taxonomy and an updated phylogeny of*Anomoloma* (Amylocorticiales, Basidiomycota). Forests 13:713.https://doi.org/10.3390/f13050713

Zhou H-M, Zhao Q, Wang Q, Wu F, Dai Y-C (2022c) Two new species of *Boletopsis* (Bankeraceae, Thelephorales) from Southwest China. MycoKeys 89:155–169.https://doi.org/10.3897/mycokeys.89.83197

Zhu L, Cui B-K (2016) Progress on the studies of medicinal mushrooms" Sanghuang" group. J Fungal Res 14(4):201–209

Zhu L, Song J, Zhou J-L, Si J, Cui B-K (2019) Species diversity, phylogeny, divergence time, and biogeography of the genus *Sanghuangporus* (Basidiomycota). Front Microbiol 10:812

Zhuang W-Y, He X-S (2007) A new pycnidioid basidiomycete family with gelatinized fruitbodies. Mycosystema 26(3):339–342

Zong T-K, Zhao C-L (2021) Morphological and molecular identification of two new species of*Phlebiella* (Polyporales, Basidiomycota) from southern China. Nova Hedwigia 112(3–4):501–514

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