Fungal Diversity (2024) 128:1–165
https://doi.org/10.1007/s13225-024-00540-z

Classes and phyla of the kingdom *Fungi*

Nalin N. Wijayawardene[1,2,3] · Kevin D. Hyde[4,5,6,7] · Kirill V. Mikhailov[8,9] · Gábor Péter[10] · André Aptroot[11] · Carmen L. A. Pires-Zottarelli[12] · Bruno T. Goto[13] · Yuri S. Tokarev[14] · Danny Haelewaters[15,16,17] · Samantha C. Karunarathna[1] · Paul M. Kirk[18] · André L. C. M. de A. Santiago[19] · Ramesh K. Saxena[20] · Nathan Schoutteten[21,90] · Madhara K. Wimalasena[3,22] · Vladimir V. Aleoshin[8,9] · Abdullah M. S. Al-Hatmi[23] · Kahandawa G. S. U. Ariyawansa[24] · Amanda R. Assunção[13] · Thushara C. Bamunuarachchige[3] · Hans-Otto Baral[25] · D. Jayarama Bhat[26,27] · Janusz Błaszkowski[28] · Teun Boekhout[29] · Nattawut Boonyuen[30] · Michael Brysch-Herzberg[31] · Bin Cao[32] · Jonathan Cazabonne[33,34] · Xue-Mei Chen[1] · Claudia Coleine[35] · Dong-Qin Dai[1] · Heide-Marie Daniel[36] · Suzana B. G. da Silva[19] · Francisco Adriano de Souza[37] · Somayeh Dolatabadi[38] · Manish K. Dubey[39] · Arun K. Dutta[40] · Aseni Ediriweera[2,41] · Eleonora Egidi[42,43] · Mostafa S. Elshahed[44] · Xinlei Fan[45,46] · Juliana R. B. Felix[13] · Mahesh C. A. Galappaththi[47] · Marizeth Groenewald[48] · Li-Su Han[1] · Bo Huang[49] · Vedprakash G. Hurdeal[50] · Anastasia N. Ignatieva[14] · Gustavo H. Jerônimo[12] · Ana L. de Jesus[12] · Serhii Kondratyuk[51,52] · Jaturong Kumla[53,54] · Martin Kukwa[55] · Qirui Li[56,57] · Juliana L. R. Lima[13] · Xiao-Yong Liu[58] · Wenhua Lu[1,53] · H. Thorsten Lumbsch[59] · Hugo Madrid[60] · Franco Magurno[61] · Guy Marson[62] · Eric H. C. McKenzie[63] · Audrius Menkis[64] · Armin Mešić[65] · Elaine C. R. Nascimento[13] · Elena S. Nassonova[66] · Yong Nie[67] · Naasson V. L. Oliveira[13] · Emilia A. Ossowska[55] · Julia Pawłowska[68] · Ursula Peintner[69] · Igor R. Pozdnyakov[70] · Bhagya M. Premarathne[71] · A. K. Hasith Priyashantha[72,73] · C. Alisha Quandt[16] · Mariana B. Queiroz[13] · Kunhiraman C. Rajeshkumar[74] · Mubashar Raza[75] · Niranjan Roy[40] · Milan C. Samarakoon[76] · Alessandra A. Santos[13] · Lidiane A. Santos[77] · Felix Schumm[78] · Laura Selbmann[35,79] · Faruk Selçuk[80] · D. Rabern Simmons[81] · Anastasia V. Simakova[82] · Maudy Th. Smith[48] · Onden Paraparath Sruthi[74] · Nakarin Suwannarach[53,54] · Kazuaki Tanaka[83] · Saowaluck Tibpromma[1] · Elias O. Tomás[13] · Merve Ulukapı[80] · Nicolas Van Vooren[84] · Dhanushka N. Wanasinghe[85] · Evi Weber[24] · Qianzhen Wu[56,57] · Er Fu Yang[1,73] · Ryuichi Yoshioka[83,91] · Noha H. Youssef[44] · Annemarie Zandijk[48] · Gui-Qing Zhang[1] · Jin-Yong Zhang[86] · Heng Zhao[87] · RuiLin Zhao[32] · Oleg A. Zverkov[9] · Marco Thines[88,89] · Sergey A. Karpov[70]

Received: 14 March 2024 / Accepted: 3 July 2024 / Published online: 15 October 2024
© The Author(s) 2024

Abstract

Fungi are one of the most diverse groups of organisms with an estimated number of species in the range of 2–3 million. The higher-level ranking of fungi has been discussed in the framework of molecular phylogenetics since Hibbett et al., and the definition and the higher ranks (e.g., phyla) of the 'true fungi' have been revised in several subsequent publications. Rapid accumulation of novel genomic data and the advancements in phylogenetics now facilitate a robust and precise foundation for the higher-level classification within the kingdom. This study provides an updated classification of the kingdom *Fungi*, drawing upon a comprehensive phylogenomic analysis of *Holomycota*, with which we outline well-supported nodes of the fungal tree and explore more contentious groupings. We accept 19 phyla of *Fungi,* viz. *Aphelidiomycota*, *Ascomycota*, *Basidiobolomycota*, *Basidiomycota*, *Blastocladiomycota*, *Calcarisporiellomycota*, *Chytridiomycota*, *Entomophthoromycota*, *Entorrhizomycota*, *Glomeromycota*, *Kickxellomycota*, *Monoblepharomycota*, *Mortierellomycota*, *Mucoromycota*, *Neocallimastigomycota*, *Olpidiomycota*, *Rozellomycota*, *Sanchytriomycota,* and *Zoopagomycota*. In the phylogenies, *Caulochytriomycota* resides in *Chytridiomycota*; thus, the former is regarded as a synonym of the latter, while *Caulochytriomycetes* is viewed as a class in *Chytridiomycota*. We provide a description of each phylum followed by its classes. A new subphylum, *Sanchytriomycotina* Karpov is introduced as the only subphylum in *Sanchytriomycota*. The subclass *Pneumocystomycetidae*

Handling Editor: Jian-Kui Liu.

Extended author information available on the last page of the article

Kirk et al. in *Pneumocystomycetes*, *Ascomycota* is invalid and thus validated. Placements of fossil fungi in phyla and classes are also discussed, providing examples.

Keywords *Caulochytriomycota* · Phylogenomic analyses · *Pneumocystomycetidae* · *Sanchytriomycotina*

Introduction

The Kingdom *Fungi* is one of the most diverse groups of living organisms on earth and its members occur across a broad range of ecosystems including extreme environments. Fungi are primarily heterotrophs that occur as uni- to multicellular organisms and are vital in ecosystem functioning (Kendrick 2000; Kirk et al. 2008; Hyde et al. 2018). Over time, understanding different aspects of fungi (i.e. taxonomy, diversity, species number, genetics, chemistry) has improved rapidly by incorporating molecular and bioinformatics tools with traditional approaches (Wijayawardene et al. 2021a). Many studies have been published based on these polyphasic approaches and these have expanded the magnitude of the kingdom (Hyde 2022). Several studies have predicted a higher diversity of different taxonomic groups (e.g. freshwater fungi *fide* Calabon et al. 2022; telemorphic *Ascomycota fide* Senanayake et al. 2022; *Basidiomycota fide* He et al. 2022a; asexually producing taxa *fide* Wijayawardene et al. 2022b). Currently, about 160,000 species of fungi are accepted by Species Fungorum (2024; accession data 12.04.2024) though the estimation of the number of species is 2–3 million (Niskanen et al. 2023). Revealing these unknown or 'missing taxa' is one of the biggest challenges, since many species do not produce any (easily) observable phenotypic characters, i.e. dark taxa (Page 2016; Wang et al. 2016a, b), and it is thus impossible to identify and describe them from conventional techniques (Mitchell and Zuccaro 2006; Seifert 2009). Over three decades, i.e. since White et al. (1990), Sanger sequencing has played a vital role in species recognition, determining the higher-level classification and other fundamental taxonomic approaches such as linking sexual and asexual or dimorphic taxa. Nevertheless, Sanger sequencing can only sequence specimens or cultures individually (Shokralla et al. 2012). Margulies et al. (2005) and Shendure et al. (2005) developed 'sequencing-by-synthesis technology' to overcome the major drawbacks of Sanger sequencing, which is currently called 'high-throughput sequencing' (HTS) or 'next-generation sequencing'(NGS) (Schuster 2008; Shendure and Ji 2008). At present, HTS/NGS plays an important role in microbial and mycological research, especially in determining dark taxa from environmental samples which could represent novel lineages in the Kingdom *Fungi* (Tedersoo et al. 2018).

Higher-ranking classification of fungi and current status

Higher-level classification of different organisms has been debated among taxonomists in different disciplines. Ruggiero et al. (2015) mentioned that 'biological classification (taxonomy) aims to simplify and order the immense diversity of life into coherent units called taxa that have widely accepted names and whose members share important properties.' The Linnaean system has played a significant role for over 250 years (since mid-eighteenth century) and is broadly adopted by taxonomists (Schuh 2003; Ruggiero et al. 2015). The molecular techniques introduced in the last three decades have progressed the Linnaean system to 'a system of modern biological classification' (Liu et al. 2016).

Nowadays, molecular systematics has become the basis for current classification schemes of fungi at various ranks. Hibbett and Donoghue (1998) discussed the importance of using DNA-based phylogenetic analyses to classify fungi. Hibbett et al. (2007) was one of the first significant studies that broadly and comprehensively discussed the higher-level ranking of fungi. Subsequently, different studies have addressed the higher-level ranking of fungi but are restricted to different taxa (Table 1).

A milestone in recent fungal classification was the study of Tedersoo et al. (2018) based on both phylogenies and divergence time estimates. In their analyses, they accepted 18 phyla based on their DNA sequence analyses, though the taxa in *Caulochytriomycota* lack DNA sequences. Galindo et al. (2021) introduced a new phylum, *Sanchytriomycota*, in *Holomycota*. Wijayawardene et al. (2020a, 2022a) accepted 20 phyla in the kingdom *Fungi* of which, 17 have been proposed to accommodate early divergent taxa, i.e., excluding *Ascomycota*, *Basidiomycota,* and *Entorrhizomycota* in *Dikarya* (Table 2). However, recent subsequent studies provided different conclusions on the classification of Early Divergent Fungi (EDF) (see below). Wijayawardene et al. (2020b) recommended the importance of maintaining a dynamic database on fungal classification.

Early divergent fungi (EDF)

The discussion of 'what delineates true fungi from fungi-like protists' has been a controversial topic for decades. The discovery and introduction of novel early lineages of *Holomycota* and the advancements in our knowledge of

Table 1 Examples of major studies that have addressed the higher-level classification of fungi

Targeted taxon (Class/Phyla/Kingdom)*	Loci	References
Kingdom *Fungi*	*rpb1* and *rpb2*	Tedersoo et al. (2018)
Kingdom *Fungi*	LSU and SSU	Voigt et al. (2021)
Kingdom *Fungi*	LSU, SSU, *rpb1* and *rpb2*	Wijayawardene et al. (2020a)
Kingdom *Fungi*	Genome	Li et al. (2021a, b)
Kingdom *Fungi*	Genome	Strassert and Monaghan (2022a, b)
Subkingdom *Mucoromyceta*	Genome	Zhao et al. (2023)
Phylum *Basidiomycota*	nrLSU, nrSSU, 5.8S, *tef*1-α, *rpb1* and *rpb2*	Zhao et al. (2017)
	Phylogenomic	Mishra et al. (2018)
Phylum *Glomeromycota*	SSU, ITS, and partial LSU	Oehl et al. (2011a,b)
Phylum *Mucoromycota*	ITS, LSU	Zhao et al. (2023)
'Zygomycota'	Conserved orthologous proteins	Spatafora et al. (2016)
Subphylum *Pucciniomycotina*	LSU, SSU, *tef*1-α, *rpb1*, *rpb2*, and 5.8 s	He et al. (2019)
Subphylum *Ustilaginomycotina*	LSU, SSU, 5.8 s, *tef*1-α, *rpb1*, and *rpb2*,	He et al. (2019)
Class *Dothideomycetes*	LSU, SSU, *tef*1-α and *rpb2*	Hongsanan et al. (2020a, b)
Class *Leotiomycetes*	Genome	Johnston et al. (2019)
Class *Sordariomycetes*	LSU, SSU, *tef*1-α and *rpb2*	Hongsanan et al. (2017) and Hyde et al. (2020)

*We only list studies published after Hibbett et al. (2007) that focus on classes and higher taxa (including intermediate/ auxiliary ranks) as this paper focuses only on them

zoosporic fungi have blurred the lines between fungi and their relatives. However, the molecular-based phylogenetic analyses have resolved many of the deepest nodes of the fungal phylogeny, and now provide a solid foundation to define the 'true fungi'. The early-diverging lineages of *Holomycota* are represented by phagotrophic nucleariids (*Cristidiscoidea*), rozellids + *Microsporidia* (collectively referred to as *Cryptomycota* or *Rozellomycota*), and aphelids, which branch off in succession from the ancestral lineage leading to the traditional fungal phyla, i.e. the 'true fungi' (Tedersoo et al. 2018; Wijayawardene et al. 2020a; Galindo et al. 2021; Mikhailov et al. 2022). The aphelids and rozellids comprise parasitic intracellular organisms, which infect the host (algae for *Aphelida* or a diverse range of hosts for *Rozellomycota*) and phagocytize the cell contents before producing zoospores. Many mycologists include rozellids + *Microsporidia* and *Aphelida* inside *Fungi*, despite their differences in the mode of nutrition (e.g. Tedersoo et al. 2018). The phagotrophic mode of nutrition is absent in true fungi, and the establishment of exclusively osmotrophic nutrition has coincided with the losses of some phagotrophy-related proteins early in their evolution (Mikhailov et al. 2022). At the same time, phagotrophic holomycotan lineages lack some of the saprotrophy-linked proteins found in the true fungi (Pozdnyakov et al. 2023). Whether this should be viewed as a basis for separating *Fungi* from the lineages of rozellids + *Microsporidia* and aphelids is a matter of debate. From a taxonomic perspective, expanding *Fungi* and dividing them into *Eumycota* and other early divergent lineages is acceptable, but it requires a clear characterization of the *Fungi*, which is presently not available. In addition, there is a temptation to expand *Fungi* to *Holomycota*, which was already suggested by Berbee et al. (2017). In the present review, we accept the broader version of *Fungi* by Tedersoo et al. (2018), but we have to keep in mind an alternative view and try to distinguish the true *Fungi* from their close relatives on the base of morpho-biological and genomic characters.

Recent phylogenomic analyses (Galindo et al. 2021; Mikhailov et al. 2022; Strassert and Monaghan 2022a, b) have shown that *Chytridiomycota* formed the earliest branch of 'true fungi'—a position contested previously by *Blastocladiomycota* in some studies (Chang et al. 2015; Li et al. 2021b). In the newer phylogenies *Blastocladiomycota* formed the next branch of 'true fungi' together with the novel phylum *Sanchytriomycota*. The relatively derived position of *Blastocladiomycota* corresponds to their advanced characters, such as sporic meiosis, hyphal-like apical growing structures (*Allomyces*), narrow sporangia exit tubes (*Catenaria*), and relatively small numbers of carbohydrate metabolism genes (Galindo et al. 2021). The *Chytridiomycota*, *Blastocladiomycota*, and *Sanchytriomycota* comprise the zoosporic lineages of fungi along with *Olpidiomycota*, which is the latest lineage to diverge from the fungal stem before the transition of fungi to terrestrial habitats (Chang et al. 2021).

Table 2 List of phyla, subphyla and classes in different subkingdoms (based on this study)

Subkingdoms	Phyla	Subphyla	Classes
Aphelidiomyceta	***Aphelidiomycota***	*Aphelidiomycotina*	*Aphelidiomycetes*
Basidiobolomyceta	***Basidiobolomycota***	*Basidiobolomycotina*	*Basidiobolomycetes*
Blastocladiomyceta	***Blastocladiomycota***	*Blastocladiomycotina*	*Blastocladiomycetes*
			Physodermatomycetes
	Sanchytriomycota	*Sanchytriomycotina* subphylum nov	*Sanchytriomycetes*
Chytridiomyceta	***Chytridiomycota***	*Chytridiomycotina*	*Caulochytriomycetes* *Chytridiomycetes*
			Cladochytriomycetes
			Mesochytriomycetes
			Lobulomycetes
			Polychytriomycetes
			Rhizophlyctidomycetes
			Rhizophydiomycetes
			Spizellomycetes
			Synchytriomycetes
	Monoblepharomycota	*Monoblepharomycotina*	*Hyaloraphidiomycetes*
			Monoblepharidomycetes
	Neocallimastigomycota	*Neocallimastigomycotina*	*Neocallimastigomycetes*
Dikarya	***Ascomycota***	*Pezizomycotina*	*Arthoniomycetes*
			Dothideomycetes
			Eurotiomycetes
			Laboulbeniomycetes
			Lecanoromycetes
			Leotiomycetes
			Lichinomycetes
			Orbiliomycetes
			Pezizomycetes
			Sordariomycetes
			Xylobotryomycetes
		Saccharomycotina	*Alloascoideomycetes*
			Dipodascomycetes
			Lipomycetes
			Pichiomycetes
			Saccharomycetes
			Sporopachydermiomycetes
			Trigonopsidomycetes
		Taphrinomycotina	*Archaeorhizomycetes*
			Neolectomycetes
			Novakomycetes
			Pneumocystomycetes
			Schizosaccharomycetes
			Taphrinomycetes
	Basidiomycota	*Agaricomycotina*	*Agaricomycetes*
			Bartheletiomycetes
			Dacrymycetes
			Tremellomycetes
		Pucciniomycotina	*Agaricostilbomycetes*
			Atractiellomycetes
			Classiculomycetes
			Cryptomycocolacomycetes

Table 2 (continued)

Subkingdoms	Phyla	Subphyla	Classes
			Cystobasidiomycetes
			Microbotryomycetes
			Mixiomycetes
			Pucciniomycetes
			Spiculogloeomycetes
			Tritirachiomycetes
		Ustilaginomycotina	*Exobasidiomycetes*
			Malasseziomycetes
			Moniliellomycetes
			Peribolosporomycetes
			Ustilaginomycetes
		Wallemiomycotina	*Wallemiomycetes*
	Entorrhizomycota	*Entorrhizomycotina*	*Entorrhizomycetes*
Mucoromyceta	***Calcarisporiellomycota***	*Calcarisporiellomycotina*	*Calcarisporiellomycetes*
	Glomeromycota	*Glomeromycotina*	*Archaeosporomycetes*
			Glomeromycetes
			Paraglomeromycetes
	Mortierellomycota	*Mortierellomycotina*	*Mortierellomycetes*
	Mucoromycota	*Mucoroymycotina*	*Endogonomycetes*
			Mucoromycetes
			Umbelopsidomycetes
Olpidiomyceta	***Olpidiomycota***	*Olpidiomycotina*	*Olpidiomycetes*
Rozellomyceta	***Rozellomycota***	*Rozellomycotina*	*Microsporidea*
			Rudimicrosporea
Zoopagomyceta	***Entomophthoromycota***	*Entomophthoromycotina*	*Entomophthoromycetes*
			Neozygitomycetes
	Kickxellomycota	*Kickxellomycotina*	*Kickxellomycetes*
			Asellariomycetes
			Barbatosporomycetes
			Dimargaritomycetes
			Harpellomycetes
			Ramicandelaberomycetes
	Zoopagomycota	*Zoopagomycotina*	*Zoopagomycetes*

Phyla of the Kingdom *Fungi*

In this compilation, we accept 19 phyla (viz., *Aphelidiomycota*, *Ascomycota*, *Basidiomycota*, *Basidiobolomycota*, *Blastocladiomycota*, *Calcarisporiellomycota*, *Chytridiomycota* (= *Caulochytriomycota*), *Entomophthoromycota*, *Entorrhizomycota*, *Glomeromycota*, *Kickxellomycota*, *Monoblepharomycota*, *Mortierellomycota*, *Mucoromycota*, *Neocallimastigomycota*, *Olpidiomycota*, *Rozellomycota*, *Sanchytriomycota* and *Zoopagomycota*).

Aphelidiomycota Tedersoo etal.
Tedersoo et al. (2018) introduced the phylum *Aphelidiomycota* to accommodate *Aphelidium* (Zopf) Gromov and three other related genera, *Amoeboaphelidium* Scherff., *Paraphelidium* Karpov et al. and *Pseudaphelidium* Schweikert & Schnepf. Members of *Aphelidiomycota* (i.e. aphelids) are a relatively poorly studied algal parasitic group (Karpov et al. 2014a, 2017a,b). On the basis of early phylogenies, Karpov et al. (2014a, 2017a,b) regarded aphelids as members of a novel superphylum *Opisthosporidia*, which also included *Rozellomycota* (= *Cryptomycota*) along with *Microsporidia*. The proposed *Opisthosporidia* were viewed as a sister group to the fungal clade, but still retained in *Holomycota*. Subsequent analyses found no support for the union of aphelids and *Rozellomycota*, thus rendering the *Opisthosporidia* unsubstantiated. Accordingly, aphelids were proposed to constitute a distinct lineage of fungi at the phylum level (*Aphelidiomycota*) or even subkingdom level (*Aphelidiomyceta*) (Tedersoo et al. 2018). Subsequent

outlines by Wijayawardene et al. (2018a, 2020a, 2022a) followed Tedersoo et al. (2018) and listed *Aphelidiomycota* as a distinct phylum in the fungal clade.

Ascomycota Caval.-Sm.

Cavalier-Smith (1998) introduced the phylum *Ascomycota*, one of the largest phyla in the kingdom. *Ascomycota* is further divided into three subphyla, *Pezizomycotina*, *Saccharomycotina* and *Taphrinomycotina* (James et al. 2006a; Liu et al. 2006; Spatafora et al. 2006; Sugiyama et al. 2006). Currently, 24 classes have been listed under the phylum which comprises fungi isolated from a broad range of environments including terrestrial and aquatic ecosystems. The subphylum *Pezizomycotina* comprises multicellular, lichenized (e.g. Class *Lecanoromycetes*) and non-lichenized taxa (e.g. Class *Dothideomycetes*). The subphyla *Saccharomycotina* and *Taprinomycotina* comprise the yeasts assigned to *Ascomycota* which are "characterized by budding or fission as the primary means of asexual reproduction, and have sexual states that are not enclosed in fruiting bodies" (Kurtzman et al. 2011). Until recently *Saccharomycotina* has comprised a single class, *Saccharomycetes* and a single order *Saccharomycetales* (Kurtzman et al. 2011). More than 1,200 species were assigned to the single class and order of this subphylum. However, based on relative evolutionary divergence (RED) analyses, Li et al. (2021a) revealed that the subphylum *Saccharomycotina* is seriously under-classified. While it is characterised by higher levels of genomic diversity and evolutionary rates than *Pezizomycotina* (Shen et al. 2020), it contained only one class as opposed to the 16 classes of *Pezizomycotina*. The other sister subphylum, *Taphrinomycotina*, although it accommodates about ten times fewer species than *Saccharomycotina*, involves six classes. Recent genome-scale phylogenetic analyses divided the subphylum *Saccharomycotina* into 12 major clades (Shen et al. 2016, 2018). Groenewald et al. (2023) proposed a new genome-informed higher rank classification of *Saccharomycotina*. Based on genome-scale phylogenetic analyses and RED analyses they proposed an updated classification of *Saccharomycotina* reflecting better the evolutionary divergence of the subphylum. According to the new classification *Saccharomycotina* consists of seven classes (*Alloascoideomycetes*, *Dipodascomycetes*, *Lipomycetes, Saccharomycetes*, *Pichiomycetes*, *Sporopachydermiomycetes* and *Trigonopsidomycetes*) and twelve orders. The third subphylum, *Taphrinomycotina*, mainly consists of yeast-like taxa.

Basidiobolomycota Doweld

Doweld (2001) introduced this phylum, to accommodate the class *Basidiobolomycetes* which also comprises of one order and one family, i.e. *Basidiobolales* Jacz. & P.A. Jacz. and *Basidiobolaceae* Engl. & E. Gilg. Tedersoo et al. (2018) introduced the subkingdom *Basidiobolomyceta* Tedersoo et al. to accommodate *Basidiobolomycota* since it showed a distinct lineage from other subkingdoms. Currently, the phylum consists of one subphylum, *Basidiobolomycotina*.

Basidiomycota R.T. Moore

Moore (1980) introduced *Basidiomycota*, which is a major phylum of the Kingdom *Fungi*, being second in species numbers to *Ascomycota* (Begerow et al. 2018; He et al. 2019). The phylum comprises four subphyla, namely *Agaricomycotina*, *Pucciniomycotina*, *Ustilaginomycotina* and *Wallemiomycotina* (He et al. 2019, 2022a, b). Whereas the typical mushroom-forming fungi are restricted to *Agaricomycotina* while *Pucciniomycotina* and *Ustilaginomycotina* are mainly characterised by phytoparasites. The members of *Basidiomycota* are mainly reported as saprobes, pathogens of animals and plants, and ectomycorrhizal species (He et al. 2022a). Traditionally, fungi producing sexually by means of basidia have been assigned to this phylum. However, based on cultural, microscopic, and molecular phylogenetic methods, several genera with asexually reproducing species were also recognised as members of *Basidiomycota* (Hyde et al. 2011; Wijayawardene et al. 2012, 2020a, 2021b, 2022a,b). *Basidiomycetous* yeasts are also an important group in this phylum and occur in *Agaricomycotina*, *Pucciniomycotina*, and *Ustilaginomycotina* (e.g. Wang et al. 2015b; Oberwinkler 2017).

Blastocladiomycota T.Y. James

James et al. (2006b) introduced the phylum *Blastocladiomycota* which was considered to be a monophyletic group within the phylum *Chytridiomycota* divergent from other zoosporic fungi, clustering among non-zoosporic fungi (Powell 2017). The phylum *Blastocladiomycota* is further divided into the subphylum *Blastocladiomycotina* (Tedersoo et al. 2018) and consists of two classes, *Blastocladiomycetes* Doweld., and *Physodermatomycetes* Tedersoo et al. with less than 200 species described. They live in aquatic and terrestrial environments as saprotrophs or parasites of algal groups (Money 2016).

Calcarisporiellomycota Tedersoo et al.

The phylum *Calcarisporiellomycota* was introduced by Tedersoo et al. (2018) and accommodates the genera *Calcarisporiella* de Hong., and *Echinochlamydosporium* Jiang et al. The phylum depicts a deep lineage with the phyla *Mucoromycota* (Hirose et al. 2012; Yamamoto et al. 2015) or *Mortierellomycota* (Jiang et al. 2011). The vegetative structure shows a branched thallus with septate hyphae with uninucleate, ovoid to ellipsoid spores. The genera are also saprotrophic in soil (Jiang et al. 2011; Hirose et al. 2012).

Chytridiomycota Doweld
= *Caulochytriomycota* Doweld

Doweld (2001) introduced the phylum *Chytridiomycota* and this was phylogenetically confirmed in subsequent studies (e.g. James et al. 2006a,b; Letcher et al. 2006; Mozley-Standridge et al. 2009). Tedersoo et al. (2018) introduced the subkingdom *Chytridiomyceta* Tedersoo et al. to accommodate *Chytridiomycota*, *Monoblepharomycota* and *Neocallimastigomycota*. Currently, the phylum comprises one subphylum and ten classes. Members of the phylum are reported from both aquatic and terrestrial ecosystems, mainly as saprotrophic, with many facultative and obligate parasites of algae (Powell and Letcher 2014; Seto and Degawa 2017). Galindo et al. (2021) and Strassert and Monaghan (2022a, b) regarded *Caulochytriomycota* as a synonym of *Chytridiomycota* and our analyses also agree with it.

Entomophthoromycota Humber

The phylum *Entomophthoromycota* was introduced by Humber (2012) and is further divided into the subphylum *Entomophthoromycotina* and three classes, *Basidiobolomycetes, Entomophthoromycetes* and *Neozygitomycetes.* The phylum *Entomophthoromycota* consists of hyphal bodies or yeast-like cells with conidiophores. They are usually parasitic on algal groups where some might subsist as saprobes. The class *Basidiobolomycetes* contains unusually large nuclei with uninucleate cells, while *Neozygitomycetes* contains nuclei with vermiform, moderately sized chromosomes, with rod-like hyphal bodies containing 3 to 5 nuclei. The class *Entomophthoromycetes* lacks uniformly uninucleate cells or uniform number of nuclei, yet consists of coenocytic mycelium or rod-like to variably-shaped hyphal bodies (Humber 2012).

Entorrhizomycota R. Bauer et al.

The phylum *Entorrhizomycota* was introduced by Bauer et al. (2015) to accommodate the genus *Entorrhiza* Weber. The phylum consists of one class, *Entorrhizomycetes*. It was further divided into order *Entorrhizales* Bauer et al., and *Talbotiomycetales* Riess et al. (Wijayawardene et al. 2022a). This taxon infects roots and its members have regularly septate coiled hypha. It is a small genus of only 14 species. However, with phylogenetic analyses and comparative studies it was found that this genus is a widespread but inconspicuous group of fungi (Bauer et al. 2015).

Glomeromycota C. Walker & A. Schüßler

Schüssler et al. (2001) introduced *Glomeromycota* to accommodate arbuscular mycorrhizal fungi and Geosiphon pyriforme (Kütz.) F.Wettst. *Geosiphon* is the only member of the monophyletic group known to form symbioses with *Nostoc* (cyanobacteria) and not with plants (Schüssler et al. 2001). The placement of *Glomeromycota* in the fungal tree was accepted by several subsequent studies (e.g. James et al. 2006a; White et al. 2006). Nevertheless, Spatafora et al. (2016) who regarded *Glomeromycota* as 'phylogenetic enigma because it lacks any known form of sexual reproduction', diminished the Phylum *Glomeromycota* to Subphylum *Glomeromycotina* in *Mucoromycota*, along with *Mucoromycotina*, and *Mortierellomycotina*. However, Tedersoo et al. (2018) accepted the Phylum *Glomeromycota* in the Subkingdom *Mucoromyceta*. The findings of Tedersoo et al. (2018) were followed by subsequent studies (Wijayawardene et al. 2018b, 2020a, 2022a; Voigt et al. 2021).

Kickxellomycota Tedersoo et al.

Tedersoo et al. (2018) introduced the phylum *Kickxellomycota* in the subkingdom *Zoopagomyceta*, along with *Entomophthoromycota*, and *Zoopagomycota*. The phylum comprises one subphylum, *Kickxellomycotina* Benny (Hibbett et al. 2007). Currently, six classes are included in *Kickxellomycota* viz., *Asellariomycetes*, *Barbatosporomycetes*, *Dimargaritomycetes*, *Harpellomycetes*, *Kickxellomycetes*, and *Ramicandelaberomycetes* (Tedersoo et al. 2018). Members of *Kickxellomycota* have been reported as insect parasites, coprophilous, and soil-inhabiting taxa.

Monoblepharomycota Doweld

Doweld (2001) introduced this phylum which is currently accommodated in subkingdom *Chytridiomyceta* (Tedersoo et al. 2018). Tedersoo et al. (2018) also introduced subphylum *Monoblepharomycotina* Tedersoo et al., the only subphylum in *Monoblepharomycota*. Currently, *Monoblepharomycota* comprises two classes, *Monoblepharidomycetes* J.H. Schaffn. and *Hyaloraphidiomycetes* Doweld. Members of *Hyaloraphidiomycetes* have been reported from both aquatic and terrestrial environments as saprobes.

Mortierellomycota Tedersoo et al.

Mortierellomycota was introduced by Tedersoo et al. (2018) and is regarded as a phylum in the subkingdom *Mucoromyceta*, along with *Calcarisporiellomycota*, *Glomeromycota*, and *Mucoromycota*. Previous studies based on phylogeny showed that his phylum has a distinct lineage (James et al. 2006a; Sekimoto et al. 2011; Spatafora et al. 2016; Tedersoo et al. 2018).

Mucoromycota Doweld

The phylum *Mucoromycota* was introduced by Doweld (2001). However, White et al. (2006) regarded *Mucorales*, the type order of *Mucoromycota*, as an order of *Zygomycota* while James et al. (2006a) and Sekimoto et al. (2011) accepted subphylum *Mucoromycotina* in *Zygomycota*. Spatafora et al. (2016) accepted *Mucoromycota* and showed three subphyla within the phylum, i.e.

Mucoromycotina, *Mortierellomycotina*, and *Glomeromycotina*. However, *Glomeromycota* has been accepted as a well-defined phylum by several authors (e.g. Walker et al. 2007; Oehl et al. 2011a, b; Tedersoo et al. 2018; Wijayawardene et al. 2020a; Voigt et al. 2021). The subphylum *Mortierellomycotina* was upgraded to a phylum by Tedersoo et al. (2018) thus *Mucoromycota* has one subphylum i.e. *Mucoromycotina.*

Neocallimastigomycota M.J. Powell
James et al. (2006a, b) recognized *Neocallimastigales* J.L. Li et al. (type: *Neocallimastix fide* Li et al. 1993) which formed a distinct clade in *Chytridiomycota.* Hibbett et al. (2007) introduced the class *Neocallimastigomycetes* and the phylum *Neocallimastigomycota* to accommodate *Neocallimastigales.* Tedersoo et al. (2018) introduced *Neocallimastigomycotina* Tedersoo et al., the only subphylum of *Neocallimastigomycota.*

Olpidiomycota Doweld
Olpidiomycota Doweld was established to accommodate *Olpidiales* (Doweld 2013a), which was earlier accepted in *Chytridiomycetes* Caval-Sm. as *Spizellomycetales* D.J.S. Barr (Barr 1980). The members of *Olpidiomycota* are cosmopolitan in distribution as parasites of economically important crop plants, algae and rotifers (Kirk et al. 2008; Powell and Letcher 2014; Lay et al. 2018; Wijayawardene et al. 2018a, 2022a, Naranjo-Ortiz and Gabaldón 2019). The recent revision of *Fungi* and fungus-like taxa (Wijayawardene et al. 2022a) accepted one class, one order, one family and four genera in *Olpidiomycota*.

Rozellomycota Doweld
The placement of *Rozellomycota* and *Microsporidia* in the kingdom *Fungi* is a controversial topic in the higher-level classification of fungi and several major studies recognized them as early divergent groups of fungi (e.g. James et al. 2006a; Hibbett et al. 2007; Corsaro et al. 2014). Nevertheless, some studies showed that *Aphelida* (*Aphelidiomycota*) and *Rozellomycota* as members of Opisthosporidia represent the sister groups to *Fungi* (Karpov et al. 2013, 2014a, 2017b; Letcher et al. 2017). In this study, we follow the treatment of Tedersoo et al. (2018) and Voigt et al. (2021) and accept *Rozellomycota* in the kingdom *Fungi*.

Sanchytriomycota Galindo et al.
Galindo et al. (2021) introduce this phylum to accommodate two genera *Sanchytrium* Karpov & Aleoshin and *Amoeboradix* Karpov, López-García, Mamkaeva et Moreira (Karpov et al. 2018), and emended the diagnoses of the class *Sanchytriomycetes* (Tedersoo et al.) Galindo et al. and the order *Sanchytriales* (Tedersoo et al.) Galindo et al. Voigt et al. (2021) accepted this phylum as a distinct phylum with a single class, order, family, and two genera.

Zoopagomycota Gryganskyi et al.
Spatafora et al. (2016) introduced this phylum and recognized three subphyla, *Entomophthoromycotina* Humber, *Kickxellomycotina* Benny and *Zoopagomycotina* Benny. However, Tedersoo et al. (2018) upgraded *Entomophthoromycotina* and *Kickxellomycotina* to phyla, thus currently *Zoopagomycota* comprises only one subphylum, *Zoopagomycotina.* Tedersoo et al. (2018) confirmed the placement of *Zoopagomycota* in the Subkingdom *Zoopagomyceta* along with *Entomophthoromycota* and *Kickxellomycota*.

Aim and the content of the compilation

This study aims to provide a broad concept of the kingdom *Fungi* and present all fundamental concepts of its taxonomy and classification. Furthermore, we provide the phylogenomic tree of phyla of the Kingdom *Fungi*. Each phylum and its classes are meticulously described, accompanied by illustrations, life modes, distribution, and notes. We have also included controversial opinions prevalent among the research communities, thereby providing a comprehensive and up-to-date view of the current scientific discourse.

Materials and methodology

Extraction of data and arrangement of the article

This manuscript focuses only on classes and phyla of the kingdom *Fungi*. We follow the higher ranks of early divergent fungi (EDF) proposed by Tedersoo et al. (2018) that have 16 phyla (*Aphelidiomycota*, *Basidiobolomycota*, *Blastocladiomycota*, *Calcarisporiellomycota*, *Caulochytriomycota*, *Chytridiomycota*, *Entomophthoromycota*, *Glomeromycota*, *Kickxellomycota*, *Monoblepharomycota*, *Mortierellomycota*, *Mucoromycota*, *Neocallimastigomycota*, *Olpidiomycota*, *Rozellomycota* and *Zoopagomycota*). Subsequently, Galindo et al. (2021) introduced *Sanchytriomycota*. However, several studies have suggested different arrangements for the higher ranks of EDF (Table 3). Besides, *Caulochytriomycota* was not accepted as a phylum by Voigt et al. (2021) and Strassert and Monaghan (2022a, b).

Placements of the phyla in *Dikarya* (i.e. *Ascomycota*, *Basidiomycota* and *Entorrhizomycota*) have been confirmed in several studies (e.g. Tedersoo et al. 2018; Wijayawardene et al. 2020a).

The nomenclature of fungi and the authors of fungal names follow Index Fungorum (2024), except for the genus originally described with *Rhizophagus populinus* P.A. Dang

Table 3 Other prevailing classes and phyla classifications of early divergent fungi

Study	Phyla in early divergent fungi	Exclusions from phyla rank/ other remarks
Spatafora et al. (2016)	*Blastocladiomycota*, *Chytridiomycota*, *Mucoromycota* (including *Glomeromycota* and *Mortierellomycota* as subphyla; i.e. *Glomeromycotina* and *Mortierellomycotina* respectively), *Zoopagomycota* (including *Entomophthoromycota* and *Kickxellomycota* as subphyla; i.e. *Entomophthoromycotina* and *Kickxellomycotina* respectively)	*Basidiobolomycetes* under *Entomophthoromycotina, Zoopagomycota*
Spatafora et al. (2017)	*Cryptomycota* (= *Rozellomycota*), *Microsporidia, Blastocladiomycota*, *Chytridiomycota* (including *Monoblepharomycota* and *Neocallimastigomycota*)*, *Mucoromycota* (including *Glomeromycota* and *Mortierellomycota* as subphyla; i.e. *Glomeromycotina* and *Mortierellomycotina* respectively), *Zoopagomycota* (including *Entomophthoromycota* and *Kickxellomycota* as subphyla; i.e. *Entomophthoromycotina* and *Kickxellomycotina* respectively)	**Monoblepharidomycetes* and *Neocallimastigomycetes* under *Chytridiomycota*
Chang et al. (2021)	*Blastocladiomycota, Chytridiomycota, Olpidiomycota, Zoopagomycota, Mucoromycota* (including *Calcarisporiella* and *Mortierella*)	
Galindo et al. (2021)	*Aphelidiomycota*, *Blastocladiomycota*, *Chytridiomycota* (including *Monoblepharomycetes, Caulochytriomycetes, Neocallimastigomycetes*), *Glomeromycota*, *Mucoromycota* (including *Mortierellomycota*), *Sanchytriomycota*, and *Zoopagomycota* (including *Basidiobolomycota*, *Entomophthoromycota*)	*Calcarisporiellomycota*, *Olpidiomycota* and *Rozellomycota*, not recognized, *Caulochytriomycota* is a synonym of *Chytridiomycota*, representative taxa of *Basidiobolomycota*, *Entomophthoromycota* clustered in *Zoopagomycota*
Strassert and Monaghan (2022a, b)	*Aphelidiomycota*, *Blastocladiomycota*, *Chytridiomycota* (including *Caulochytriomycota*), *Glomeromycota*, *Monoblepharomycota*, *Mortierellomycota*, *Mucoromycota*, *Neocallimastigomycota*, *Olpidiomycota*, *Rozellomycota*, *Sanchytriomycota*, and *Zoopagomycota* (including *Basidiobolomycota, Entomophthoromycota* and *Kickxellomycota* as subphyla; i.e. *Basidiobolomycotina, Entomophthoromycotina* and *Kickxellomycotina* respectively)	*Calcarisporiellomycota* not included, *Caulochytriomycota* is a synonym of *Chytridiomycota*
Mikhailov et al. (2022)	*Rozellomycota* (*Rozellida* + *Microsporidia*), *Aphelida*, *Chytridiomycota* (including *Monoblepharomycetes, Caulochytriomycetes*, *Neocallimastigomycetes*)#, *Blastocladiomycota*, *Zoopagomycota*, *Mucoromycota*	#no formal classes were there, but representatives are included

as type species of *Rhizophagus*, later replaced by *Rhizophagus intraradices*. We have adopted the arguments presented by Sieverding et al. (2015) and have opted to use the generic name *Rhizoglomus* Sieverd., G.A. Silva & Oehl instead of *Rhizophagus*. Nevertheless, this arrangement needs to be approved by the International Commission of Taxonomy of Fungi.

Phylogenomic analysis

The dataset for phylogenomic analysis was prepared using a set of 300 orthologous groups, constructed for phylogeny inferences in an earlier study (Mikhailov et al. 2022). We have updated the original dataset, which featured 45 species of Holomycota, to include 40 more members of the fungal lineage, with emphasis on improving the sampling of poorly represented phyla. The genomic and transcriptomic data were collected from the NCBI GenBank database (https://www.ncbi.nlm.nih.gov/genbank/) and the JGI GenomePortal (https://genome.jgi.doe.gov/portal/). Prefiltered transcriptomes of *Aphelidium* species were obtained from a public repository (https://figshare.com/projects/Aphelida_Extended_Data/111539) (Galindo et al. 2022). Orthologous sequences were identified in the assembled collection of proteomes using a previously developed dataset expansion pipeline (Tikhonenkov et al. 2020), involving HMMER searches (Eddy 2011) with the alignment profiles, and reciprocal BLAST searches (Altschul et al. 1997). The sets of identified orthologous sequences were processed using an automated quality filtering procedure of PREQUAL (Whelan et al. 2018) with all-against-all sequence comparisons and a posterior probability filtering threshold of 0.95. The filtered sets of sequences were aligned with MAFFT using the localpair (L-INS-i) algorithm (Katoh and Standley 2013), followed by manual inspection of alignments using BioEdit (Hall 1999). Phylogenetic trees were reconstructed for each of the 300 orthologous groups using IQ-TREE (Nguyen et al. 2015) to identify and eliminate contamination detected in the sequence sets, specifically extraneous sequences found in the *Coelomomyces lativittatus* transcriptomic data. The cleaned alignments were finally processed using a custom mask, designed to exclude ambiguously aligned and low-complexity regions. The trimmed alignments were concatenated using SCaFoS (Roure et al. 2007) into a matrix with 113 K amino acid sites.

Bayesian inference with the concatenated alignment was performed with PhyloBayes MPI (Lartillot et al. 2013) using the site-heterogeneous CAT-GTR model with four discrete Gamma-distributed rate categories. Four independent chains were run for 10 K cycles and monitored for convergence. The consensus Bayesian tree was reconstructed using the four chains with a 25% burn-in. Trees were also reconstructed for each of the analysis chains independently to confirm convergence to a unique tree topology within each chain. The mean posterior relative exchangeabilities and site-specific equilibrium frequencies were extracted from the chain files with a 25% burn-in using the PhyloBayes readpb utility, and converted for downstream analyses using the available scripts (Szantho et al. 2023).

Maximum likelihood analysis with the concatenated alignment was performed with IQ-TREE (Nguyen et al. 2015). Tree reconstruction employed the LG + C60 + F + G4 profile mixture model, and node support was evaluated using the ultrafast bootstrap approximation (Hoang et al. 2018) with 1000 replicates. Additionally, tree inferences were conducted using the posterior mean site frequency model (Wang et al. 2018), employing the exchangeabilities and site-specific frequencies derived from the PhyloBayes analysis, as introduced by the CAT-PMSF approach (Szantho et al. 2023). The CAT-PMSF inference utilized PhyloBayes-optimized parameters obtained without a fixed tree topology constraint, although the sampled portions of the analysis chains displayed strict preference for a unique tree topology. Accordingly, tree reconstruction with the CAT-PMSF approach was also carried out independently with the parameters obtained from each of the four PhyloBayes chains. Node support for the CAT-PMSF tree inference was evaluated similarly with ultrafast bootstrap approximation using 1000 replicates.

Approximately unbiased tests (Shimodaira 2002) with alternative tree topologies were performed by IQ-TREE with 100,000 resamplings using the RELL method. The tree topologies, representing the conceivable phylogenetic relationships around the contentious nodes of the fungal phylogeny, were constructed using the MEGA software (Kumar et al. 2016). Site-wise likelihoods were calculated under the LG + C60 + F + G4 evolutionary model using the original ML tree for parameter estimation, and under the CAT-PMSF model in four variations, corresponding to the parameters derived from the four PhyloBayes analysis chains.

Results and discussion

Phylogenomic tree of *Holomycota*

The phylogeny reconstructions were performed using maximum likelihood (ML) and Bayesian methods with a 300-gene dataset and a taxonomic selection balanced toward early-diverging fungal lineages (the dataset is available at Mendeley Data, https://doi.org/10.17632/9jchyjrxmy.1). For both reconstruction methods, we employed site-heterogeneous models of sequence evolution, as they provide a better approximation of natural processes (Lartillot and Philippe 2004; Quang le et al. 2008) and are generally more robust to reconstruction artefacts than site-homogenous models

(Philippe et al. 2011). The phylogenies produced by both methods show agreement across most of tree nodes, yet similarly to earlier analyses (Galindo et al. 2021; Li et al. 2021a; Strassert and Monaghan 2022a, b; Mikhailov et al. 2022), some of the key nodes of fungal phylogeny are unstable or show discordance between the analyses (Fig. 1).

Both ML and Bayesian trees fully support the early split of *Rozellomycota* from the fungal stem lineage, and the

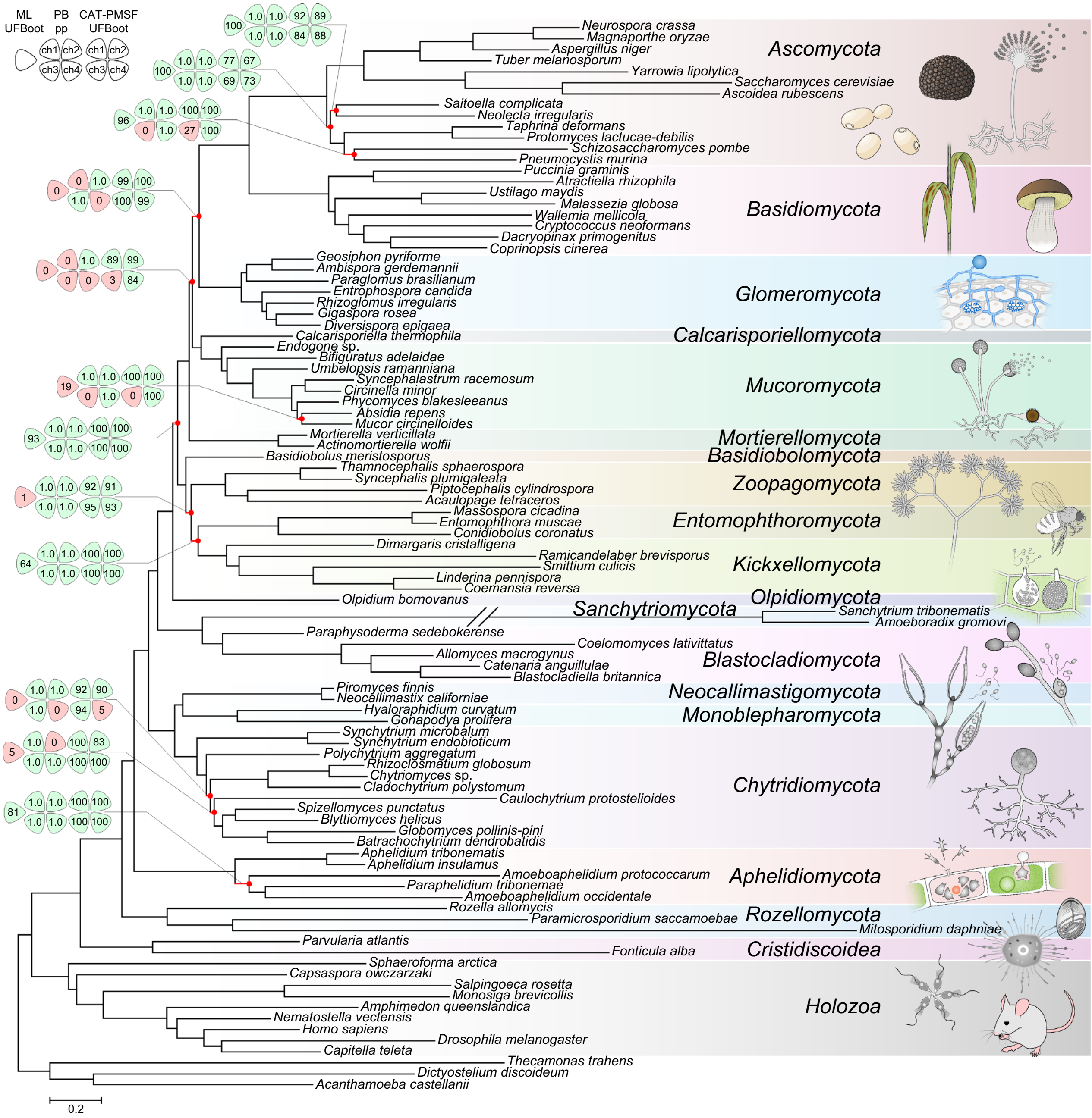


Fig. 1 Phylogeny of *Holomycota* reconstructed with a 300-gene dataset. The consensus tree obtained using four CAT-PMSF inferences with parameters from each of the four chains of PhyloBayes, featuring support values from different reconstruction methods: ML inference with the LG+C60+F+G4 profile mixture model, Bayesian inference with the CAT-GTR model of PhyloBayes, and ML inference under CAT-PMSF; tree nodes where the reconstruction methods fail to achieve maximal support, or are in disagreement, are highlighted in red, and the corresponding support values are shown; the support values in the ML analyses correspond to the ultrafast bootstrap approximation; the support values for PhyloBayes inference are posterior probabilities; for the Bayesian inference and the CAT-PMSF reconstructions the support values are depicted for each of the four analysis chains in the four-leaf clover arrangements, with the red-coloured clover leaves highlighting instances where the best tree for the chain/analysis deviated from the consensus shown here; the branch of *Sanchytriomycota* was shortened by one-third for the illustration

subsequent separation of *Aphelidiomycota* from the ancestral lineage of true fungi. This result is in agreement with the previous large-scale phylogenies (Torruella et al. 2018; Galindo et al. 2022), which similarly found no support for the superphylum *Opisthosporidia*, hypothesized to house *Aphelidiomycota* and *Rozellomycota* (Karpov et al. 2014a). The trees also agree on the sister position of *Neocallimastigomycota* and *Monoblepharomycota* to the *Chytridiomycota*, and the placement of the whole lineage as the earliest branch of true fungi.

The sole sequenced representative of the proposed phylum *Caulochytriomycota* (Doweld 2014a), *Caulochytrium protostelioides*, is found nested within *Chytridiomycota*, joining support for its deranking to a member of *Chytridiomycota* (Ahrendt et al. 2018; Strassert and Monaghan 2022a, b). Yet, the reconstructions fail to find the exact placement of *Caulochytrium* relative to the chytrid orders—its position within chytrids varies in both ML and Bayesian analyses (Supplementary Figs. 1 & 2). The newly proposed phylum *Sanchytriomycota* (Galindo et al. 2021), which includes two species, *Amoeboradix gromovii* and *Sanchytrium tribonematis*, with highly divergent sequences, is fully supported as a sister group to *Blastocladiomycota*, together forming the second earliest branch of true fungi. The last lineage to diverge from the fungal stem before the emergence of terrestrial non-zoosporic fungi is a chytrid-like fungus *Olpidium* (Chang et al. 2021). The Bayesian reconstruction fully supported the sister position of *Olpidium* to the non-zoosporic fungi. In the ML analysis, however, the support wavered, with 7% of bootstrap replicates instead placing *Olpidium* further into the clade of non-zoosporic fungi, sister to the group uniting *Mucoromycota*, *Mortierellomycota*, *Calcarisporiellomycota*, *Glomeromycota*, and *Dikarya*.

Remarkably, most internal tree nodes, where the analyses failed to reach a consensus, involve groups of terrestrial fungi rather than the deeper branching zoosporic fungal phyla. The most prominent conflict is observed in the relative branching of *Mucoromycota*, *Mortierellomycota*, *Glomeromycota*, and *Dikarya*. While all reconstructions agree on the sister position of *Calcarisporiellomycota* to *Mucoromycota*, confirming earlier rDNA trees (Hirose et al. 2012; Tedersoo et al. 2018), the exact phylogenetic context of the *Mucoromycota* + *Calcarisporiellomycota* group varies in the analyses. In the ML tree the *Mucoromycota* (incl. *Calcarisporiellomycota*), *Mortierellomycota*, and *Glomeromycota* form a fully-supported monophyletic group sister to *Dikarya*, with *Glomeromycota* being more closely related to *Mucoromycota* than *Mortierellomycota*, at 89% bootstrap support (Supplementary Fig. 1). In the Bayesian inference, which was conducted using four independent analysis chains, we observed three different arrangements for these phyla; one variant repeating the ML tree branching order, and the other variants placing *Glomeromycota* sister to *Dikarya*, with *Mortierellomycota* appearing either as sisters to *Mucoromycota* + *Calcarisporiellomycota* or as sisters to the whole lineage comprising *Mucoromycota, Glomeromycota,* and *Dikarya* (Supplementary Fig. 2). Lineages of former zygomycete fungi that were collectively referred to as *Zoopagomycota* in prior taxonomic revisions (Spatafora et al. 2016) formed a monophyletic group sister to other terrestrial fungi in all analyses, but the relationship between the constituent phyla—*Basidiobolomycota*, *Entomophthoromycota*, *Kickxellomycota*, *Zoopagomycota* sensu stricto—differed between the analyses. The Bayesian inference fully supported the early branching of *Basidiobolus* within the group and the sister position of *Zoopagomycota* to the monophyletic group uniting *Entomophthoromycota* and *Kickxellomycota* (Supplementary Fig. 2). The ML tree placed *Basidiobolus* sister to *Zoopagomycota*, but neither the *Basidiobolomycota* + *Zoopagomycota* nor the *Entomophthoromycota* + *Kickxellomycota* were highly supported (Supplementary Fig. 1).

The conflicting results of the ML and Bayesian trees around the position of *Glomeromycota* were noted previously in phylogenomic analyses (Galindo et al. 2021; Mikhailov et al. 2022; Strassert and Monaghan 2022a, b), and were shown to stem from the inherent limitations of the site-heterogeneous profile mixture model implemented in the ML tree-building software (Strassert and Monaghan 2022a, b). Thus, the disagreement between the ML and Bayesian trees on the relative branching of *Mucoromycota*, *Mortierellomycota*, *Glomeromycota*, and *Dikarya* was anticipated for the updated dataset. Unexpectedly, however, our Bayesian inference itself also failed to converge on a single branching arrangement for these groups. Past 1.5 K cycles and up to 10 K cycles, when the run was halted, each independent chain of the inference strictly adhered to its own tree topology, resulting in an ambiguous relationship between these groups in the consensus of the four chains. In an attempt to resolve this ambiguity, we have applied the CAT-PMSF method (Szantho et al. 2023), reconstructing additional ML trees using the evolutionary model parameters obtained from the Bayesian analysis chains. Reconstructions under the CAT-PMSF managed to reconcile the position of *Glomeromycota*, placing the group sister to *Dikarya* with nearly full support for all four chains, despite the conflicting result of the Bayesian inference (Fig. 1). The CAT-PMSF reconstruction also switched toward supporting the sister position of *Caulochytrium* to the *Spizellomycetales* and *Rhizophydiales* in *Chytridiomycota* for the one chain of Bayesian inference, where an alternative placement of *Caulochytrium* sister to *Cladochytriales* and *Chytridiales* was observed. In other instances where the individual Bayesian trees were incongruent, the CAT-PMSF trees also reproduced the disagreement. These include the placement of *Mortierellomycota*, the positions of *Pneumocystis* and *Schizosaccharomyces* in *Taphrinomycotina*, the relative branching of *Mucor*, *Absidia*, and *Phycomyces* in *Mucoromycota*, and the position of *Polychytrium* in *Chytridiomycota*.

Notably, CAT-PMSF analysis also lowered support for several tree nodes where the Bayesian trees were resolute and even fully supported by the original ML analysis with the site-heterogeneous profile mixture model. The latter include the positions of *Saitoella* and *Neolecta*, and the monophyly of *Taphrinomycotina* (Fig. 1).

To characterize the spectrum of ambiguous tree topologies systematically, we carried out hypothesis testing with an exhaustive set of alternatives around the conflicting nodes of fungal phylogeny. The hypotheses were tested using the approximately unbiased (AU) test under the site-heterogeneous profile mixture model and the CAT-PMSF models derived from the Bayesian inference. For the tree nodes involving the relative branching of *Mucoromycota*, *Mortierellomycota*, *Glomeromycota*, and *Dikarya*, the profile mixture model accepts only two variants, both of which include the union of *Mucoromycota*, *Mortierellomycota*, and *Glomeromycota* (Supplementary Table 1). In contrast, tests under the CAT-PMSF reject any such variant at the 5% significance level. CAT-PMSF did not reject only variants with *Glomeromycota* sister to *Dikarya*. These include a variant with *Mortierellomycota* sister to the whole lineage of *Mucoromycota*, *Glomeromycota*, and *Dikarya* or a variant with a more commonly seen sister relationship between *Mortierellomycota* and *Mucoromycota* (incl. *Calcarisporiellomycota*). The latter group, however, was rejected in one of the three chains tested with CAT-PMSF. In *Chytridiomycota* the profile mixture model fails to reject 6 out of 15 possible arrangements for the lineages of *Caulochytrium*, *Polychytrium*, *Spizellomycetales* + *Rhizophydiales*, and *Cladochytriales* + *Chytridiales*. With CAT-PMSF there are only two accepted topologies for chytrids, which include a sister relationship between *Caulochytrium* and *Spizellomycetales* + *Rhizophydiales*, with *Polychytrium* emerging either as a sister to *Cladochytriales* + *Chytridiales* or at the base of the whole group. In one of the chains, an additional topology with *Caulochytrium* sister to *Cladochytriales* + *Chytridiales* also appears as a likely variant. Tests for the relative branching of *Basidiobolomycota*, *Entomophthoromycota*, *Kickxellomycota*, and *Zoopagomycota* fail to reject 5 out of 15 arrangements with the profile mixture model. With CAT-PMSF only two topologies for these groups are accepted, which include a monophyletic group of *Entomophthoromycota* + *Kickxellomycota* with either *Basidiobolus* or *Zoopagomycota* as its sister lineages. Tests with CAT-PMSF reject an alternative placement of *Olpidium* within non-zoosporic fungi, which was observed in a small percentage of bootstrap replicates of the original ML tree and was accordingly not rejected by the test with the profile mixture model. For members of *Taphrinomycotina,* all but one of the tree topologies were rejected by the test with the profile mixture model. CAT-PMSF, on the other hand, failed to reject four topologies, including those where *Saitoella* is sister to *Taphrinomycotina* or where *Taphrinomycotina* are polyphyletic and *Saitoella* + *Neolecta* emerge as the earliest branch of *Ascomycota* or *Saitoella* alone moves to the *Pezizomycotina* + *Saccharomycotina* branch.

Taxonomy

In this section, all the phyla are provided with important taxonomic data, history, distribution, life cycle data, and life or nutritional modes. The classes of each phylum (Fig. 2) are listed according to the placements in the respective subclasses (if more than one subclass).

APHELIDIOMYCOTA Tedersoo, Sanchez-Ramirez, Kõljalg, Bahram, M. Döring, Schigel, T.W. May, M. Ryberg & Abarenkov, Fungal Diversity 90: 147 (2018)

Syn. *Aphelida* Karpov, Aleoshin & Mikhailov

Index Fungorum Registration Identifier 553,990

Amoeboid endobiotic parasites of algae. Dispersal amoeboid zoospores attach to a new host cell and encyst (either sessile on the substrate or producing a stalk; "apophyse"; Gromov 2000). Amoeboid body penetrates the host's cell through a cyst stalk. The intracellular amoeba engulfs the contents of the host's cell, forming food vacuoles that transport food into the central digestive vacuole. An excretory body is formed in the digestive vacuole. The amoeboid trophont grows into a plasmodium, which totally replaces the cytoplasm of a host cell; the multinuclear plasmodium develops into an unwalled sporangium and divides into uninucleate amoeboid zoospores. Intracellular resting spores are present (Karpov et al. 2014a).

Life modes and distribution: Parasites of algae

Notes: The aphelids are a small group of intracellular parasites of algae, including three freshwater genera, *Aphelidium* (Zopf) Gromov (Fig. 3), *Amoeboaphelidium* Scherff., *Paraphelidium* Karpov et al. and a marine genus, *Pseudaphelidium* Schweikert & Schnepf (Schweikert and Schnepf 1996, 1997; Gromov 2000; Karpov et al. 2017a).

Only the asexual part of the life cycle is known for aphelids: amoeboid zoospore attaches to the host algae, and involves a flagellum and encysts. A cyst germinates and penetrates the host cell wall with an infection tube and injects the cyst contents into the host. The parasite becomes the intracellular phagotrophic amoeba which engulfs the host cytoplasm with pseudopodia and forms a central digestive vacuole containing a red residual body. The parasite grows forming an endobiotic multinucleate plasmodium with the residual body in a large central vacuole while it consumes the whole cytoplasm of the host cell. The mature plasmodium then divides into a number of uninucleated cells. After maturation, the amoeboid zoospores are released from the empty host cell through the hole made earlier by the infection tube and infect other algae.

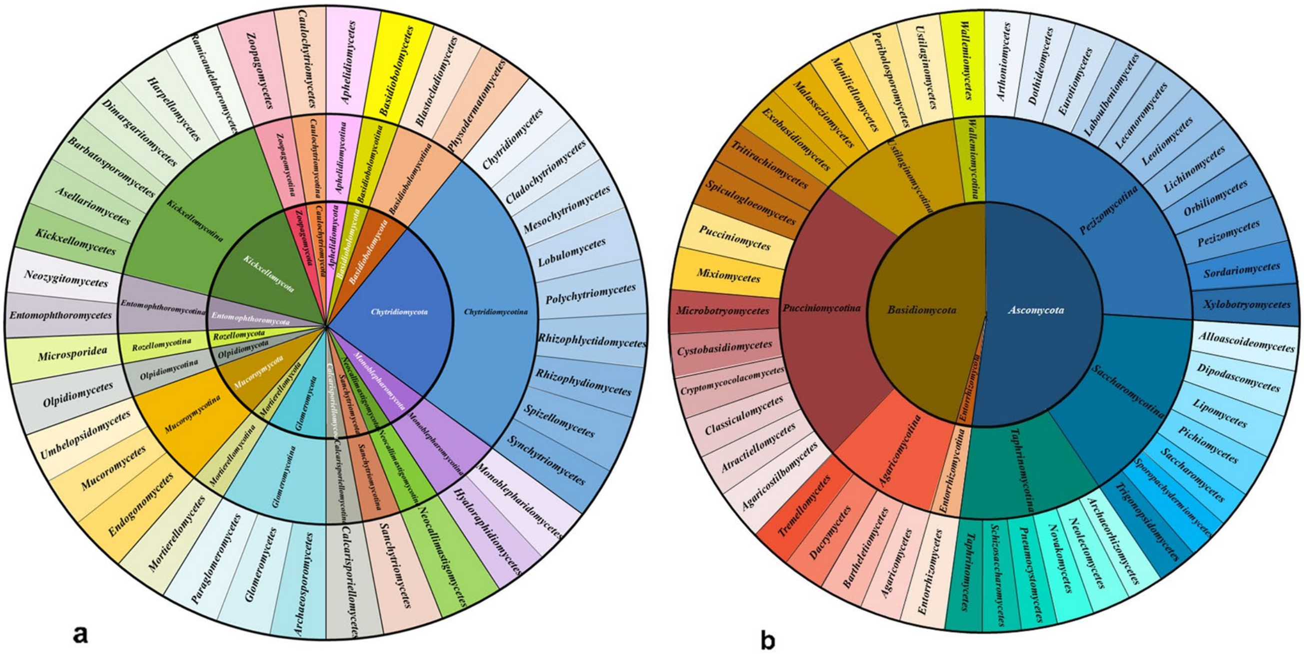


Fig. 2 Diagrammatic representation of phyla, subphyla and classes of the kingdom *Fungi*; **a** EDF. **b** *Dikarya*

All known aphelids can produce multiple infections, thus, the trophonts from different strains/populations may fuse to each other during the development of plasmodium which can possess more than one sort of nuclei (Tcvetkova et al. 2023).

The phylogenetic position of the aphelids became clear after five genes sequencing of *Amoeboaphelidium protococcorum* (Karpov et al. 2013). Subsequently, Letcher et al. (2013) confirmed this result on the base of SSU gene sequence of *Am. occidentale*. The aphelids grouped with *Rozella* and microsporidia forming a cluster sister to *Fungi*, which was called the super phylum *Opisthosporidia* a year later (Karpov et al. 2014a). The rank of the aphelids has been raised from the class *Aphelidae* (Gromov 2000) to the phylum *Aphelida* (Karpov et al. 2014a, b). The position of the aphelids on ribosomal trees was not stable. It varied from sister group to *Fungi* + *(Rozella* + *Microsporidia*) (Corsaro et al. 2014, 2019), to *Rozella* + *Microsporidia* (in most published trees), and to the Fungi (Tedersoo et al. 2018). Many mycologists included aphelids in the *Fungi* based predominantly on their life cycle, which superficially resembles those of zoosporic fungi, and on the monophyly of the cluster including *Fungi* and *Opisthosporidia* (James et al. 2013). The subsequent outline by Wijayawardene et al. (2020a) followed Tedersoo et al. (2018) and listed *Aphelidiomycota* as a distinct phylum in the fungal clade.

Intensive study of the aphelids during last decade gave more knowledge based on the light microscopic and ultrastructural observations, and molecular phylogeny including genomics. A new genus *Paraphelidium* with two species was described (Karpov et al. 2017a,b), several new species in *Aphelidium* (Letcher et al. 2017; Tcvetkova et al. 2019; Seto et al. 2020, 2022) and *Amoeboaphelidium* (Letcher et al. 2015) were added based on morphological and molecular data. Genomes of three (Mikhailov et al. 2022; Pozdnyakov et al. 2023) and transcriptomes of four aphelid species (Torruella et al. 2018; Galindo et al. 2022) were assembled, and a multigene phylogeny unambiguously showed a sister position of the *Aphelida* and fungi.

Karpov et al. (2014a, b) believe that phylum *Aphelidiomycota* (= *Aphelida*) having a phagotrophic cellular mode of nutrition does not belong to the kingdom *Fungi* with the totally saprotrophic cellular mode of nutrition. From this view, the original phylum name *Aphelida* (Karpov et al. 2014a, b) has to be retained. We temporarily accept the layout of the present paper dealing with *Fungi* sensu lato, which also includes here the phagotrophic rozellids and follows the taxonomy by Tedersoo et al. (2018).

Currently, the phylum consists of one subphylum (*Aphelidiomycotina*) and one class (*Aphelidiomycetes*).

Aphelidiomycetes Tedersoo, Sánchez-Ramírez, Kõljalg, Bahram, Döring, Schigel, T. May, M. Ryberg & Abarenkov, Fungal Diversity 90: 147 (2018); Fig. 3

Index Fungorum Registration Identifier 553991

The class description is similar to the description of the phylum

Type order: ***Aphelidiales*** Tedersoo, Sánchez-Ramírez, Kõljalg, Bahram, Döring, Schigel, T. May, M. Ryberg & Abarenkov 2018

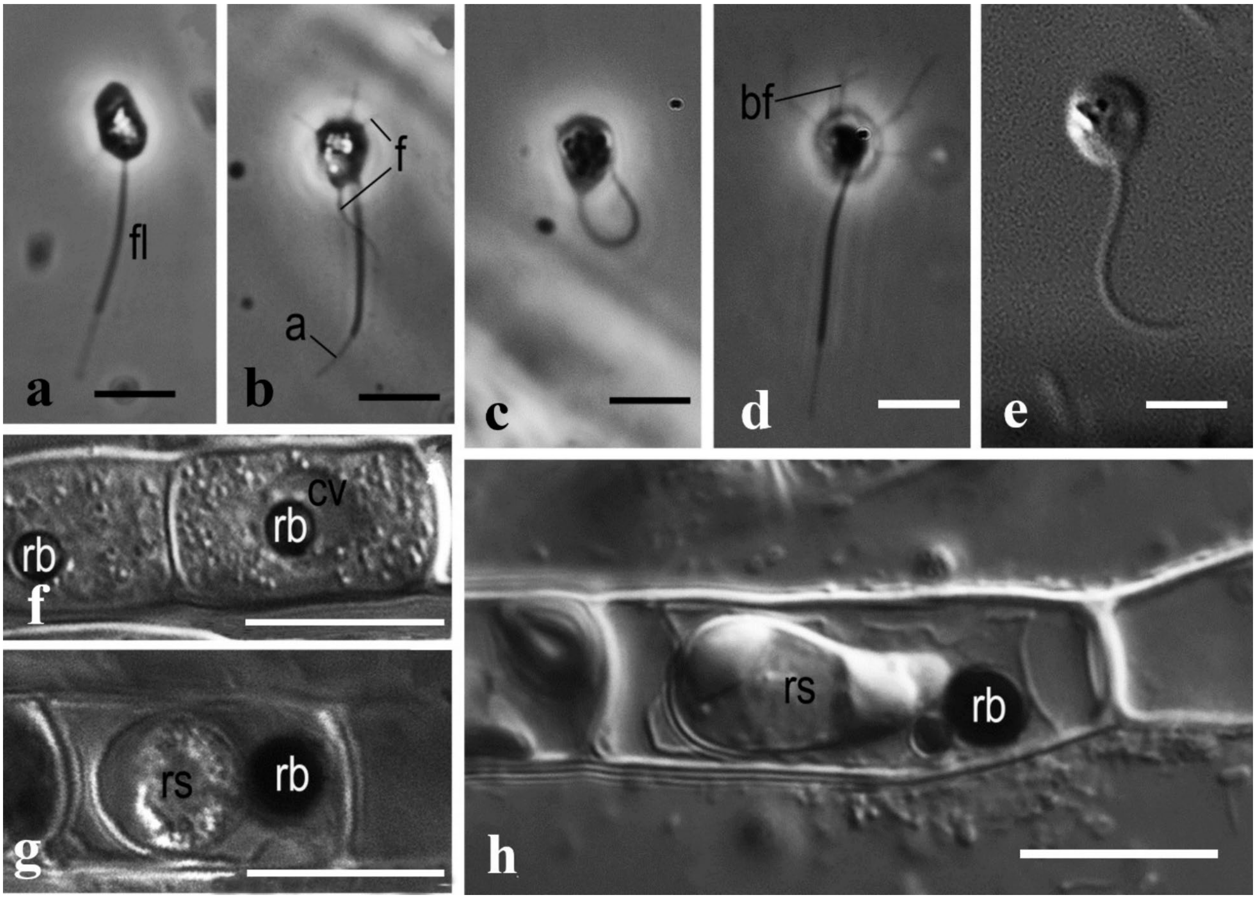


Fig. 3 Light microscopic images of three stages of life cycle of *Aphelidium* spp. life cycle. Modified after: Karpov et al. (2014a) (**e**, **f**, **g**), 2020 (**a**, **b**, **h**), Tcvetkova et al. (2019) (**c**, **d**). **a**–**e** – zoospores of *Aph. insulamus* (**a**, **b**), *Aph. arduennense* (**c**, **d**) and *Aph. melosirae* (**e**); **a**, **c**, **e** Swimming zoospores. **b**, **d** Crawling zoospores with simple filopodia (**f**) and branching filopodia (bf). **f** Plasmodium of *Aph. melosirae* in the host cell with central digestive vacuole (cv) containing residual body (rb). **g** Rounded resting spore (rs) of *Aph. melosirae*. **h** elongated resting spore (rs) of *Aph. insulamus*. Scale bars: **a**–**e** = 3 μm, **f**–**h** = 10 μm

Type family: ***Aphelidiaceae*** Tedersoo, Sánchez-Ramírez, Kõljalg, Bahram, Döring, Schigel, T. May, M. Ryberg & Abarenkov, Fungal Diversity 90: 147 (2018)
Type genus: *Aphelidium* Zopf, Encyklop. Naturwiss. (Breslae): 30 (1885)
Type species: *Aphelidium deformans* Zopf, Encyklop. Naturwiss. (Breslae): 30 (1885)

ASCOMYCOTA Caval.-Sm., Biol. Rev. 73: 247 (1998)

Index Fungorum Registration Identifier 90031

Sexual morph: Reproducing by formation of an ascoma or rarely naked, without an organised ascoma. Ascomata when present apothecial, perithecial, pseudothecial or cleistothecial. Ascomatal cavity when present with a centrum or hamathecium composed of cellular or filamentous, thread-like paraphyses or pseudoparaphyses. Asci unitunicate—operculate, unitunicate-inoperculate, prototunicate, bitunicate. Ascospores with varied shapes, colour, septation, size, with or without surface ornamentation and appendages. Asexual morph: coelomycetous—producing pycnidia or acervuli or intermediate forms. Hyphomycetous—producing sporodochia, synnemata or individual conidiophores; conidia produced by different modes—arthric, blastic (holoblastic and enteroblastic), phialidic, annelidic, basauxic; conidia with different shapes, sizes, dry or wet, with or without surface appendages. Yeasts—budding or fission as the primary means of asexual reproduction, and have sexual morph that are not enclosed in fruiting bodies.

Life modes and habitats: Saprobes, pathogens of plants and animals, or lichen-forming, lichenicolous, fungicolous, endophytes, yeast-like or filamentous.

Notes: Whittaker (1959) introduced the term Ascomycota which was invalid. Cavalier-Smith (1998) introduced the legitimate term, and subsequent studies accepted it (e.g. Hibbett et al. 2007). *Ascomycota* is the largest phylum in the kingdom of *Fungi*. The higher-level classification of the phylum was first compiled as the ‘Outline of *Ascomycota*’ by Eriksson and Hawksworth (1986). Subsequent updates and changes were published by Eriksson and Winka (1997), and Lumbsch and Huhndorf (2007, 2010). Important studies of the taxonomy and classification of *Ascomycota* and its classes since Lumbsch and Huhndorf (2010) are listed in Table 4.

Table 4 Important studies (on taxonomy and classification) published since Lumbsch and Huhndorf (2010) on *Ascomycota* and its classes

Article	Rank	Content
Rosling et al. (2011)	*Archaeorhizomycetes*	Taxonomy/classification/phylogeny
Gazis et al. (2012)	*Xylonomycetes*	Taxonomy/classification
Hansen et al. (2013)	*Pezizomycetes*	Phylogeny/classification
Hustad et al. (2013)	*Geoglossomycetes*	Phylogeny/classification
Hyde et al. (2013)	*Dothideomycetes*	Taxonomy/classification
Prieto et al. (2013)	*Candelariomycetes*	Phylogeny/classification
Beimforde et al. (2014)	*Ascomycota*	Estimating the Phanerozoic history
Ertz et al. (2014)	*Arthoniomycetes*	Phylogeny/classification
Gueidan et al. (2014)	*Eurotiomycetes*	Phylogeny/classification
Johnston et al. (2014)	*Leotiomycetes*	Taxonomy/classification
Menkis et al. (2014)	*Archaeorhizomycetes*	Phylogeny/classification
Miądlikowska et al. (2014)	*Lecanoromycetes*	Phylogeny/classification
Haelewaters et al. (2015)	*Laboulbeniomycetes*	Phylogeny/classification
Maharachchikumbura et al. (2015)	*Sordariomycetes*	Taxonomy/classification
Shen et al. (2016)	*Saccharomycotina*	Taxonomy/phylogeny
Baral et al. (2018)	*Xylonomycetes*	Phylogeny
Ekanayaka et al. (2017)	*Neolectomycetes*	Taxonomy/classification
Hongsanan et al. (2017)	*Sordariomycetes*	Phylogeny/classification based on molecular clock evidence
Liu et al. (2017)	*Dothideomycetes*	Ranking higher taxa using divergence times
Lücking et al. (2017)	*Arthoniomycetes*	Taxonomy/classification
Lücking et al. (2017)	*Lichinomycetes*	Taxonomy/classification
Wijayawardene et al. (2017a)	*Ascomycota*	Notes for the genera in *Ascomycota*
Baral et al. (2017)	*Orbiliomycetes*	Taxonomy/classification
Goldmann and Weir (2018)	*Laboulbeniomycetes*	Phylogeny/classification
Hibbett et al. (2018)	*Ascomycota*	Phylogenetic taxon definition
Rikkinen et al. (2018)	*Coniocybomycetes*	Fossil study
Tedersoo et al. (2018)	*Collemopsidiomycetes*	Phylogeny
Wijayawardene et al. (2018a)	*Ascomycota*	Outline/classification
Ametrano et al. (2019)	*Dothideomycetes*	Phylogeny
Haelewaters et al. (2019)	*Laboulbeniomycetes*	Phylogeny/classification
Johnston et al. (2019)	*Leotiomycetes*	Phylogeny/classification
Samarakoon et al. (2019)	*Ascomycota*	Divergence time calibrations for ancient lineages
Voglmayr et al. (2019)	*Candelariomycetes*	Phylogeny/classification
Voglmayr et al. (2019)	*Xylobotryomycetes*	Phylogeny/classification
Blackwell et al. (2020)	*Laboulbeniomycetes*	Evolution
Haelewaters et al. (2020)	*Laboulbeniomycetes*	Phylogeny/taxonomy/classification
Hyde et al. (2020)	*Sordariomycetes*	Taxonomy/classification
Shen et al. (2020)	*Ascomycota*	Phylogeny
Hongsanan et al. (2020a,b)	*Dothideomycetes*	Taxonomy/classification
Čadež et al. (2021)	*Novakomycetes*	Phylogeny/classification
Haelewaters et al. (2021a)	*Laboulbeniomycetes*	Phylogeny/classification
Haelewaters et al. (2021c)	*Leotiomycetes*	Phylogeny/taxonomy/classification
Hashimoto et al. (2021)	*Xylonomycetes*	Phylogeny/classification
Latinne et al. (2021)	*Pneumocystidomycetes*	Phylogeny/host specificity
Díaz-Escandón et al. (2022)	*Lichinomycetes*	Phylogeny
Brysch-Herzberg et al. (2022, 2023)	*Schizosaccharomycetes*	Taxonomy/phylogeny

Table 5 Subphyla and classes of *Ascomycota*

Phylum	*ASCOMYCOTA*		
Subphyla	*Pezizomycotina*	*Saccharomycotina*	*Taphrinomycotina*
Classes	*Arthoniomycetes* *Dothideomycetes* *Eurotiomycetes* *Laboulbeniomycetes* *Lecanoromycetes* *Leotiomycetes* *Lichinomycetes* *Orbiliomycetes* *Pezizomycetes* *Sordariomycetes* *Xylobotryomycetes*	*Alloascoideomycetes* *Dipodascomycetes* *Lipomycetes* *Pichiomycetes* *Saccharomycetes* *Sporopachydermiomycetes* *Trigonopsidomycetes*	*Archaeorhizomycetes* *Neolectomycetes* *Novakomycetes* *Pneumocystomycetes* *Schizosaccharomycetes* *Taphrinomycetes*

Currently, *Ascomycota* comprises three subphyla and 24 classes (Table 5).

Pleomorphism and one fungus one name

Saccardo (1904) suggested implementing the Dual Nomenclature system for pleomorphic fungi. Many ascomycetous taxa have been named with two names when they are reported with two different morphs. However, on 30 July 2011, the dual nomenclature system was abandoned, thus it was encouraged to link different morphs and propose one name for one fungus. Several important publications have been published during the last decade, and these are summarized in Table 6.

Evolutionary studies of *Ascomycota*

In recent years, *Ascomycota* have been the focus of in-depth molecular dating, paleoecological reconstruction, and morphological character evolution studies. Taylor and Berbee (2006) reviewed the molecular-based divergence time estimation for fungi and provided estimated divergence times for the major lineages of the Fungal Tree of Life. A remarkable fossil, *Paleopyrenomycites devonicus*, discovered in the cortex just beneath the epidermis of aerial stems and rhizomes of the vascular plant *Asteroxylon* (Taylor et al. 2005), shaped the subsequent evolutionary studies in *Ascomycota* significantly. Based on different calibrations, including significant ascomycetous fossil data, the divergence of the *Ascomycota* may have occurred during the 512–588 MYA (Gueidan et al. 2011; Prieto and Wedin 2013; Beimforde et al. 2014; Pérez-Ortega et al. 2016). A recent genome-scale evolutionary study shows the origin of the *Ascomycota* has taken place at 563 MYA (631–495 MYA), while the origin of the *Pezizomycotina* is at 407.7 MYA (631–405 MYA), the *Saccharomycotina* at 438.4 MYA (590–304 MYA), and the *Taphrinomycotina* at 530.5 MYA (620–417 MYA) (Shen et al. 2020). Table 7 summarizes the significant publications related to the evolution of *Ascomycota* published after Taylor and Berbee (2006).

Table 6 Important studies focused on one fungus, one name in *Ascomycota*

Rank	Study
Ascomycota	Rossman et al. (2016)
Dothideomycetes	Wijayawardene et al. (2014), (2017a), Rossman et al. (2015b)
Diaporthales	Rossman et al. (2015a)
Leotiomycetes	Johnston et al. (2014)
Magnaporthales	Zhang et al. (2016)
Orbiliaceae (Orbiliomycetes)	Baral et al. (2018)
Pezizomycetes	Healy et al. (2016)
Sordariomycetes	Réblová et al. (2016)
Xylariales	Wendt et al. (2018)

Subphylum *Pezizomycotina* O.E. Erikss. & Winka, Myconet 1(1): 9 (1997)

Index Fungorum Registration Identifier 501468

Notes: Eriksson and Winka (1997) introduced the subphylum *Pezizomycotina* to accommodate *Arthoniomycetes*, *Dothideomycetes*, *Eurotiomycetes*, *Lecanoromycetes, Leotiomycetes*, *Pezizomycetes* and *Sordariomycetes.* Hibbett et al. (2007) listed *Laboulbeniomycetes* under *Pezizomycotina*. Subsequent studies by Eriksson et al. (2003), Reeb et al. (2004) and Voglmayr et al. (2019) introduced *Lichinomycetes*, *Orbiliomycetes*, and *Xylobotryomycetes* respectively. Currently, *Pezizomycotina* has eleven classes (Table 5).

Arthoniomycetes O.E. Erikss. & Winka, Myconet 1(1): 4 (1997)

Index Fungorum Registration Identifier 501475; Fig. 4

Thallus lichenized with chlorococcoid or trentepohlialean algae or non-lichenized, usually well-developed, crustose, leprarioid, byssoid, placodioid or fruticose, or in form of black yeasts (*Phaeococcomyces* de Hoog) or stromatic; vegetative lichenized diaspores (isidia, soredia or pseudoisidia)

Table 7 Important studies (evolution and ancestral character reconstruction related) published since Taylor and Berbee (2006) on *Ascomycota* and its classes and subclasses

Article	Rank	Content
Vijaykrishna et al. (2006)	*Ascomycota*	Molecular dating and ancestral state reconstructions with emphasis on freshwater fungi
Gueidan et al. (2008)	*Pezizomycotina*	Molecular dating and the ancestral state reconstructions with emphasis on rock-inhabiting fungi
Lücking et al. (2009)	*Ascomycota* and selected classes (*Eurotiomycetes, Lecanoromycetes, Sordariomycetes*)	Molecular dating of fungal divergences
Schoch et al. (2009)	*Ascomycota*	Molecular dating of major lineages and the ancestral state reconstructions with emphasis on ecology, lichenization, mature sporocarp, and ascus dehiscence
Wang et al. (2010)	*Ascomycota*	Evolutionary rate of *Ascomycota* and *Basidiomycota*, with emphasis on ascomycetous subclasses
Amo de Paz et al. (2011)	*Lecanoromycetes*	Molecular dating of fungal divergences of major lineages
Yang et al. (2012)	*Ascomycota*	Molecular dating and the evolution of carnivorous fungi
Prieto and Wedin (2013)	*Ascomycota*	Molecular dating of major lineages and diversification
Beimforde et al. (2014)	*Ascomycota*	Molecular dating of major lineages and ecological diversity
Hongsanan et al. (2017)	*Ascomycota* (*Sordariomycetes*)	Molecular dating of major lineages and the ancestral state reconstructions with emphasis on fungal epiphytes
Pérez-Ortega et al. (2016)	*Ascomycota*	Molecular dating of fungal divergences and introducing a new order (*Collemopsidiales*)
Samarakoon et al. (2016)	*Sordariomycetes*	Molecular dating of subclasses
Habibi and Banihashemi (2017)	*Sordariomycetes* and *Leotiomycetes*	Molecular dating of major lineages
Hongsanan et al. (2017)	*Sordariomycetes*	Molecular dating for higher ranking of fungi
Hyde et al. (2017)	*Fungi, Ascomycota*	Molecular dating for higher ranking of fungi
Liu et al. (2017)	*Dothideomycetes*	Molecular dating of major lineages and standardized taxonomic system
Lücking and Nelsen (2018)	*Ascomycota*	Review and assessment of the evolution of lichenization in fungi
Tedersoo et al. (2018)	*Fungi, Ascomycota*	Molecular dating of higher-level fungal lineages
Zhang et al. (2018a, b)	*Ascomycota*	Molecular dating of major lineages with emphasis on cave fungi
Dayarathne et al. (2019)	*Savoryellomycetidae*	Molecular dating of major lineages
Lücking (2019)	*Fungi, Ascomycota*	Review on molecular dating based temporal banding approach for higher level fungal classification
Naranjo-Ortiz and Gabaldón (2019)	*Fungi, Ascomycota*	Review on traits and their diversity, focusing on the evolutionary relationships among the main fungal lineages
Samarakoon et al. (2019)	*Ascomycota*	Review of fossil *Ascomycota* for calibrating molecular clocks
Haelewaters et al. (2019)	*Ascomycota*	Molecular clock analysis of major lineages with emphasis on Laboulbeniomycetes
Muggia et al. (2020)	*Ascomycota*	Evolutionary aspects of genomics and proteomics
Shen et al. (2020)	*Ascomycota*	Genome based molecular dating and genomic properties of major lineages
Chethana et al. (2021)	*Fungi, Ascomycota*	Ancestral state reconstructions for appressorial types in the main phyla of fungi and fungus-like organisms
Li et al. (2021a)	*Fungi, Ascomycota*	Genome based molecular dating of major lineages
Samarakoon et al. (2022)	*Xylariomycetidae*	Molecular dating and ancestral state reconstructions
Chen et al. (2023a, b)	*Sordariomycetes*	Genome based molecular dating of major lineages

present in some species; ascomata usually present, stromatic (e.g., *Etayoa* Diederich & Ertz, *Lichenostigma* Hafellner), apothecioid, rounded to stellate, lirelliform or not well-defined and globose asci loosely scattered in the thallus (*Crypthothecia* Stirt., *Myriostigma* Kremp.); hamathecium present in form of paraphysoids (between asci or enclosing the asci) or absent; asci bitunicate, globose to clavate, with a strongly thickened tholus, with K, I + blue ring in the

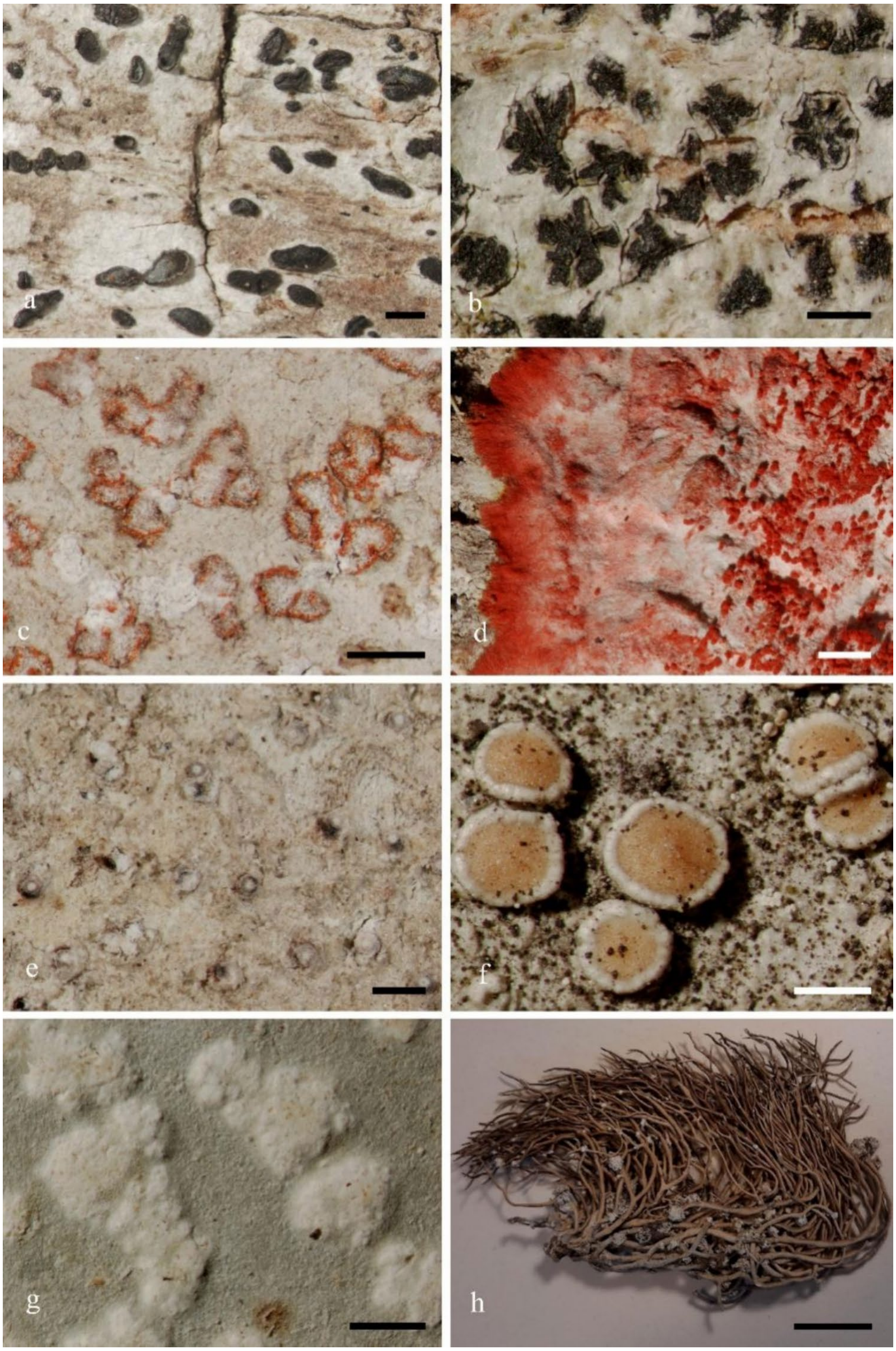


Fig. 4 Morphology of selected members of *Arthoniomycetes*. **a** *Alyxoria varia* (Poland, UGDA L-41544). **b** *Arthonia radiata* – type species (Poland, UGDA L-60149). **c** *Coniocarpon cinnabarinum* (Poland, UGDA L-20564). **d** *Herpothallon rubrocinctum* with pseudoisidia (Bolivia, UGDA L-19608). **e** *Lecanactis abietina* with pycnidia (Poland, UGDA L-25338). **f** *Lichenostigma chlaroterae*, stromata on *Lecanora pulicaris* (Poland, UGDA L-21140). **g** *Myriostigma napoense* with not well-defined ascomata (Bolivia, UGDA L-19564). **h** *Roccella tinctoria* (Canary Islands, UGDA L-20824). Scale bars: **a**, **b**, **c**, **e**, **f** = 500 µm; **d**, **g** = 1000 µm; **h** = 10 mm

lower part of the apical dome (near the ocular chamber), sometimes also ascus tholus amyloid; ascospores hyaline to brown, simple, transversely septate or muriform. *Conidia* simple to muriform, produced by budding or in conidiomata (pycnidia or sporodochia). Lichenized species often produce secondary lichen metabolites. In general taxa can be included in *Arthoniomycetes* based on unique to the class asci with thickened tholus, with KI + blue ring in the lower part of the apical dome, and/or on the molecular data, especially in case of sterile, peculiar species (Tehler et al. 2010; Ertz and Tehler 2011; Ertz et al. 2011, 2014, 2015; Diederich et al. 2012; Frisch et al. 2014, 2015; Thiyagaraja et al. 2020).

Life modes and distribution: Lichenized, saprotrophic or lichenicolous (parasitic or commensals), on bark of trees, wood, rocks, leaf litter, and other lichens (apothecia or thallus), epiphyllous, cosmopolitan, members of several cryptogamous communities, but do not play important role in building main biomes (Lutzoni et al. 2004; Spatafora et al. 2006; Ertz et al. 2009, 2011, 2014, 2015; Tehler et al. 2010; Ertz and Tehler 2011; Diederich et al. 2012; Frisch et al. 2014, 2015; Thiyagaraja et al. 2020), cosmopolitan, but common in temperate to tropical regions, in coastal, desert, mountainous, or forest habitats.

Notes: At first, the species now placed in *Arthoniales* were accepted in two orders, *Arthoniales* and *Opegraphales* M. Choisy ex D. Hawksw. & O.E. Erikss., by Hawksworth and Eriksson (1986). The similarity and close relationships of *Arthoniales* and *Opegraphales* were pointed out by Hafellner (1988) and later included in the class *Arthoniomycetes* by Eriksson and Winka (1997) within the newly established superclass *Leotiomyceta* O.E. Erikss. & Winka. Lutzoni et al. (2004) suggested a sister relationship with *Dothideomycetes* O.E. Erikss. & Winka, but with low support, and Spatafora et al. (2006) confirmed this relationship. At present, *Arthoniomycetes* includes two orders, *Arthoniales* (syn. *Opegraphales*) and *Lichenostigmatales*, the latter with one family (*Phaeococcomycetaceae* McGinnis & Schell) and three genera. The majority of taxa are placed in *Arthoniales*, within seven families (*Andreiomycetaceae* B.P. Hodk. & Lendemer, *Arthoniaceae*, *Chrysotrichaceae* Zahlbr., *Lecanographaceae* Ertz, Tehler, G. Thor & Frisch, *Opegraphaceae* Körb. ex Stizenb., *Roccellaceae* Chevall., *Roccellographaceae* Ertz & Tehler), however, 21 genera are considered *incertae sedis* and perhaps more families can be established when more species are included in the phylogeny of the class (Wijayawardene et al. 2022a).

Type order: *Arthoniales* Henssen ex D. Hawksw. & O.E. Erikss., Syst. Ascom. 5(1): 177 (1986).
Type family: *Arthoniaceae* Reichenb. ex Reichenb., Deut. Bot. Herb.-Buch: 13 (1841).
Type genus: *Arthonia* Ach., Neues J. Bot. 1(3. Stück): 3 (1806).

Type species: *Arthonia radiata* (Pers.) Ach., K. Vetensk-Acad. Nya Handl. 29: 131 (1808).

Dothideomycetes O.E. Erikss. & Winka, Myconet 1(1): 5 (1997).
Index Fungorum Registration Identifier 501,481; Fig. 5

Sexual morph: *Ascomata* stromatic, uni- or multi-loculate, pseudothecial, thyriothecial, cleistothecial, hysterothecial or apothecial, solitary to gregarious, globose to subglobose, pyriform to depressed, crustose or stellate, discoid to cupulate, immersed to superficial, coriaceous, with or without ostioles, glabrous to setose, periphysate, brown to black. *Peridium* single or multi-layered, composed of angular to globose or filiform, black to hyaline cells towards the inside lighter. *Hamathecium* comprising or lacking pseudoparaphyses. *Asci* cylindrical to clavate or ellipsoidal to subglobose, bitunicate, fissitunicate, with or without an ocular chamber. *Ascospores* filiform or ellipsoidal to fusiform, aseptate or septate, hyaline or colored, smooth- or rough-walled, with or without guttules, thin- or thick-walled, with or without various types of appendages and/or sheaths. **Asexual morph:** coelomycetous or hyphomycetous. **Coelomycetes:** *Conidiomata* acervular or pycnidial, solitary or gregarious, immersed to erumpent, uni- or multi-loculate, with or without an ostiole. *Conidiomatal wall* composed of angular to globose or filiform, hyaline to brown cells. *Conidiophores* cylindrical to ampulliform or filiform, septate, branched to unbranched, sometimes reduced to conidiogenous cells. *Conidiogenous cells* holoblastic, enteroblastic, phialidic, annellidic, arthric or tretic, integrated to discrete, doliiform, lageniform or cylindrical, sometimes with sympodial or percurrent proliferations, hyaline to brown. *Conidia* globose to oblong, cylindrical to filiform, hyaline to dark brown, aseptate or septate, smooth, striate, spinulose or verruculose, thin- or thick-walled, with or without appendages or gelatinous sheaths. **Hyphomycetes:** *Conidiomata* sporodochial or synnematal, solitary to gregarious, with or without setae. *Conidiophores* macronematous to micronematous, mononematous or synnematous, straight or flexuous, aseptate or septate, unbranched or branched, hyaline to brown. *Conidiogenous cells* blastic, phialidic, annellidic or tretic, integrated or discrete, determinate or proliferating sympodially or percurrently, cylindrical to oblong. *Conidia* solitary or catenate, acrogenous, pleurogenous or acropleurogenous, globose to ellipsoidal, cylindrical, clavate to obclavate, fusiform, filiform or reniform to sickle-shaped, straight to curved or helicoid, rounded or obtuse to truncate at apex, truncate at base, aseptate or septate, hyaline to dark brown, smooth or verruculose.

Life modes and distribution: The members of *Dothideomycetes* are distributed in a wide range of ecosystems around the world and have diverse life modes. Saprobic fungi are found in all environments and are important for decomposition and nutrient cycles in ecosystems (e.g. *Hysterium*, *Lindgomyces*). Phytopathogenic fungi are responsible for causing leaf, stem, root, and fruit diseases (e.g. *Alternaria*, *Botryosphaeria*, *Cercospora*, *Mycosphaerella*), while some have been reported as pathogenic to arthropods and mammals (e.g. *Hortaea*, *Medicopsis*, *Myriangium*, *Piedraia*). Lichens (e.g. *Monoblastia*, *Strigula*, *Trypethelium*) are found in the tropics and subtropics (Hongsanan et al. 2020b). Lichenicolous fungi (e.g. the *Phoma* complex) are also reported (Lawrey

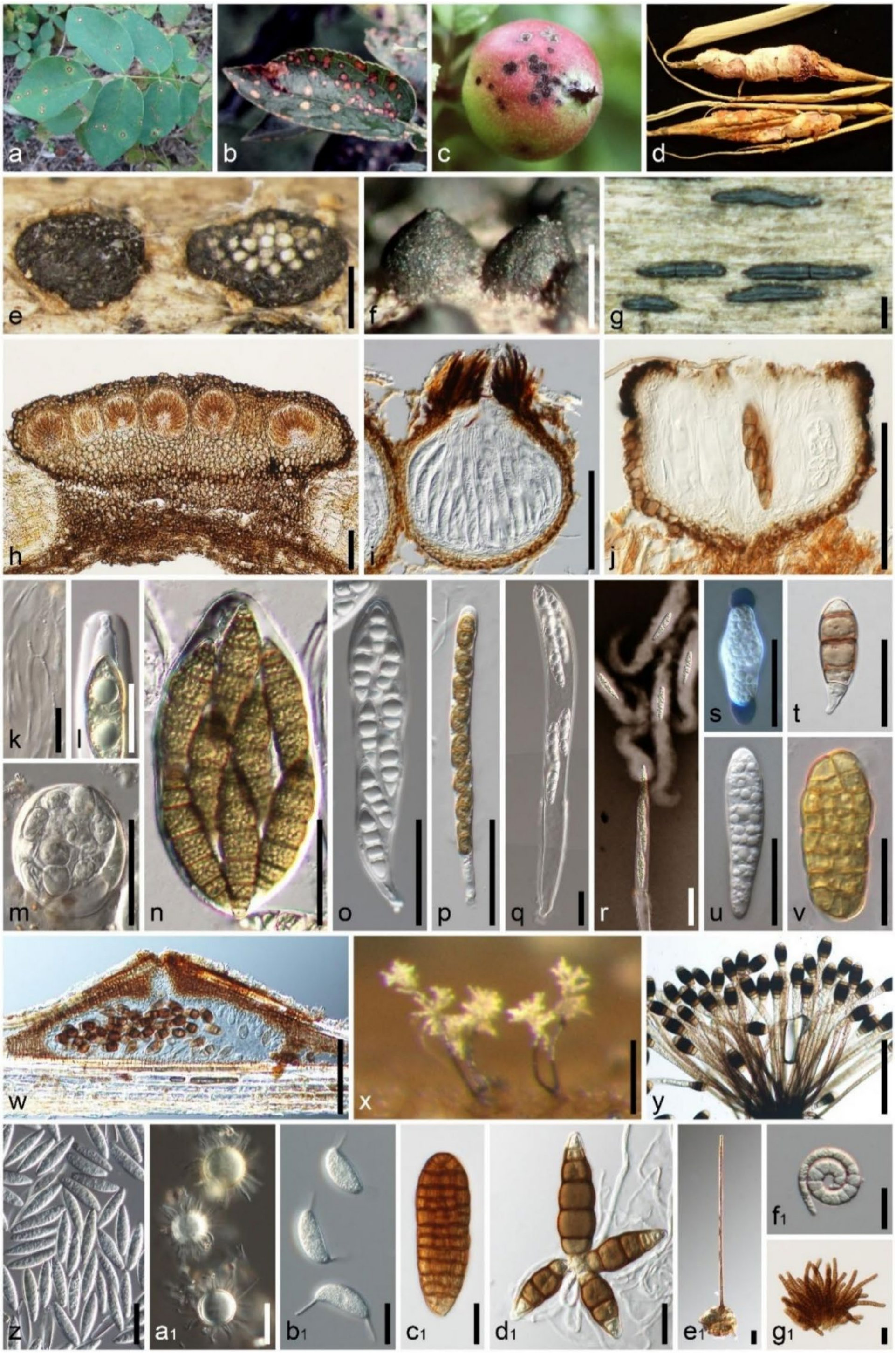


Fig. 5 Morphology in species of *Dothideomycetes*. **a–d** Symptoms (**a** *Pseudocercospora cladrastidis* on leaves of *Maackia amurensis*. **b** *Alternaria alternata* on apple leaf. **c** *Venturia inaequalis* on apple fruit **d** *Shiraia bambusicola* on bamboo). **e–g** Ascomata on host surface (**e** *Dothidea puccinioides*. **f** *Caryospora minima*. **g** *Hysterium angustatum*). **h–j** Ascomata in vertical sections (**h** *D. puccinioides*. **i** *Keissleriella quadriseptata*. **j** *Minutisphaera japonica*). **k** pseudoparaphyses (*Lineolata rhizophorae*). **l** Ascus apex (*Jahnula* sp.). **m–p** Asci (**m** *Asterina aucubae*, **n** *Hadrospora fallax*. **o** *Massarina eburnea*. **p** *Neoheleiosa* sp.). **q** Fissitunicate ascus with extending endoascus (*Lindgomyces cinctosporus*). **r** Fissitunicate ascus and discharged ascospores with an elongated sheath (*Tingoldiago graminicola* (mounted in India ink)). **s–v** Ascospores (**s** *Phyllosticta* sp. (stained with blue-black ink). **t** *Rebentischia abietis*. **u** *Patellaria* sp. **v** *Stemphylium* sp.). **w** Conidioma in vertical section (*Versicolorisporium triseptatum*). **x** Macronematous conidiophores (*Cladosporium* sp.). **y** Synnema (*Phragmocephala atra*). **z–f$_1$** conidia (**z** *Botryosphaeria dothidea*. **a$_1$** *Periconia macrospinosa* (bleached using NaClO). **b$_1$** *Muyocopron* sp. **c$_1$** *Berkleasmium concinnum*. **d$_1$** *Prosthemium intermedium*. **e$_1$** *Quadricrura meridionalis*. **f$_1$** *Tubeufia* sp.). **g$_1$** Propagule (*Collapsimycopappus styracis*). Scale bars: **e–g** = 500 µm, **h–j**, **w–y** = 100 µm, **m–r** = 50 µm, **k**, **l**, **s–v**, **z–g$_1$** = 20 µm

et al. 2012; Valenzuela-Lopez et al. 2018). Some members are endophytic (e.g. *Alfoldia*, *Aquilomyces*, *Camarosporidiella*, *Neohendersonia*, *Ramichloridium*), mycorrhizal (e.g. *Cenococcum*), fungicolous (e.g. *Ampelomyces*, *Trichothyrium*) and coprophilous (e.g. *Delitschia*, *Preussia*). There are some rock-inhabiting fungi (e.g. *Coniosporium*, *Cryomyces*) and their species diversity is becoming clearer. The ancestors of *Dothideomycetes* are presumed to have been saprobic and then evolved into other lifemodes such as phytopathogens and lichens (Schoch et al. 2009a; Haridas et al. 2020).

Notes: *Dothideomycetes*, the largest and most phylogenetically diverse class of *Ascomycota*, were introduced by Eriksson and Winka (1997). This class encompasses the majority

Table 8 Economically significant studies

Species name	Host	References (major refs in last 5 years)
Cercospora beticola	Sugar beet (*Beta vulgaris*)	Imbusch et al. (2021)
Corynespora cassiicola	Soybean (*Glycine max*)	Edwards Molina et al. (2019)
Lasiodiplodia spp.	Jute (*Corchorus* spp.)	Mandal et al. (2023)
Pseudocercospora fijiensis	Banana (*Musa* spp.)	Yonow et al. (2019)
Zymoseptoria tritici	Wheat (*Triticum* spp.)	Garnault et al. (2019)

Table 9 Medicinally significant studies

Species name	Human/ animal	References (major refs in last 5 years)
Hortaea werneckii	Human	Chamroensakchai et al. (2021)
Medicopsis romeroi	Human	Chanyachailert et al. (2019)

Table 10 Industrial applications

Species name	Industry	References (major refs in last 5 years)
Cladosporium halotolerans	Silver nanoparticles (AgNPs)	Ameen et al. (2023)
Paraconiothyrium brasiliense	Anticancer drug	Nakashima et al. (2019)
Phoma sp.	Melanin pigment production	Surendirakumar et al. (2022)

of species previously classified under *Loculoascomycetes* (Luttrell 1955) and is characterized by ascolocular development and fissitunicate asci. The classification of sexually typified genera within *Dothideomycetes* was provided by Lumbsch and Huhndorf (2007, 2010) alongside the Phylum *Ascomycota*. Similarly, asexual-typified genera in this class were incorporated into the natural classification systems by Wijayawardene et al. (2014), where molecular data are available. The most recent monographs of families of *Dothideomycetes* were presented by Hongsanan et al. (2020a, b).

Dothideomycetes comprising 49 orders, 222 families and 1748 genera (Wijayawardene et al. 2022a) are divided into two subclasses: *Dothideomycetidae* and *Pleosporomycetidae*. Most orders and families are treated as *incertae sedis* within this class (Schoch et al. 2006). Within the subclass *Dothideomycetidae*, there are ten accepted orders, namely: *Aureoconidiellales*, *Capnodiales*, *Cladosporiales*, *Comminutisporales*, *Dothideales*, *Mycosphaerellales*, *Myriangiales*, *Neophaeothecales*, *Phaeothecales*, and *Racodiales* (Wijayawardene et al. 2022a). In the *Pleosporomycetidae* subclass, *Gloniales*, *Hysteriales*, *Mytilinidiales*, and *Pleosporales* are accepted (Wijayawardene et al. 2022a), whereas 35 orders are categorized as *Dothideomycetes* orders *incertae sedis*.

One fungus one name: In recent years, DNA sequencing and molecular phylogenetic analysis have made it possible to confirm sexual and asexual relationships and to propose one name for a single species or genus (Crous et al. 2009; Bensch et al. 2012; Manamgoda et al. 2012; Phillips et al. 2013; Hyde et al. 2013, 2014). Thus, it was proposed to adopt one name (between two generic names) when the links between the morphs are confirmed.

The members of *Dothideomycetes* are well-known as pathogens of both plants and animals, and industrially important taxa. Some studies focusing on economically, clinically and industrially important taxa are summarized in Tables 8, 9 and 10 respectively (examples that were published in the last 5 years).

Type order: ***Dothideales*** Lindau, in Engler & Prantl, Nat. Pflanzenfam., Teil. I (Leipzig) 1(1): 373 (1897).

Type family: ***Dothideaceae*** Chevall. [as ‘Dothideae’], Fl. gén. env. Paris (Paris) 1: 446 (1826).

Type genus: ***Dothidea*** Fr., Observ. mycol. (Havniae) 2: 347 (1818).

Type species: ***Dothidea sambuci*** (Pers.) Fr., Syst. mycol. (Lundae) 2(2): 551 (1823).

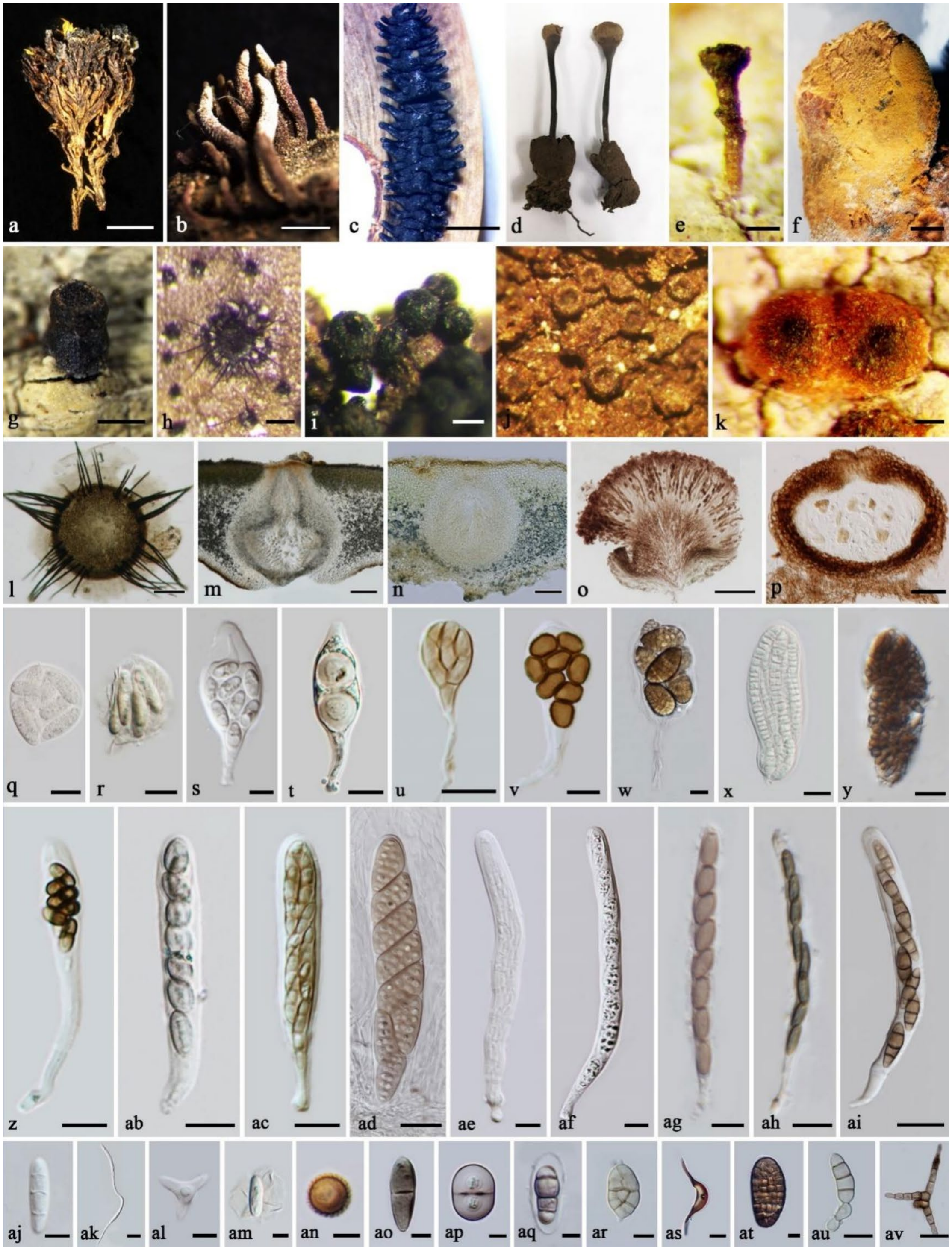
Eurotiomycetes O.E. Erikss. & Winka, Myconet 1(1): 6 (1997).

Index Fungorum Registration Identifier 501483; Fig. 6

Thallus: Yeast-like to filamentous. **Sexual morph**: *Stromata* occasionally present, reduced, usually pulvinate or (sub)globose, sometimes stipitate, white, brown or black. *Ascomata* apothecial, ascostromatal, cleistothecial, gymnothecial, perithecioid, or mazaediate, mostly (sub)globose, pyriform or variously shaped, sometimes setose or with distinct peridial appendages, light-coloured to black, solitary to aggregated. *Hamathecium* absent or including paraphyses, pseudoparaphyses, periphysoids and periphyses in different combinations. *Asci* usually 8-spored, sometimes 2-spored or polysporous, mostly (sub)globose, clavate or obpyriform, unitunicate or bitunicate, with fissitunicate to evanescent dehiscence. Ascospores usually allantoid, bivalved, ellipsoidal, globose, oblate, (ob)ovoid, reniform or star-shaped, aseptate, transversely septate or dictyoseptate, hyaline, light-coloured or brown, smooth or showing an equatorial furrow, rim or crests, a reticulum, ridges, spines, warts or other ornamentations, sometimes surrounded by a sheath. **Asexual morph**: coelomycetous or hyphomycetous. **Coelomycetes:** *Conidiomata* pycnidial or pycnothyrial, with or without a central ostiole, commonly flat to globose, brown, immersed to erumpent. *Conidiomatal wall* often of *textura angularis* or *textura epidermoidea* at the outer portion, inner wall covered with hyaline to dark brown, ampulliform, cylindrical, ellipsoidal, fusiform, oval or lens-shaped phialidic conidiogenous cells, or with pale brown toruloid conidiophores producing cheiroid conidia. *Conidia* aseptate, mostly cylindrical to ellipsoid, hyaline or cheiroid, consisting of a central globose, medium brown, verruculose cell giving rise to up to 6 radiating arms of subglobose to ellipsoidal cells, each forming lateral branches. **Hyphomycetes:** *Conidiomata* present or absent, scattered or aggregated, sporodochia or synnemata. *Setae* sometimes present. *Conidiophores* micronematous to macronematous, hyaline to brown, solitary to fasciculate, aseptate or septate, simple or branched, smooth-walled to verrucose, *Conidial ontogeny* enteroblastic, holoblastic, holothallic or thallic-arthric. *Conidiogenous cells* intercalary, lateral or terminal, sometimes extending percurrently or sympodially, sometimes denticulate or with dark or refractive scars. *Conidia* solitary or produced in mucilaginous masses or chains, aseptate, transversely septate or dictyoseptate, highly diverse in shape, usually (sub)cylindrical, (ob)clavate, doliiform, ellipsoid, (sub)globose, falcate, fusiform or guttuliform, smooth-walled or ornamented, usually with more or less developed spines or warts, with or without a basal frill, secession rhexolytic or schizolytic.

Life modes and distribution: Members of *Eurotiomycetes* are abundant both in terrestrial and aquatic ecosystems worldwide, occurring in an extremely broad range of habitats. While most of these fungi are degraders of decaying material of plant or animal origin, many species cause diseases in animals (e.g. *Exophiala cancerae*, an agent of Lethargic Crab Disease in the mangrove crab *Ucides cordatus fide* de Hoog et al. 2011) (Table 11), plants (e.g. *Dolabra nepheliae* on rambutan and lychee *fide* Rossman et al. 2010), or other fungi (e.g. *Cladophialophora pucciniophila* on *Puccinia polygoni-amphibii fide* Park and Shin 2011). This order includes a remarkably high number of clinically relevant species causing diverse pathologies in humans and other animals, including agents of life-threatening systemic mycoses, such as blastomycosis, coccidioidomycosis, histoplasmosis, and paracoccidioidomycosis, as well as fungi causing chromoblastomycosis, dermatophytosis, hyalohyphomycosis, mycetoma, and phaeohyphomycosis (de Hoog et al. 2020). Certain lineages in *Eurotiomycetes* contain lichenized fungi, e.g. *Pyrenulales*, *Verrucariales*, and some *Celotheliaceae* (Gueidan et al. 2014; Pykälä et al. 2020; Miranda-González et al. 2022) or lichenicolous species (e.g. *Knufia peltigerae* and *Sclerococcum* spp. *fide* Untereiner et al. 2011; Diederich et al. 2018).

Notes: The class *Eurotiomycetes* was erected by Eriksson and Winka (1997) based on phylogenetic analysis of the 18S rRNA gene (SSU). The original circumscription of this class included most fungi referred to as "Plectomycetes", which were roughly characterized by thin-walled prototunicate asci (unitunicate asci with walls which disintegrate at maturity to release the ascospores passively within the ascoma), ascomata lacking a distinct hymenial layer and with asci scattered within the ascomatal cavity, aseptate ascospores, ascomata gymnothecial to cleistothecial, the latter sometimes produced within a stroma, and morphologically diverse blastic or thallic asexual morphs (Alexopoulos et al. 1996; Geiser et al. 2006). Eriksson and Winka (1997) included two orders in this class, i.e. *Eurotiales* and *Onygenales*. The former included the families *Elaphomycetaceae*, *Monascaceae* and *Trichocomaceae*, and the latter included *Arthrodermataceae*, *Ascosphaeraceae*, *Eremascaceae*, *Gymnoascaceae* and *Onygenaceae*. The monophyly of this class was confirmed subsequently in a SSU-based phylogenetic analysis by Geiser and LoBuglio (2001). Unexpectedly, early phylogenetic studies (Spatafora et al. 1995; Berbee 1996; Silva-Hanlin and Hanlin 1999) revealed that the "monophyletic Plectomycetes" shared a common ancestry with members of the order *Chaetothyriales*, which produce perithecioid ascomata and bitunicate asci with an active, fissitunicate spore release mechanism (Müller et al. 1987; Barr 1991). The order *Coryneliales* has been considered a "missing link" between the "monophyletic Plectomycetes" and chaetothyrialean genera and related fungi. *Coryneliales* produce ascolocular ascomata and asci which are initially bitunicate, but whose outer layer breaks away early in their development, so that asci appear unitunicate at maturity, releasing spores passively by degradation of the inner ascal wall (Johnston and Minter 1989). Multi-locus phylogenetic studies placed this order basal to the clade comprising *Eurotiales* and *Onygenales* (Geiser et al. 2006), supporting the view that the ascomata of Plectomycetes evolved by loss of the bitunicate ascus and its active spore release mode (Eriksson 1982). The boundaries of *Eurotiomycetes* have been broadened significantly in recent years and, at present, it includes six ecologically, morphologically, and phylogenetically diverse subclasses, i.e. *Chaetothyriomycetidae*, *Coryneliomycetidae*, *Cryptocaliciomycetidae*, *Eurotiomycetidae*, *Mycocaliciomycetidae*, and *Sclerococcomycetidae*



(Prieto et al. 2021). The class *Eurotiomycetes* currently encompasses twelve orders, 34 families and ca. 291 genera.

Numerous species of *Eurotiomycetes* are pleomorphic, producing sexual and asexual morphs which were traditionally named separately. Recent phylogenetic studies (Réblová et al. 2013; Samson et al. 2014; Yilmaz et al. 2014; Diederich et al. 2018; Sun et al. 2019a, b; Houbraken et al. 2020; Kandemir et al. 2022) have applied unitary nomenclature in different genera in this class, in the pursuit of taxonomic stability.

Type order: ***Eurotiales*** G.W. Martin ex Benny & Kimbr., Mycotaxon 12(1): 23 (1980).

◂ **Fig. 6** Macro and micro morphological characteristics of eurotiomycetous taxa. **a**, **g–k** ascomata (**a** *Agonimia tristicula* (*Verrucariaceae*, *Verrucariales*, *Chaetothyriomycetidae*; **g** *Pyrgillus americanus* (*Pyrenulaceae*, *Pyrenulales*, *Chaetothyriomycetidae*); **h** *Chaetothyrium guaraniticum* (*Chaetothyriaceae*, *Chaetothyriales*, *Chaetothyriomycetidae*); **i**: *Dolabra nepheliae* (*Celotheliaceae*, *Phaeomoniellales*, *Chaetothyriomycetidae*); **j** *Coccodinium bartschii* (*Coccodiniaceae*, *Chaetothyriales*, *Chaetothyriomycetidae*); **k** *Pyrenowilmsia ferruginosa* (*Pyrenulaceae*, *Pyrenulales*, *Chaetothyriomycetidae*). **b** Synnema of *Penicilliopsis clavariiformis* (*Aspergillaceae*, *Eurotiales*, *Eurotiomycetidae*). **c** Ascostroma of *Corynelia tripos* (*Coryneliaceae*, *Coryneliales*, *Coryneliomycetidae*). **d** Stipewith volva of *Pseudotulostoma volvatum* (*Elaphomycetaceae*, *Eurotiales*, *Eurotiomycetidae*). **e** Apothecia of *Mycocalicium parietinum* (*Mycocaliciaceae*, *Mycocaliciales*, *Mycocaliciomycetidae*). **f** Stromata *Dendrosphaera eberhardtii* (*Aspergillaceae*, *Eurotiales*, *Eurotiomycetidae*). **h** Ascomata with black setae of *Chaetothyrium guaraniticum* (*Chaetothyriaceae*, *Chaetothyriales*, *Chaetothyriomycetidae*). l Squash mount of ascoma of *Actinocymbe separato-setosa* (*Chaetothyriaceae*, *Chaetothyriales*, *Chaetothyriomycetidae*). **m**, **n**, **p** Vertical section of ascoma (**m** *Dermatocarpon miniatum* (*Verrucariaceae*, *Verrucariales*, *Chaetothyriomycetidae*); **n** *Dermatocarpella yoshimurae* (*Verrucariaceae*, *Verrucariales*, *Chaetothyriomycetidae*). **o** Vertical section of apothecia of *Phaeocalicium praecedens* (*Mycocaliciaceae*, *Mycocaliciales*, *Mycocaliciomycetidae*). **q–ai** Asci with ascospores. (**q** *Phaeosaccardinula diospyricola* (*Chaetothyriaceae*, *Chaetothyriales*, *Chaetothyriomycetidae*). **r** *Samarospora potamogetonis* (*Eurotiomycetidae incertae sedis*). **s** *Dermatocarpon miniatum* (*Verrucariaceae*, *Verrucariales*, *Chaetothyriomycetidae*). **t** *Corynelia clavata* (*Coryneliaceae*, *Coryneliales*, *Coryneliomycetidae*). **u** *Caliciopsis pinea* (*Coryneliaceae*, *Coryneliales*, *Coryneliomycetidae*). **v** *Fitzpatrickella operculata* (*Coryneliaceae*, *Coryneliales*, *Coryneliomycetidae*). **w** *Sporodictyon schaererianum* (*Verrucariaceae*, *Verrucariales*, *Chaetothyriomycetidae*). **x** *Actinocymbe separato-setosa* (*Chaetothyriaceae*, *Chaetothyriales*, *Chaetothyriomycetidae*). **y** *Muellerella polyspora* (*Verrucariaceae*, *Verrucariales*, *Chaetothyriomycetidae*). **z** *Clypeopyrenis microsperma* (*Pyrenulaceae*, *Pyrenulales*, *Chaetothyriomycetidae*). **ab** *Melanotheca coccorum* (*Pyrenulaceae*, *Pyrenulales*, *Chaetothyriomycetidae*). **ac** *Pyrenowilmsia ferruginosa* (*Pyrenulaceae*, *Pyrenulales*, *Chaetothyriomycetidae*). **ad** *Heufleridium pentagastricum* (*Pyrenulaceae*, *Pyrenulales*, *Chaetothyriomycetidae*). **ae** *Dolabra nepheliae* (*Celotheliaceae*, *Phaeomoniellales*, *Chaetothyriomycetidae*). **af** *Parathelium polysemum* (*Verrucariaceae*, *Verrucariales*, *Chaetothyriomycetidae*). **ag** *Phaeocalicium praecedens* (*Mycocaliciaceae*, *Mycocaliciales*, *Mycocaliciomycetidae*). **ah** *Chaenothecopsis rubescens* (*Mycocaliciaceae*, *Mycocaliciales*, *Mycocaliciomycetidae*). **ai** *Moriola descensa* (*Verrucariaceae*, *Verrucariales*, *Chaetothyriomycetidae*). **aj-at** Ascospores. (**aj** *Verrucaria tartarina* (*Verrucariaceae*, *Verrucariales*, *Chaetothyriomycetidae*). **ak** *Rhaphidicyrtis trichosporella* (*Incertae sedis*, Pyrenulales, *Chaetothyriomycetidae*). **al** *Tripospora tripos* (*Coryneliaceae*, *Coryneliales*, *Coryneliomycetidae*). **am** *Samarospora potamogetonis* (*Eurotiomycetidae* genera *incertae sedis*). **an** *Lagenulopsis bispora* (*Coryneliaceae*, *Coryneliales*, *Coryneliomycetidae*). **ao** *Heterocarpon ochroleucum* (*Verrucariaceae*, *Verrucariales*, *Chaetothyriomycetidae*). **ap** *Parapyrenis aurora* (*Pyrenulaceae*, *Pyrenulales*, *Chaetothyriomycetidae*). **aq** *Phaeospora rimosicola* (*Verrucariaceae*, *Verrucariales*, *Chaetothyriomycetidae*). **ar** *Ceratocarpia cactorum* (*Chaetothyriaceae*, *Chaetothyriales*, *Chaetothyriomycetidae*). **as** *Bicornispora exophiala* (*Rutstroemiaceae*, *Helotiales*, *Leotiomycetidae*). **at** *Sporodictyon schaererianum* (*Verrucariaceae*, *Verrucariales*, *Chaetothyriomycetidae*). **au**, **av** Spores (**au** *Coccodinium bartschii* (*Coccodiniaceae*, *Chaetothyriales*, *Chaetothyriomycetidae*). **av** *Chaetothyrium spinigerum* (*Chaetothyriaceae*, *Chaetothyriales*, *Chaetothyriomycetidae*). Scale bars: **a**, **b** = 2000 μm, **c**, **f** = 1000 μm, **e**, **h**, **i**, **k–o** = 100 μm, **g** = 500 μm, **p** = 50 μm, **q**, **w**, **ad**, **ai**, **av** = 20 μm, **r–v**, **x–ac**, **ae–ah**, **ak**, **al**, **as–au** = 10 μm, **aj**, **am–ar** = 5 μm (photo credit to Qing Tian)

Type family: ***Aspergillaceae*** Link, Abh. dt. Akad. Wiss. Berlin 1824: 165. 1826.

= *Eurotiaceae* Clem. & Shear, Gen. fung., Edn 2 (Minneapolis): 50 (1931).

Type genus: ***Aspergillus*** P. Micheli ex Haller, Hist. stirp. Helv. (Bernae) 3: 113 (1768).

Type species: ***Aspergillus glaucus*** (L.) Link 1809 (Designated by Clements & Shear, Gen. fung., Edn 2 (Minneapolis): 386. 1931).

= *Eurotium herbariorum* (F.H. Wigg.) Link ex Nees, Syst. Pilze (Würzburg): 96 (1816) [1816–17].

Laboulbeniomycetes Engler & Prantl, Nat. Pflanzenfam., Teil. I (Leipzig) 1: vi (1897).

Index Fungorum Registration Identifier 501,485; Fig. 7

Laboulbeniales **and** ***Herpomycetales***: No production of hyphae; three-dimensional thallus solitary or multiple, determinate growth, formed by divisions of two-celled ascospore, composed of up to several thousand cells; perithecia composed of two-layered walls, systematically to rarely haustorial (rhizoid-like), haustoria simple or branched, single or multiple per thallus, no asexual reproduction; host specific, habitat specific, and position specific, on single arthropod-only hosts, ascospores transmitted primarily through direct contact between hosts. ***Laboulbeniales*****:** Thalli averaging 200–300 μm, microscopic and multicellular, perithecial wall generally arises from perithecial basal cells, with inner cell wall starting at different level outer cell walls, rows of outer wall cells growing upwards around and after carpogonial extension, melanin-rich cell walls, unculturable (or if growth, no more than a few cells), rarely haustorial (rhizoid-like), single per thallus; from four to eight two-celled ascospores per ascus, septum positioned near the lower end separating a smaller (directed downward) and larger cell (directed upwards), asci generated from a single series of ascogenic cells, sticky ascospores transmitted directly from infected to uninfected hosts during mating or other contacts; known from all continents (except Antarctica), wide variety of hosts including cockroaches, termites, beetles, flies, true bugs, ants, crickets and allies, lice, and thrips, moderately to highly host-specific. ***Herpomycetales*****:** Dioecious; four-celled primary axis of thallus developing directly from ascospore; suprabasal cell in female thallus giving rise to secondary axis (or axes), producing perithecia and connecting directly with integument of the host; perithecia multi-tiered, outer wall rows consisting of many cells equal in height, develop before carpogonial upgrowth which extends between the outer wall cells, bearing single to three apex projections; haustorial, multiple per thallus; ascospores 8 per ascus with median septum resulting in two equal cells; asci produced sequentially from two series of ascogenic

Table 11 Medicinally/clinical significance, examples:

Species name	Human/ animal	References
Aspergillus fumigatus	Main agent of aspergillosis worldwide in human and various warm-blooded animals	Tsang et al. (2018), Houbraken et al. (2020), Ortiz et al. (2022)
Blastomyces dermatitidis	Causative agent of blastomycosis in humans and other mammals	Dukik et al. (2017), Jiang et al. (2018), Linder & Kauffman (2020)
Cladophialophora carrionii	Main agent of human chromoblastomycosis in arid regions	Deng et al. (2015), de Hoog et al. (2020)
Cladophialophora bantiana	Agent of phaeohyphomycosis in humans and other mammals, usually affecting the brain	Kantarcioglu et al. (2017), de Hoog et al. (2020)
Coccidioides immitis	Agent of human coccidioidomycosis	de Hoog et al. (2020), Kandemir et al. (2022), Kirkland et al. (2022)
Exophiala dermatitidis	Agent of various forms of phaeohyphomycosis in humans	Song et al. (2017), Kirchhoff et al. (2019)
Fonsecaea pedrosoi	Main agent of human chromoblastomycosis in humid regions	Schneider et al. (2019)
Histoplasma capsulatum	Agent of human histoplasmosis	Sepúlveda et al. (2017), Valdez et al. (2022)
Paracoccidioides brasiliensis	Agent of paracoccidioidomycosis in humans and other mammals	Pinheiro et al. (2020), Hahn et al. (2022), Rodrigues et al. (2023), Vilela et al. (2023)
Talaromyces marneffei	Agent of talaromycosis in humans and other mammals	Cao et al. (2019), Pruksaphon et al. (2022), Wang et al. (2023a)
Trichophyton rubrum	Human, agent of dermatophytosis	de Hoog et al. (2017), Chanyachailert et al. (2023)

cells, host-specificity restricted to cockroaches. ***Pyxidiophorales*****:** Three-morph life-cycle with hyphal growth, including an independent sexual (meiosporic origin) state and two asexual (mitosporic origin) states associated with arthropods for dispersal, some mycoparasitic forming two-celled ascospores dividing into asexual state (*Thaxteriola* Speg.); perithecia produced from a mycelium, composed of single-layered cell walls, reduced number of ascospores per ascus; heteroecious, with fungal host (which is parasitized) and arthropod host (for dispersal), sometimes associated on ephemeral substrates such as herbivore dung.

Life modes and distribution: Perithecial fungi obligatorily associated with arthropod integuments, either as ectobionts or for dispersal, on a wide range of terrestrial and aquatic hosts; forming teleomorphic thalli on specific or unspecific positions on the host integument, sometimes involved in hyperparasitic associations; or mycoparasitic and producing anamorphic morphs dispersed by arthropods (Fig. 8).

Notes: *Laboulbeniomycetes* is a class of microscopic fungi within *Ascomycota* exhibiting an obligate association with arthropods. Three named (*Laboulbeniales*, *Herpomycetales* and *Pyxidiophorales*) and two unnamed (*Chantransiopsis* and *Laboulbeniopsis*) clades are currently accepted (Haelewaters et al. 2021a). However, the circumscription of these clades has been impeded by numerous taxonomic and phylogenetic misunderstandings and misinterpretations, resulting in a *turbulent* taxonomic history (*fide* Haelewaters et al. 2021b). Initially mistaken for parasitic worms or red algal relatives, there was no consensus among biologists and mycologists regarding the fungal nature of these organisms during the twentieth century, mainly due to the lack of "typical" fungal characters. Charles P. Robin (1821–1885) was the first one to recognize *Laboulbeniomycetes* as fungi, alongside Roland Thaxter (1891–1931) who later considered them to be ascomycetes (Blackwell et al. 2020). Thaxter's efforts led to the description of over half of the currently known diversity of *Laboulbeniomycetes*, inevitably based on morphological characters (e.g. perithecium morphology or asci development).

Since Engler (1898) erected the class *Laboulbeniomycetes*, the accumulation of empirical data and the development of molecular-based tools considerably improved our understanding of life history traits and phylogenetic relationships within this group. The class was for the first time confirmed by molecular data by Weir and Blackwell (2001) and while molecular-based studies show clear advantages over field-based observations (Cazabonne et al. 2022), numerous phylogenetic relationships within *Laboulbeniomycetes* remain to be elucidated. Goldmann and Weir (2018) demonstrated that *Laboulbeniomycetes* is a monophyletic group within *Ascomycota*, closely related to *Sordariomycetes*, confirming the previous placement of the *Laboulbeniales*-*Pyxidiophora* clade (Weir and Blackwell 2001). The uncertain placement of the genus *Herpomyces* was resolved by Haelewaters et al. (2019) by the introduction of the order *Herpomycetales* based on molecular phylogenetic, morphological, developmental, and host usage data. Despite those recently undertaken efforts, deeper nodes remain unresolved and the sister group of *Laboulbeniomycetes* is yet to be discovered

Fig. 7 *Laboulbeniomycetes*, including (**a**–**l**) *Laboulbeniales*, (**m**–**n**) *Herpomycetales*, and (**o**–**p**) *Pyxidiophorales*. **a** *Stigmatomyces majewskii*. **b** *Teratomyces actobii*. **c** *Rhachomyces anophthalmi*. **d** *Laboulbenia notiophili*. **e** *Dimeromyces rugosus*. **f** Laboulbenia anisodactyli. **g** *Arthrorhynchus eucampsipodae*. **h** *Gloeandromuces cusucoensis*. **i** *Laboulbenia oioveliicola*. **j** *Haplomyces texanus*. **k** *Hesperomyces harmoniae*. **l** *Gloeandromyces plesiosaurus* f. *plesiosaurus*. **m** *Herpomyces stylopygae*. **n** *Herpomyces shelfordellae*. **o** *Thaxteriola* sp. **p** *Pyxidiophora bialowiezensis*. Scale bars: **a**, **c**, **d**, **h**, **l**–**o** = 50 µm; **b**, **e**, **g**, **j**, **k**, **p** = 100 µm; **f** = 10 µm; **i** = 20 µm. Photos: Danny Haelewaters; drawings: Jingyu Liu

(Blackwell et al. 2020). Fossil records for *Laboulbeniomycetes* are limited to *Columnomyces electri* from Dominican amber (Perreau et al. 2021) and *Stigmatomyces succini* from Bitterfeld amber (Rossi et al. 2005).

Type order: ***Laboulbeniales*** Lindau, in Engler & Prantl, Nat. Pflanzenfam., Teil. I (Leipzig) 1(1): 47 (1897).
Type family: ***Laboulbeniaceae*** G. Winter [as 'Laboulbenieae'], Rabenh. Krypt.-Fl., Edn 2 (Leipzig) 1.2: 918 (1886).

Type genus: ***Laboulbenia*** Mont. & C.P. Robin, in Robin, Histoire naturelle des Vegetaux Parasites (Paris): 622 (1853).
Type species: ***Laboulbenia rougetii*** Mont. & C.P. Robin, in Robin, Histoire naturelle des Vegetaux Parasites (Paris): 622 (1853).

Lecanoromycetes O.E. Erikss. & Winka, Myconet 1(1): 7 (1997).

Index Fungorum Registration Identifier 501486; Fig. 9

Fig. 8 Hosts of *Laboulbeniomycetes* microfungi. **a** *Harmonia quadripunctata* (Coleoptera, Coccinellidae) with *Hesperomyces harmoniae*. **b** *Bembidion femoratum* (Coleoptera, Carabidae) with *Laboulbenia vulgaris*. **c** *Bradycellus harpalinus* (Coleoptera, Carabidae) with *Laboulbenia eubradycelli*. **d** A dried, pinned specimen of *Crepidogaster bioculata* (Coleoptera, Carabidae) with *Laboulbenia* sp. **e** *Myrmica sabuleti* (Hymenoptera, Formicidae) with *Rickia wasmannii*. **f** *Penicillidia conspicua* (Diptera, Nycteribiidae) with *Arthrorhynchus nycteribiae*. Photos: a: Gilles San Martin; b, c: Bart Horvers; d: Ondřej Koukol; f: Walter P. Pfliegler; E. Theodoor Heijerman

Sexual morph: *Thallus* usually superficial on the substratum, more rarely immersed, poikilohydric, usually long-lived (on average perennial, up to thousands of years), composed of hyphae and green algae and/or cyanobacteria in defined tissues. *Ascomata* apothecia, often present but unknown in many species, solitary or aggregated, round to linear, variously coloured, disc usually without algae or cyanobacteria, margin often containing algae or cyanobacteria. *Hamathecium* composed of paraphyses. *Asci* often eight-spored, but varying between 1-spored and multi (> 100)-spored, cylindrical to fusiform or clavate, incompletely bitunicate, often with J + staining tholus. *Ascospores*

Fig. 9 *Lecanora saepiphila.* **a** habitat on wood. **b** section through apothecium, mounted in water. **c** section through apothecium, mounted in 10% KOH. Pictures by L.A. dos Santos

filamentous, globose, ellipsoidal or fusiform, aseptate or septate, hyaline or brown, often surrounded by a gelatinous sheath. **Asexual morph:** coelomycetous. *Conidiomata* frequently present, pycnidial, developing on the same thalli as the apothecia, usually immersed, globose, coriaceous, with a single locule, dark brown to black, ostiolate. *Conidiomata wall* carbonized. *Conidiophores* lining the inner cavity or reduced, septate, sometimes branched. *Conidiogenous cells* phialidic, discrete, lageniform, hyaline to pale yellow, smooth, producing microconidia and sometimes mesooconidia. *Conidia* hyaline, aseptate to multiseptate, without appendages.

Life modes and distribution: Lichen-forming with green algae and/or cyanobacteria, or more rarely parasitic on lichens or saprobic; on bark, wood, rock, soil, detritus, other lichens and/or living leaves. Showing a worldwide distribution, but most abundant in boreal to arctic regions.

Notes: The class *Lecanoromycetes*, one of the largest classes of phylum *Ascomycota*, was introduced by Eriksson and Winka (1997). It comprises the vast majority of the lichenized fungi. Apart from this, it accommodates some species that are parasitic on lichens, either with their own separate algae, or without separate algae and using the algae of the host; there are also some groups with a saprobic life style. Rambold and Triebel (1992) provided a discussion and list of such species.

Based on Lücking et al. (2017) and Wijayawardene et al. (2022a), the class comprises 21 orders, 82 families, around 775 genera and around 15,500 species. The saprobic life style is largely restricted to a small part of the *Ostropales*.

The members of the *Lecanoromycetes* are distributed over a broad range of ecosystems. They are most conspicuous in boreal, (ant) arctic and alpine ecosystems, where they cover vast areas of soil and rock. In other ecosystems they are present on tree bark and living leaves. As with almost every group, they are most diverse in the tropics. They are themselves often host to other, so-called intralichenic, filamentous fungi and/or yeasts (Spribille et al. 2016; Grimm et al. 2021).

The main use of *Lecanoromycetes* is for the biomonitoring of air pollution (Giordani 2019). Many species are sensitive to sulphur dioxide, while other species respond positively to ammonia pollution.

Type order: ***Lecanorales*** Nannf., Nova Acta R. Soc. Scient. upsal., Ser. 4 8(no. 2): 68 (1932).

Type family: ***Lecanoraceae*** Körb. [as 'Lecanoreae'], Syst. lich. germ. (Breslau): 104 (1855).

◂ **Fig. 10** *Leotiomycetes* fungi. **a** *Lachnellula willkommii*, rehydrated apothecia showing dense hairs on the outside, on branch of *Larix decidua*, Sampeyre, Italy (*Lachnaceae*, *Helotiales*). **b** *Phialocephala* sp., Calf Island, Boston Harbor Islands, Massachusetts USA (*Mollisiaceae*, *Helotiales*). **c** *Chlorosplenium cusucoense* (as *Chlorosplenium* sp. 1 in Haelewaters et al. 2021), Boquete, Panama (*Chlorospleniaceae*, *Helotiales*). **d** *Sclerencoelia fraxinicola*, erumpentapothecia on branch of *Fraxinus excelsior*, Tübingen, Germany (*Cenangiaceae*, *Helotiales*). **e** *Propolis farinosa*, erumpent apothecia on branch of Populus sp., Peddocks Island, Boston Harbor Islands, Massachusets, USA (*Marthamycetaceae*, *Rhytismatales*). **f** *Leotia* sp. nov., Koussoucoingou, Benin (*Leotiaceae*, *Leotiales*). **g** *Pezoloma* sp., apothecia on dead leaf of *Acer saccharinum*, New Durham, New Hampshire, USA (*Discinellaceae*, *Helotiales*). **h** *Hymenoscyphus* serotinus, on *Fagus sylvatica* twig, Kaiserslautern, Germany (*Helotiaceae*, *Helotiales*). **i** *Pezoloma* sp., transverse section of 2–4-mm wide apothecium (*Discinellaceae*, *Helotiales*). **j** *Hymenoscyphus* sp. nov., ascus p in Melzer's reagent, Caribou, Colorado. **k** *Ascocoryne* sp., asci in Melzer's reagent, World's End Peninsula, Boston Harbor Islands, Massachusets, USA (*Gelatinodiscaceae*, *Helotiales*). Scale bars: j, k = 10 µm. Photos: a, d. Hans-Oto Baral; b, c, k. Danny Haelewaters; e. Alden C. Dirks; f. Meike Piepenbring; g, i. Jason M. Karakehian; h. Petra Behrens; j. Candice C. Perrota

Type genus: ***Lecanora*** Ach., in Luyken, Tentam. Histor. Lichen. Gen. Prim. Lin. Distrib. nov., Göttingae: 90 (1809).
Type species: ***Lecanora argentata*** (Ach.) Röhl., Deutschl. Fl. (Frankfurt) 3(2): 82 (1813).

Leotiomycetes O.E. Erikss. & Winka, Myconet 1(1): 7 (1997).

Index Fungorum Registration Identifier 501,487; Fig. 10

Ascomata typically small (<2 cm) in size; often apothecial (cup-shaped), of various sizes and forms including cups to earth tongues to perithecioid apothecia, rarely naked asci developing from hyphae due to lack of ascomata (e.g. in *Thelebolales*, genus *Antarctomyces*); frequently open apothecium, closed until maturity (e.g., in *Lahmiales*, *Rhytismatales*) or permanently closed (cleistothecia) (e.g., in *Amorphothecaceae*, *Erysiphaceae*, *Myxotrichaceae*, *Pleuroascaceae*, *Rutstroemiaceae*, *Thelebolaceae*); single or multicelular ascomata when closed. Hymenium exposed or not during ascomata maturation. *asci* inoperculate, with apical ring amyloid, inamyloid, or hemiamyloid, frequently not surrounded by tissue (open apothecia); rarely splitting open at maturity. *Ascospores* frequently without ornamentation, actively (e.g. open apothecia) or passively discharged through wall disintegration (e.g. cleistothecia). *Paraphyses* produced in open apothecia and absent in cleistothecia; some lineages amenable to growth in axenic culture; common in environmental DNA samples; asexual reproduction frequent, certain taxa only known from asexual morphs; yeast forms rare.

Life modes and distribution: *Leotiomycetes* have a global distribution and are found on all continents, although historically they have been unevenly sampled (Quandt and Haelewaters 2021). There are numerous extremophiles, including psychrophiles (in *Thelebolales*; de Menezes et al. 2017; Villanueva et al. 2021). Environmental DNA studies have shown that *Leotiomycetes* are dominant in many different habitats, including arctic tundras, southern temperate forests, and peat bogs (Tedersoo et al. 2014; Lamit et al. 2017). *Helotiales* is a speciose and a diverse order with numerous ecologies including saprotrophs, plant pathogens, mycorrhizae, and endophytes (Baral et al. 2015; Ekanayaka et al. 2019; Johnston et al. 2019). *Chaetomellales*, *Lahmiales*, *Marthamycetales*, *Micraspidales*, and *Rhytismatales* are dominated by taxa growing within and fruiting on living or dead plant tissues (Quandt and Haelewaters 2021). *Leotiales* is ecologically diverse, with saprotrophic, lichenized, plant-pathogenic, and potentially mycorrhizal representatives. *Thelebolales* comprises saprotrophs, coprophiles, psychrophiles, and mammal associates including pathogens (Landvik et al. 1998; de Hoog et al. 2005; Minnis and Lindner 2013; Haelewaters et al. 2021d). *Phacidiales* includes saprotrophs and parasites of plants, fungi, and lichens (Quandt and Haelewaters 2021). *Lauriomycetales* and *Umbellidiales* are only known from asexual morphs found in leaf litter (Hernández-Restrepo et al. 2017; Barreto et al. 2023). *Medeolariales* only includes one described species that is a plant pathogen (LoBuglio and Pfister 2010).

Notes: Eriksson and Winka (1997) erected the class *Leotiomycetes* to classify ascomycetes with inoperculate asci, which include the morphological group of the inoperculate discomycetes. Eriksson (2005) excluded *Geoglossaceae* and added *Pseudeurotiaceae* to the class. Later, Wang et al. (2006) recognized the following higher taxa: *Cyttariales*, *Erysiphales*, *Helotiales*, *Rhytismatales*, *Thelebolales*, *Myxotrichaceae*, and *Pseudeurotiaceae*. Rossman et al. (2004) determined a close relationship between *Chaetomella* and *Pilidium* within *Leotiomycetes*. *Chaetomellaceae* was erected to accommodate the two genera *Chaetomella* and *Pilidium* (Baral et al. 2015) and later recognized as an ordinal-level clade by Crous et al. (2017). Using genomic data, Johnston et al. (2019) recognized *Chaetomellales*, *Helotiales*, *Leotiales*, *Marthamycetales*, *Phacidiales*, *Rhytismatales*, and *Thelebolales*. Recent ordinal-level additions include: *Lauriomycetales* (Hernández-Restrepo et al. 2017; Haelewaters et al. 2021c), *Lichinodiales* (Prieto et al. 2019), *Micraspidales* (Quijada et al. 2020), and *Umbellidiales* (Barreto et al. 2023). Haelewaters et al. (2021c) formally recognized *Cyttariales* and *Erysiphales* as family-level clades in *Helotiales*, and *Lichinodiales* as a family-level clade in *Leotiales*.

Over time, the following trends can be observed in the class: (1) in general, some genera have been studied significantly more than others. For example, the type genus *Leotia* has not received any taxonomic additions in over forty years (Otani 1982). (2) Many species and genera have frequently changed placement both among different higher taxa and between taxonomic levels (in both directions). A consequence of this has been an expansive definition of the now massive order *Helotiales*. (3) The class has been plagued by systematic inconsistencies among different studies (Quandt and Haelewaters 2021). Currently, the following orders are recognized: *Chaetomellales*, *Helotiales*, *Lahmiales*, *Lauriomycetales*, *Leotiales*, *Marthamycetales*, *Medeolariales*, *Micraspidales*, *Phacidiales*, *Rhytismatales*, *Thelebolales*, and *Umbellidiales*.

Phylogenetic relationships within *Leotiomycetes*

The classification system and taxonomy of *Leotiomycetes* were traditionally based on morphology, in particular sexual and asexual diagnostic characteristics. However, morphologically defined taxa grouped in erected genera, families, and orders are often not supported by molecular phylogenies (e.g., Quijada et al. 2018; Ekanayaka et al. 2019; Johnston et al. 2019; Haelewaters et al. 2021c; Quandt and Haelewaters 2021). In addition, even after the use of DNA characters, molecular phylogenies are often inconsistent and unresolved. The first molecular phylogenies of helotialean taxa were based on SSU and LSU (Platt and Spatafora 2000; Gernandt et al. 2001). Note that for some of the currently recognized orders, sequence data does not currently exist (*Lahmiales fide* Quandt and Haelewaters 2021) or has only been generated for ribosomal loci (*Medeolariales fide* LoBuglio and Pfister 2010). In general, limited DNA data are available for most members of the class, notably regarding type specimens.

Based on the most recent studies, current classifications recognize the following classifications and associations. The first diverging order of the class is *Lauriomycetales*, followed by *Umbellidiales* (Barreto et al. 2023). Phylogenies disagree on the relationships of other early diverging orders in the class: *Chaetomalleles*, *Leotiales*, *Marthamycetales*, *Micraspidales*, *Phacidiales*, *Rhytismatales*, and *Thelebolales*, and their respective relationships to *Helotiales* (Ekanayaka et al. 2019; Johnston et al. 2019; Haelewaters et al. 2021d; Quijada et al. 2022; Barreto et al. 2023). Historically there has been confusion about how these non-helotialean *Leotiomycetes* taxa are related to one another (Gernandt et al. 2001; Lantz et al. 2011; Quijada et al. 2018; Karakehian et al. 2019). Within *Helotiales*, 53 families were recognized by Quandt and Haelewaters (2021), and Johnston et al. (2019) recognized the discinelloid, erysiphoid, helotioid, hyaloscyphoid, mollisioid, pezizelloid, and sclerotinioid clades.

The total number of species in the class differs depending on the classification system. According to Wijayawardene et al. (2020a), *Leotiomycetes* comprises 13 orders and 52 families, for a total of 626 accepted genera and 6,453 species, with a major part of *incertae sedis* genera and species distributed in *Helotiales*. Quandt and Haelewaters (2021) synthesized the numbers of genera and species per family in the then-current classification of *Leotiomycetes* and presented 13 orders, with 43 families, 630 genera, and a total of 6,440 species. The most recent compilation of known species and genera of *Leotiomycetes* was presented by Wijayawardene et al. (2022a) and resulted in eleven orders, 55 families, 633 genera, and 6,451 species.

Type order: ***Leotiales*** Korf & Lizoň, Czech Mycol. 52(4): 256 (2001).
Type family: ***Leotiaceae*** Corda, Icon. fung. (Prague) 5: 37 (1842).
Type genus: ***Leotia*** Pers., Neues Mag. Bot.: 31 (1794).
Type species: ***Leotia lubrica*** (Scop.) Pers., Neues Mag. Bot.: 31 (1794).

Lichinomycetes V. Reeb, Lutzoni & Cl. Roux, Mol. Phylogen. Evol. 32(3): 1055 (2004).

= *Candelariomycetes* Voglmayr & Jaklitsch, in Voglmayr, Fournier & Jaklitsch, Persoonia 42: 41 (2018).

= *Coniocybomycetes* M. Prieto & Wedin, Cladistics 39(3): 305 (2013).

= *Geoglossomycetes* Zheng Wang, C.L. Schoch & Spatafora, Persoonia 22: 131 (2009).

= *Sareomycetes* Beimforde, A.R. Schmidt, Rikkinen & J.K. Mitch., Fungal Systematics and Evolution 6: 33 (2020).

= *Xylonomycetes* Gazis & P. Chaverri, in Gazis, Miądlikowska, Lutzoni, Arnold & Chaverri, Mol. Phylogen. Evol. 65(1): 301 (2012).

Index Fungorum Registration Identifier 501,488; Fig. 11

Sexual morph: *Thallus* when lichen-forming superficial on the substratum, which is usually rock or soil (rarely bark), when not lichen-forming immersed in soil, plants or insects, composed of hyphae or yeast cells. *Ascomata* apothecia, often present, solitary, round and immersed in or superficial on thallus, or on substrate surface and often stalked. *Hamathecium* composed of paraphyses. *Asci* often eight-spored, but up to multi (> 100)-spored, cylindrical to fusiform or clavate, incompletely bitunicate, often with J + staining tholus. *Ascospores* filamentous, globose, ellipsoidal or fusiform, aseptate or septate, hyaline. **Asexual morph:** coelomycetous. *Conidiomata* infrequently present, pycnidial, developing on the same thalli as the apothecia, usually immersed, globose, with a single locule, pale, ostiolate. *Conidiomata wall* not carbonized. *Conidiophores* lining the inner cavity or reduced, septate, sometimes branched. *Conidiogenous cells* phialidic, discrete, lageniform, hyaline, smooth, producing microconidia. *Conidia* hyaline, aseptate, without appendages.

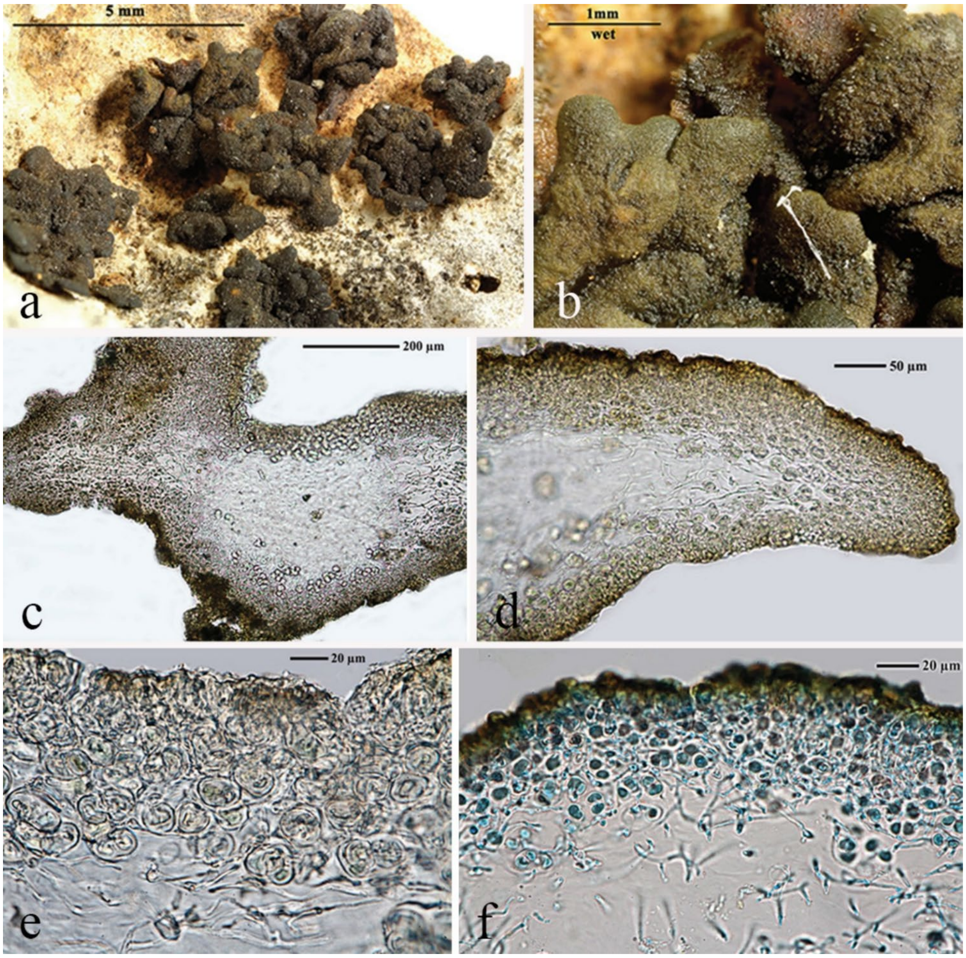


Fig. 11 *Digitothyrea polyglossa*. **a**, **b** habitus on rock. **c**–**f** sections through the thallus. Pictures by F. Schumm

Life modes and distribution: Lichen-forming with cyanobacteria or green algae, or more rarely putative mycorrhizae, endophytes, and yeast-like insect symbionts.

Notes: The class *Lichinomycetes* was until recently regarded as one of the smaller classes of the Phylum *Ascomycota,* including only some ascomycetes that are lichenized with cyanobacteria (Díaz-Escandón et al. 2022). The study by Díaz-Escandón et al. (2022) however showed that several other fungal classes with widely varying life modes cluster in the clade of *Lichinomycetes*. It regards the (former) classes *Candelariomycetes, Coniocybomycetes, Geoglossomycetes, Sareomycetes,* and *Xylonomycetes*, all of which have to be subsumed into the *Lichinomycetes* following this study.

Based on Lücking et al. (2017), Díaz-Escandón et al. (2022), and Wijayawardene et al. (2022a), the class comprises 7 orders, 13 families, around 75 genera, and around 600 species.

The members of the *Lichinomycetes* are distributed over a broad range of ecosystems. They are most conspicuous in desert ecosystems, where they cover vast areas of rock and soil. In all other ecosystems, they are present but less conspicuously. As with almost every group, they are most diverse in the tropics (Schumm and Aptroot 2023).

The main use of *Lichinomycetes* is that they are often a component of soil crusts in desert environments.

Type order: ***Lichinales*** Henssen & Büdel, in Eriksson & Hawksworth, Syst. Ascom. 5(1): 138 (1986).
Type family: ***Lichinaceae*** Nyl., Mém. Soc. Sci. nat. Cherbourg 2: 8 (1854).
Type genus: ***Lichina*** C. Agardh, Syn. Alg. Scand.: xii, 9 (1817).
Type species: ***Lichina pygmaea*** (Lightf.) C. Agardh, Syn. Alg. Scand.: xii, 9 (1817).

Orbiliomycetes O.E. Erikss. & Baral, in Eriksson, Baral, Currah & Hansen, Myconet 9: 96 (2003).

Index Fungorum Registration Identifier 501492; Fig. 12

Sexual morph: *Ascomata* solitary or aggregated, cupulate to flat or convex, sessile or sometimes distinctly stalked, erumpent or superficial, usually non-gelatinous, hyaline to bright-coloured (yellow, red, pink etc.), rarely black, exterior


a
b
c
d
e
f
g
h
i
j
k
1
2
l
1
2
3
4
m
1
2
3
4
5
6
7
8
9
10
11
12
n
1
2
3
4
5
6
7

◀ **Fig. 12** Macro- and micromorphological characteristics of *Orbiliomycetes*. **a–j** Apothecia; a *Hyalorbilia inflatula*. **b** *Orbilia claviliformis*. **c** *Lilapila oculisporella*. **d** *Orbilia mirabilis*. **e** *O. patellarioides*. **f** *O. orientalis*. **g** *O. rubrovacuolata*. **h** *O. xanthostigma*. **i** *O. fimbriata*. **j** *O. crenatomarginata*; **k** Asci; **k$_1$** *Lecophagus ellipsoideus*. **k$_2$** *O. multiaustraliensis*; **l** Paraphyses; **l$_1$** *O. sarothamni*. **l$_2$** *O. carpoboloides*. **l$_3$** *O. eucalypti*. **l$_4$** *O. amarilla*; **m.** Ascospores; **m$_1$** *Lilapila oculispora*. **m$_2$** *O. subsphaerospora*. **m$_3$** *Amphosoma resinicola*. **m$_4$** *Hyalorbilia fusispora*. **m$_5$** *O. flavida*. **m$_6$** *O. cercidicola*. **m$_7$** *O. xanthoguttulata*. **m$_8$** *O. menageshae*. **m$_9$** *O. carpoboloides*. **m$_{10}$** *O. bicknellensis*. **m$_{11}$** *O. myriomuscula*. **m$_{12}$** *O. subaristata*; **n** Conidia; **n$_1$** *O. fissilis*. **n$_2$** *O. aprilis*. **n$_3$** *O. auricolor*. **n$_4$** *O. subvinosa*. **n$_5$** *O. eucalypti*. **n$_6$** *O. patellarioides*. **n$_7$** *Hyalorbilia inflatula*

smooth or with short to long, thin-to thick-walled hairs or glassy processes that are frequently agglutinated as teeth. *Ectal excipulum* composed of hyaline isodiametric to prismatic cells. *Medullary excipulum* of hyaline intricate to isodiametric texture. *Hamathecium* composed of paraphyses that are septate, apically uninflated to inflated (knob-shaped to spathulate or lanceolate), often covered by exudate, with anastomoses at the base, branched below or also above. *Vacuolar bodies* and *cytoplasmic bodies* typical of various species. *Asci* arising from croziers or usually from simple septa with often bifurcate base, 8–128-spored with often some of the spores inversely oriented, ± cylindrical in the region of pars sporifera, unitunicate, forcibly ejecting ascospores as a single compact entity, inamyloid, apex of dead asci hemispherical to truncate (saddle-shaped), thin- or thick-walled, without apical ring. *Ascospores* variously shaped, mostly aseptate, hyaline, smooth-walled, thin-walled, mostly with one or sometimes several globose to lens-shaped or tear-shaped to filiform spore bodies which are often associated with some lipid bodies. **Asexual morph:** hyphomycetous; *Conidiomata* solitary, sometimes sporodochial or synnematal. *Setae* lacking. *Conidiophores* macronematous to micronematous, mononematous, scattered or gregarious, hyaline, straight, septate, unbranched or branched, smooth-walled. *Conidiogenous cells* monoblastic, terminal, proliferating sympodially, rarely synchronously, conidial secession schizolytic. *Conidia* solitary, acrogenous, hyaline, thin-walled, smooth, aseptate to multiseptate, unbranched (obovoid, fusiform, cylindrical, falcate, sometimes with protuberances) or variously branched, truncate at the base, eguttulate or guttulate. *Trapping organs* present in *Lecophagus*, *Hyalorbilia*, and *Orbilia* section *Arthrobotrys*: adhesive pegs capturing rotifers, peg-like knobs capturing rhizopods, adhesive knobs, columns or networks, constricting and non-constricting rings capturing nematodes or rarely arthropods.

Life modes and distribution: Members of *Orbiliomycetes* are distributed worldwide in a very broad range of ecosystems with very different climatic conditions. Numerous members are drought-tolerant and show their maximum diversity in semihumid to semiarid regions, growing on dead xeric parts of woody plants, while only a smaller part is adapted to moist to semi-aquatic habitats. Various taxa include a parasitic phase: members of *Lecophagus* are adapted to attract and exploit rotifers and some of *Hyalorbilia* prey on rhizopods, while a few closely related species of *Orbilia* section *Arthrobotrys* (*O. alba*, "*Dactylellina*" *copepodii,* "*D.*" *entomopaga*, "*D.*" *ferox*) trap and exploit different small arthropods, such as copepods, collemboles, and insects. Many members of section *Arthrobotrys* prey on nematodes and are potential agents in controlling root damage in agriculture. Very few taxa have been exclusively reported as fungicolous, e.g., *Hyalorbilia orbiliicola* growing parasitic on *Orbilia* spp. (Baral et al. 2020).

Notes: The class *Orbiliomycetes* was introduced by Eriksson and Baral in Eriksson et al. (2003) based on extraordinary morphologies and molecular data to include the family *Orbiliaceae* which has extremely increased in the past decades to around 500 species with a known teleomorph (Baral et al. 2020). The extraordinary morphology of the bilateral-symmetrical ascus apex and the living ascospores with their spore bodies were first addressed by Baral (1994). Important comprehensive works on the classification of the group were those by Boudier (1904–1910), Velenovský (1934), Svrček (1954) and Spooner (1987) for the teleomorphs. A large number of authors have worked on the predacious anamorphs of *Orbiliomycetes*, one of the most important being Drechsler (e.g., Drechsler 1937). A survey of nematode-trapping taxa was provided by Rubner (1996) and Yu et al. (2014).

Pfister (1997) and Hagedorn and Scholler (1999) were the first to apply DNA sequence-based methods to the family to connect sexually and asexually typified taxa and to suggest relationships for taxa with similar trapping devices by replacing previous concepts that were based on the different types of conidiophores and conidia.

According to Baral et al. (2020), the class currently comprises one order, one family, and ten genera. This was accepted by Wijayawardene et al. (2020a, 2022a).

One fungus one name: A large number of members of *Orbiliomycetes* have been reported as pleomorphic taxa, and numerous genera have been recognized to accommodate them based on the different types of conidiophores and conidia (Baral et al. 2018). About 15 of these genera have been accepted prior to the new rules of adopting only one name for one taxon. Different opinions exist about the circumscription of a genus. Baral et al. (2020) proposed a rather wide concept by recognizing a very large genus *Orbilia*.

Type order: ***Orbiliales*** Baral, O.E. Erikss., G. Marson & E. Weber, in Eriksson, Baral, Currah & Hansen, Myconet 9: 96 (2003).

Type family: ***Orbiliaceae*** Nannf., Nova Acta R. Soc. Scient. upsal., Ser. 4 8(no. 2): 250 (1932).
Type genus: ***Orbilia*** Fr., Fl. Scan.: 343 (1836).
Type species: ***Orbilia xanthostigma*** (Fr.) Fr. 1849 (designated by Bachman, Ann. rep. Ohio State Acad. Sci. 5(no. 2): 57. 1909); *fide* Index Fungorum (2023).

Pezizomycetes O.E. Erikss. & Winka, Myconet, 1(1): 8 (1997).

Index Fungorum Registration Identifier 501,493; Fig. 13

Sexual morph: *Ascomata* epigeous or hypogeous, of apothecia or cleistothecia types, more rarely of perithecia type, exceptionally without a complex structure, i.e. asci produced on a simple hyphal structure. Apothecia of various shape, e.g. discoid, cupuliform, pulvinulate, cerebriform, saddle-shaped, etc., stipitate or not. Cleisthotecia usually more or less spherical or potato-like. Flesh of apothecia compound with an exposed hymenium and an excipulum, the latter made of a single structure or more complex (multi-layered). Flesh of cleistothecia (also called gleba) has a differentiate hymenium or not, accompanied with sterile tissues, surrounded by a peridium. *Asci* with a single wall (unitunicate), inamyloid or amyloid (more or less diffusely in the whole length, or more strongly at the apex), operculate with an operculum placed at the top or eccentrically, or sometimes without differentiated apical structure, breaking down before maturity (prototunicate), more rarely evanescent, mainly 8-spored, sometimes 2-, 4-, 16-, 32-spored or more, with or without croziers at the base. *Ascospores* always aseptate, mainly symmetrical, smooth or variously ornamented, with or without oil drops, mainly containing 1 to 4 nuclei, hyaline, more rarely coloured. *Paraphyses* present, septate, simple or branched, sometimes anastomosing, hyaline or containing various type of granular, vacuolar or cristalloid pigments (e.g. carotenoids), sometimes also with external pigments that may form an epithecium. **Asexual morph:** Hyphomycetous, of various types, e.g. chromelosporium-like and oedocephalum-like in *Pezizaceae*, dichobotrys-like in *Pyronemataceae* and *Pyropyxidaceae*, mollardiomyces-like in *Sarcoscyphaceae*, conoplea-like in *Sarcosomataceae*, verticicladium-like in *Chorioactidaceae*, costantinella-like in *Morchellaceae*, etc. The conidia are formed blastically. Some genera are only known to be anamorphic, e.g. *Glaziella*, *Heydenia*, *Phymatotrichopsis*.

Life modes and distribution: *Pezizomycetes* are present all around the world, in a wide range of habitats, although they seem more represented in temperate and boreal zones, as well as in Mediterranean basin. They are mainly saprobic and terrestrial but can be found on other substrates such as decaying wood, dead plants or dung. Some genera are known to have species that form ectomycorrhizae (Hobbie et al. 2001; Tedersoo et al. 2006, 2010), including hypogeous members of these genera. There are also some parasitic genera or species, e.g. *Octospora* Hedw. and *Lamprospora* De Not. are bryoparasites (Döbbeler 1979; Benkert 1993), *Rhizina undulata* Fr. parasites the roots of pine trees, especially those damaged by fire (Sierota 1998; Lee et al. 2005), the asexual morph of *Caloscypha fulgens* (Pers.) Boud. — previously known under the name *Geniculodendron pyriforme* — is a seed pathogen of conifers (Salt 1974; Schröder et al. 2002), the anamorph *Phymatotrichopsis omnivora* (Shear) Hennebert is a root pathogen of dicotyledonous plants (Uppalapati et al. 2010). Some species are also known to be strictly pyrophilous, growing in postfire environments (Petersen 1970). Many of them are known to be endophytes or endolichenic fungi (Raudabaugh et al. 2020; Healy et al. 2021).

Notes: *Pezizomycetes* was introduced by Eriksson and Winka (1997). This class includes only one order, *Pezizales*, the so-called "operculate discomycetes", a group of cup-fungi distinguished from the other fleshy ascomycetes by Boudier (1885) based on the dehiscence mode of asci, i.e. presence of an operculum. This systematics was widely used during the twentieth century, until the works of Berthet (1964), Eckblad (1968) and Korf (1972) who proposed some changes based on morphological characters and nomenclatural aspects. Main changes were introduced in the molecular era with the first phylogenetic works by Gargas and Taylor (1995), Landvik et al. (1997), Norman and Egger (1999), Hansen and Pfister (2006) and Perry et al. (2007). Kirk et al. (2008) listed 16 families, 200 genera and about 1684 species. Jaklitsch et al. (2016) also listed 16 families, but 172 genera and about 1608 species, while Ekanayaka et al. (2018) listed 21 families and 218 accepted genera. During the last years, three new families were added (Kraisitudomsook et al. 2020; Van Vooren 2021; Zeng et al. 2022). There are about 235 accepted genera based on our last count.

Beyond their roles in natural ecosystems, some *Pezizomycetes* have an important economic impact on the food industry, i.e. truffles culture (Oliach et al. 2021) and wild mushrooms collecting like morels (Malone et al. 2022).

For a more detailed view of *Pezizomycetes*, see Pfister and Healy (2021).

Type order: ***Pezizales*** J. Schröt., *in* Engler & Prantl, Nat. Pflanzenfam., I: 173 (1897) [as "*Pezizineae*"].
Type family: ***Pezizaceae*** Dumort. Analyse des familles des plantes: 72 (1829).
Type genus: ***Peziza*** Dill. ex Fr., Syst. mycol. (Lundae) 2(1): 40 (1822).
Type species: ***Peziza vesiculosa*** Bull., Hist. Champ. Fr., 1(2): 270 (1790), *nom. sanct.*

Fig. 13 Macro morphologies of taxa in *Pezizomycetes*. **a** *Peziza vesiculosa*. **b** *Daleomyces brunneoviolaceus*. **c** *Cheilymenia crucipila*. **d** *Helvella monachella*. **e** *Caloscypha fulgens*. **f** *Morchella deliciosa*. **g** *Neournula pouchetii*. **h** *Ascobolus lignatilis*. **i** *Discina perlata*. **j** *Tuber melanosporum*. **k** *Scutellinia nigrohirtula*. **l** *Wilcoxina gregaria*. **m** *Genea verrucosa*. **n** *Pyronema domesticum*. **o** *Orbicula parietina*. **p** *Lamprospora leptodictya*. (All photos by N. Van Vooren, except *Orbicula parietina* with the courtesy of M. Poulain)


a
b
c
d
e
f
g
h
i
j
l
n
k
m
o
p
q
r
s
t
u
v
w
x
y
z
aa
bb
cc
dd
ee
ff
gg
hh
ii
jj
kk
ll
mm
nn
oo
pp

◂ **Fig. 14** Morphological features of different taxa in *Sordariomycetes*. **a** Stromata of *Xylaria* sp. **b** stromata of *Collodiscula* sp. **c** Stromata of *Daldinia* sp. **d** Stromata of *Xylaria bambusicola*. **e** Fruiting bodies of *Nectria pseudotrichia*. **f** Fruiting bodies of *Eutypa linearis*. **g** Stromata of *Xylaria* sp. **h** Fruiting bodies of *Astrocystis mirabilis*. **i** Longitudinal section of the fruiting bodies of *Daldinia bambusicola*. **j, k** Longitudinal section of *Eutypa linearis*. **l, m** Longitudinal section of *Arthrinium longistromum*. **n** Longitudinal section of *Leptosporella bambusae*. **o** Longitudinal section of perithecium of *Anthostomella* sp. **p** Longitudinal section of *Daldinia bambusicola*. **q** Longitudinal section of perithecium of *Lopadostoma* sp. **r** Longitudinal section of perithecium of *Fasciatispora* sp. **s** Longitudinal section of perithecium of *Nigropunctata* sp. **t** Conidia arrangement of *Pleurophragmium bambusinum*. **u** Ascus of *Reticulosphaeria* sp. **v** Ascus of *Xylaria* sp. **w** Ascus of *Fasciatispora* sp. **x** Ascus of *Pemphidium* sp. **y** Ascus of *Nigropunctata* sp. **z** Ascus of *Collodiscula* sp. **aa** Ascus of *Arecophila* sp. **bb** Ascus of *Eutypella* sp. **cc** Ascus of *Arthrinium rasikravindrae*. **dd** Ascus of *Leptosporella bambusae*. **ee** Ascospore of *Collodiscula* sp. **ff** Ascospore *Spirodecospora* sp. **gg** Ascospore *Anthostomella* sp. **hh** Ascospore *Reticulosphaeria* sp. **ii** Ascospore *Durotheca* sp. **jj** Ascospore *Pseudomassaria* sp. **kk** Ascospore of *Pleurophragmium bambusinum*. **ll** Ascospore of *Cytospora* sp. **mm** Ascospore of order *Diaporthales* sp. **nn** Ascospore of *Arthrinium* sp. **oo** Conidia of *Arthrinium yunnanum*.**pp** Ascospore of *Pustulomyces bambusicola*

Sordariomycetes O.E. Erikss. & Winka, Myconet 1(1): 10 (1997).

Index Fungorum Registration Identifier 90,350; Fig. 14

Sexual morph: *Stromata* immersed to erumpent, composed of orange, brown or black parenchymatous tissues, ascomata embedded in stromatic tissues. *Ascomata* solitary or aggregated, subglobose to cylindrical or ovoid to ellipsoidal, immersed to superficial, ostiolate, papillate or epapillate, periphysate, brown to black. *Hamathecium* composed of paraphyses or internal structures absent; centrum initially filled with a hyaline pseudoparenchyma, dissolving at maturity. *Asci* four-spored or eight-spored or multi, cylindrical to fusiform or clavate to ellipsoidal, unitunicate, deliquescent, with J-, apical ring or indistinct. *Ascospores* filamentous or ellipsoidal to fusiform, aseptate or septate, hyaline or brown or becoming dark at maturity, allantoid, clavate, cylindrical to ellipsoid, 0–3-septate, smooth-walled, with or without guttules, thick- or thin-walled, with or without apical chambers. **Asexual morph:** coelomycetous or hyphomycetous. **Coelomycetes:** *Conidiomata* acervular or pycnidial or intermediate, scattered or aggregated, immersed, globose, coriaceous, with single or multi locules, yellow or orange or dark brown to black, ostiolate or aostiolate. *Conidiomata wall* comprising thin-walled, almost hyaline to brown cells of *textura angularis*. *Conidiophores* lining the inner cavity or reduced to basal layer sometimes reduced to conidiogenous cells, occasionally, septate, branched. *Conidiogenous cells* holoblastic, enteroblastic to phialidic, discrete, lageniform, subcylindrical to cylindrical, hyaline to pale yellow, smooth, producing macroconidia and sometimes microconidia from same conidiogenous cell. *Conidia* hyaline when young, hyaline or brown to dark brown at maturity, aseptate to multiseptate, thick-walled or smooth-walled, guttulate or egutulate, with appendage or not. **Hyphomycetes:** *Conidiomata* solitary, sporodochia or synnemata. *Setae* lacking, or present occasionally. *Conidiophores* macronematous to micronematous, mononematous, scattered or gregarious, brown, straight, aseptate or septate, unbranched or branched, smooth-walled. *Conidiogenous cells* monoblastic, terminal, integrated or discrete, percurrent or proliferating sympodially. *Conidia* solitary, acrogenous, brown to dark brown, aseptate to septate, obclavate, fusiform, cylindrical, pyriform to obovoid, straight, subtruncate to obtuse at the apex, truncate or swollen at the base, with or without basal frill eguttulate or guttulate.

Life modes and distribution: The members of *Sordariomycetes* are distributed in a broad range of ecosystems (worldwide) and are reported as different life modes. Phytopathogenic members of the class are responsible for causing leaf, stem, root, and fruit diseases (e.g. *Cytospora chrysosperma*, *Coniella vitis*, *Diaporthe eres*), while some are reported as pathogenic to arthropods and mammals (e.g. *Sporothrix*, *Fusarium*). Some members are endophytes (e.g. *Pestalotiopsis*) and some are saprobic taxa that are important in decomposition and nutrient cycling (e.g. *Chaetomium*, *Neurospora*). Some taxa have been exclusively reported to be fungicolous.

Notes: The class *Sordariomycetes*, one of the largest classes of the phylum *Ascomycota* was introduced by Eriksson and Winka (1997). Nevertheless, previous exceptional studies by Barr (1983, 1987, 1990) and Eriksson and Hawksworth (1986, 1993) provided a comprehensive background for the classification of these unitunicate fungi. Classification of sexually typified genera in *Sordariomycetes* was provided along with the Phylum *Ascomycota* by Lumbsch and Huhndorf (2007, 2010).

Hyde et al. (2011) made the first attempt at compiling asexually typified genera of the kingdom *Fungi* and listed the genera and morphologically doubtful genera (like genera) according to their ‘natural classification’. After completion, Hyde et al. (2011) provided the asexually typified genera in *Sordariomycetes,* and subsequent studies by Wijayawardene et al. (2012, 2017b, 2022b) updated the lists with the notes, and Wijayawardene et al. (2021b) provided the entries for all pleomorphic genera in *Sordariomycetes*. Maharachchikumbura et al. (2015) provide the first attempts at assembling both sexually and asexually typified genera, along with morphology and DNA sequence-based phylogenies. Hongsanan et al. (2017) provided the divergence time estimates for the various orders and families in the class. Hyde et al. (2020) is the latest study that provides a comprehensive background on the taxonomy of the genera and the higher-level classification of *Sordariomycetes*.

Sordariomycetes have been recognized with six subclasses i.e. *Hypocreomycetidae*, *Sordariomycetidae* and *Xylariomycetidae* (Eriksson and Winka 1997), *Diaporthomycetidae*, *Lulworthiomycetidae* (Maharachchikumbura et al. 2016), and *Savoryellomycetidae* (Hongsanan et al. 2017).

Many members of *Sordariomycetes* have been reported as pleomorphic taxa (Kirk et al. 2008). Thus, it was proposed to adopt one name (between two generic names) when the links between the morphs are confirmed. Rossman et al. (2015b) and Réblová et al. (2016) are important publications that deal with the recent nomenclatural changes.

Type order: *Sordariales* Chadef. ex D. Hawksw. & O.E. Erikss., Syst. Ascom. 5(1): 182 (1986).
Type family: ***Sordariaceae*** G. Winter [as 'Sordarieae'], Rabenh. Krypt.-Fl., Edn 2 (Leipzig) 1.2: 162 (1885).
Type genus: *Sordaria* Ces. & De Not., Comm. Soc. crittog. Ital. 1(fasc. 4): 225 (1863).
Type species: *Sordaria fimicola* (Roberge ex Desm.) Ces. & De Not. 1863.

Xylobotryomycetes Voglmayr & Jaklitsch, Persoonia 42: 41 (2018).

Index Fungorum Registration Identifier 826,791; Fig. 15

Sexual morph: *Stromata* superficial ascomata bearing branched or unbranched. *Ascomata* perithecioid, perithecioid, subglobose to ellipsoid. *Ostiolar* canal periphysate. *Hamathecium* filiform, septate, hyaline, thin-walled, embedded in a gelatinous matrix, paraphyses. *Asci* 4–8-spored, bitunicate, fissitunicate, apex with an inamyloid apical ring. *Ascospores* ellipsoid to fusiform, 2-celled, brown, septate, with longitudinal germ slits (Voglmayr et al. 2019). **Asexual morph: Coelomycetous:** pycnidial, cylindrical, unilocular. *Conidiogenous cells* meristem, producing pigmented, septate arthroconidia. *Conidia* pigmented, septate (Voglmayr et al. 2019).

Life modes and distribution: The members of *Xylobotryomycetes* are distributed in a broad range of ecosystems viz., tropical, subtropical to warm temperate, humid areas and are reported as different life modes (Réblová and Seifert 2012; Voglmayr et al. 2019). Most of the members are saprobic.

Notes: Voglmayr et al. (2019) introduced *Xylobotryomycetes* with *Xylobotryales* based on unique morphological features and phylogeny analyses. This order contains two families, *Cirrosporiaceae* and *Xylobotryaceae* (type family) and each family has a single genus *Cirrosporium* and *Xylobotryum*, respectively. The morphology of the type genus of *Xylobotryaceae*, *Xylobotryum*, is very similar to *Xylaria* species, as they produce dark carbonaceous stromata, but *Xylobotryum* produces naked perithecia and two-celled ascospores (Trierveiler-Pereira et al. 2008). The position of *Xylobotryum* within *Ascomycota* was uncertain until Voglmayr et al. (2019) used molecular data to determine its placement. Classification of the type genus of *Cirrosporiaceae* (*Cirrosporium*) within *Eurotiomycetes*, which is close to *Mycocaliciales,* has been suggested by Réblová and Seifert (2012), which can be a new order. An extensive analysis of *Ascomycota* by Schoch et al. (2009) resolved the ancestor of the *Eurotiomycetes* and Voglmayr et al. (2019) showed that *Cirrosporium* is basal to the *Eurotiomycetes*.

Type Order: *Xylobotryales* Voglmayr & Jaklitsch, in Voglmayr, Fournier & Jaklitsch, Persoonia 42: 41 (2018).
Type Family: *Xylobotryaceae* Voglmayr & Jaklitsch, in Voglmayr, Fournier & Jaklitsch, Persoonia 42: 42 (2018).
Type Genus: *Xylobotryum* Pat., in Patouillard & Lagerheim, Bull. Herb. Boissier 3(1): 69 (1895).
Type Species: *Xylobotryum andinum* Pat., in Patouillard & Lagerheim, Bull. Herb. Boissier 3(1): 69 (1895).

Subphylum *Saccharomycotina* O.E. Erikss. & Winka, Myconet 1(1): 10 (1997).

Index Fungorum Registration Identifier 501,470.

Notes: Eriksson and Winka (1997) introduced this subphylum to accommodate a single class, *Saccharomycetes*. Groenewald et al. (2023) comprehensively addressed *Saccharomycotina* and introduced *Alloascoideomycetes*, *Dipodascomycetes*, *Lipomycetes*, *Pichiomycetes*, *Sporopachydermiomycetes* and *Trigonopsidomycetes*. Hence, the subphylum consists of seven classes.

Alloascoideomycetes M. Groenew., Hittinger, Opulente & A. Rokas Stud. Mycol. 105: 7 (2023).

Index Fungorum Registration Identifier 847278; Fig. 16a, b-d

Sexual reproduction: Firm walled *asci* are ellipsoidal to elongate and form laterally or terminally on hyphae, singly or in small whorls. Greater than eight and up to 400 *ascospores* can form in an *ascus* and released by apical deterioration. *Ascospores* are ellipsoidal but can also appear hat-shaped due to a unilateral, mucilaginous brim. **Asexual reproduction:** Colonies are cream-colored and can be dry or slimy. Budding cells, *pseudohyphae* and *true hyphae* are present or absent as species are often dimorphic, with colonies being restricted and yeast-like or expanding and hyphal. Cell division is by multilateral budding and formation of *pseudohyphae* and septate *hyphae*. Clavate *blastoconidia* of variable size form on

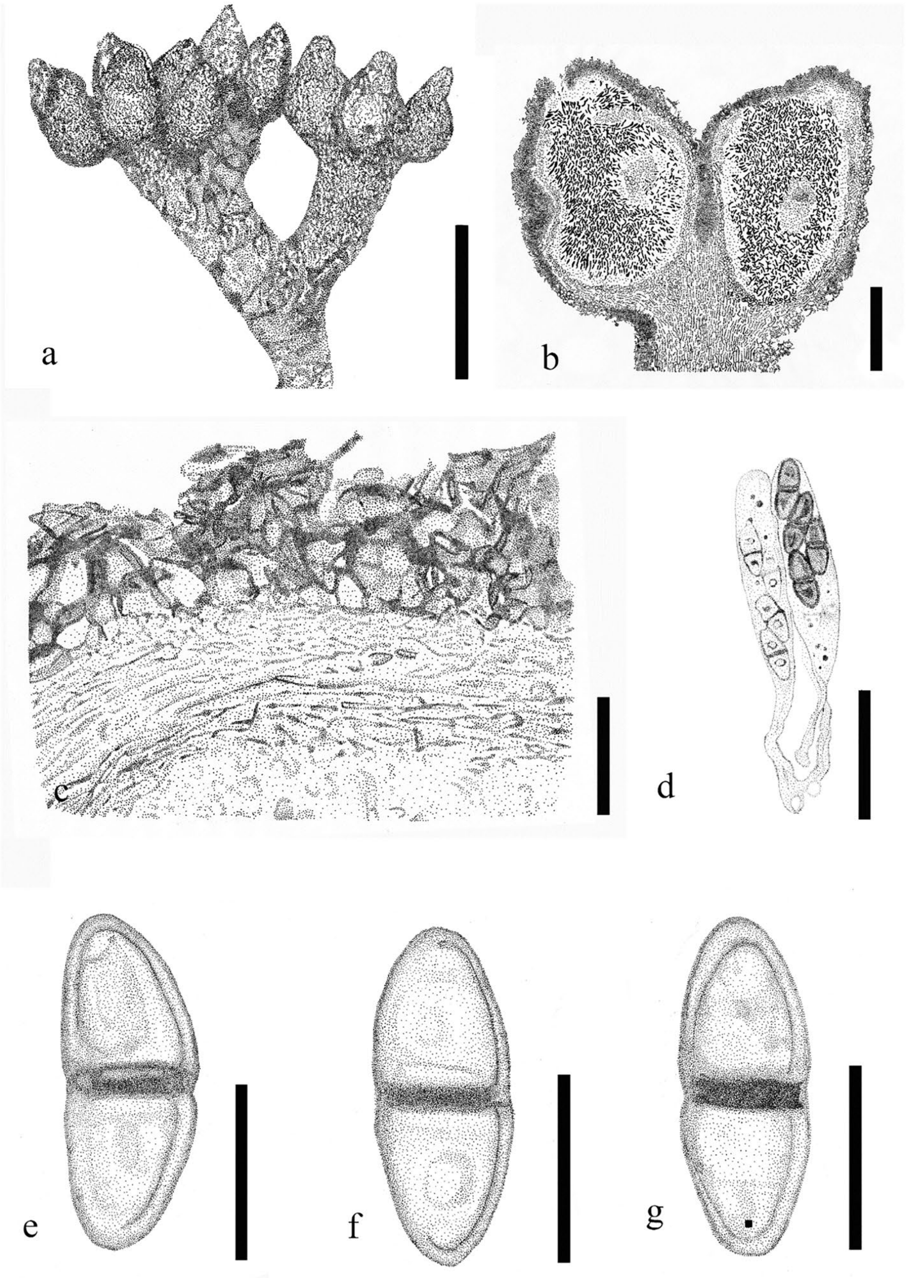
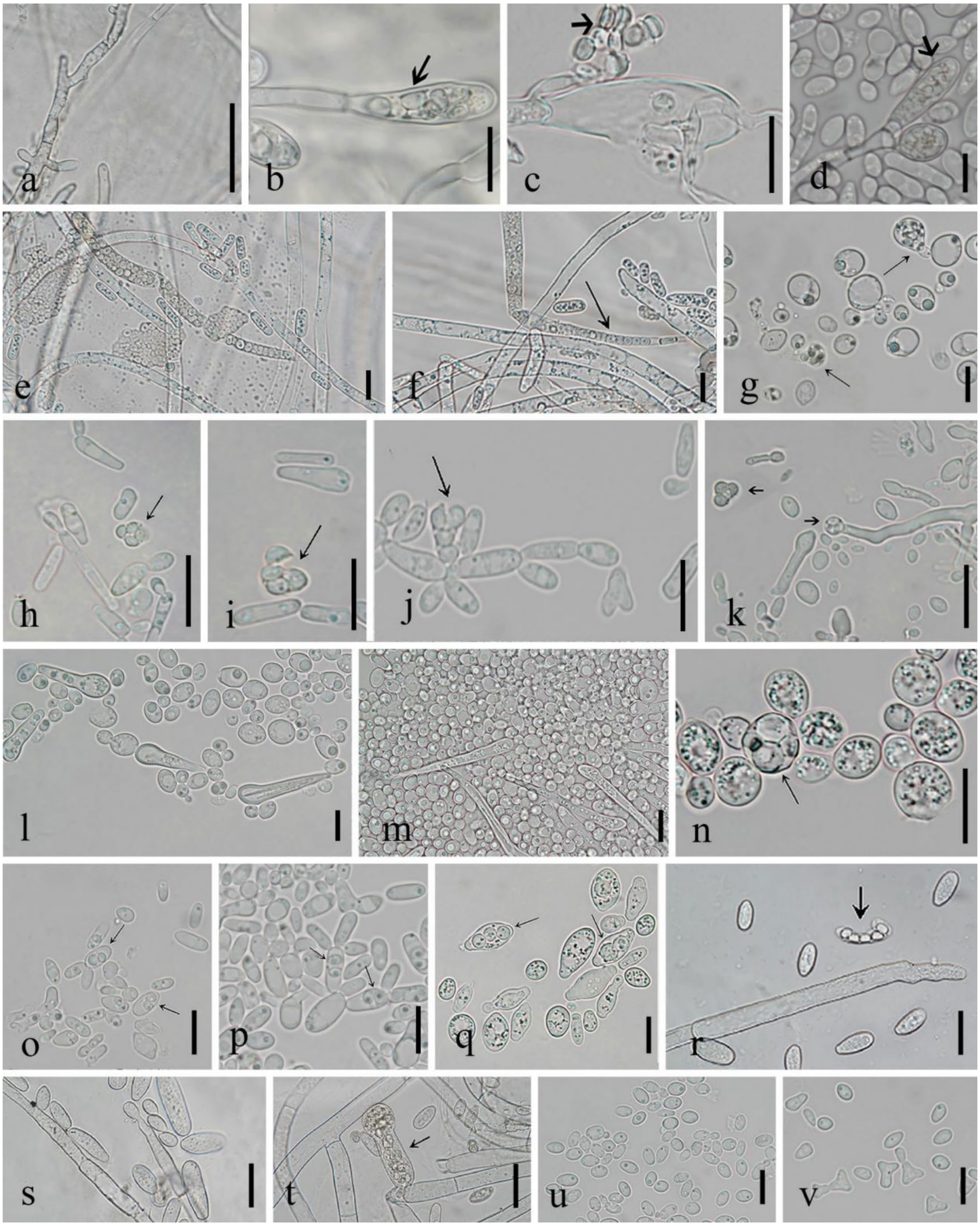


Fig. 15 *Xylobotryum andinum* (WU 39969, epitype). **a** Heads of branched stroma showing ascomata (MJF 07074). **b** Ascomata in vertical section. **c** Peridium. **d** Immature and mature asci. **e–g** Ascospores. Scale bars: **a** = 1 mm, **b** = 0.2 mm, **c**, **d** = 20 µm, **e**–**g** = 5 µm. Redrawn from Voglmayr et al. (2019)

wide *hyphae* and may be sessile or arise from denticles and occur singly or in short, branched chains. **Physiology/biochemistry:** Fermentation is absent and relatively few carbon compounds are assimilated. Urease activity is absent. The diazonium blue B reaction is negative or, rarely, weak. **Molecular analyses:** The class can be distinguished by the following molecular characteristics. Class-specific protein families OG0009556 and OG0024318 (Groenewald et al. 2023) as well as phylogenetic analyses using DNA sequences encoding LSU rDNA, SSU rDNA, *tef1-α*, *rpb1*, and *rpb2* (Kurtzman and Robnett 2013a).

Life mode and distribution: The small number of *Alloascoideomycetes* members have been primarily reported from wood, including decaying wood and oak trees (*Quercus* sp., *Fagaceae*) and on occasion associated with bark beetles (*Hylecoetus dermestoides*) and once from a larvae in West Africa (Kurtzman et al. 2011).

Notes: The class *Alloascoideomycetes* in subphylum *Saccharomycotina* was introduced by Groenewald et al. (2023), who, based on the analysis of genomic data, proposed the distribution of the yeasts assigned to *Saccharomycotina* among seven classes. They provided a diagnosis



of *Alloascoideomycetes* with class-specific orthologous groups of proteins (OGs). For more details, see the entry *Saccharomycetes*. Analysis of the two yeast DNA barcodes, LSU rDNA, SSU rDNA, and the gene sequence for the D1/D2 domain of the LSU rDNA (Kurtzman and Robnett 1998) indicated that two *Ascoidea* species, *Ascoidea africana* and *Ascoidea hylecoeti* are not closely related to *Ascoidea rubescens*. Kurtzman and Robnett (2013a) clearly divided *Ascoidea* species into two genera, *Ascoidea* and *Alloascoidea*, where the latter was included as the sole genus in the family *Alloascoideaceae*. *Alloascoidea* was found to be homothallic and produces clusters of more than eight ascospores in an ascus (Kurtzman and Robnett 2013a). Groenewald et al. (2023) is the latest study that provides a comprehensive background on the taxonomy of the higher-level classification of *Alloascoideomycetes*. Although only two species of *Alloascoidea* are presented by the class, Groenewald et al. (2023) proposed the separation of *Alloascoidea*

◂ **Fig. 16** Microscopic features of taxa in *Saccharomycotina*. **a** Septate non-sporulating hyphae and pseudohyphae of *Alloascoidea hylecoeti* (*Alloascoideaceae*, *Alloascoideales*, *Alloascoideomycetes*). **b–d** *Alloascoidea africana* (*Alloascoideaceae*, *Alloascoideales*, *Alloascoideomycetes*) asci with ascospores and released ascospores (indicated with arrows). **e, f** *Dipodascus albidus* (*Dipodascaceae*, *Dipodascales*, *Dipodascomycetes*). **e.** Ascospores within hyphae and released ascospores. **f** Hyphae, arthroconidia and ascospores (indicated by arrow). **g** *Lipomyces starkeyi* (*Lipomycetaceae*, *Lipomycetales*, *Lipomycetes*) conjugation between a cell and its bud, ascus with ellipsoidal ascospores (indicated by arrows). **h–j** *Pichia membranifaciens* (*Pichiaceae*, *Pichiales*, *Pichiomycetes*) budding cells and asci with hat-shaped ascospores (indicated by arrows). **k** *Pachysolen tannophilus* (*Pachysolenaceae*, *Alaninales*, *Pichiomycetes*) budding cells, ascus with ascospores and liberated ascospores (indicated by arrow). **l, m** *Metschnikowia bicuspidata* (*Metschnikowiaceae*, *Serinales*, *Pichiomycetes*). **l** *M. bucuspidata* var. *californica* budding cells and needle-shaped ascospores. **m** *M. bucuspidata* var. *chathamia* budding cells and needle-shaped ascospores. **n** *Saccharomyces cerevisiae* (*Saccharomycetaceae*, *Saccharomycetales*, *Saccharomycetes*) budding cells and unconjugated, persistent ascus with globose ascospores (indicated by arrow). **o, p** *Phaffomyces opuntiae* (*Phaffomycetaceae*, *Phaffomycetales*, *Saccharomycetes*). **o** Budding cells and asci with hat-shaped ascospores (indicated by arrows). **p** Budding cells in short chains and asci with hat-shaped ascospores (indicated by arrows). **q** *Saccharomycodes ludwigii* (*Saccharomycodaceae*, *Saccharomycodales*, *Saccharomycetes*) bipolar cell division of budding cells and asci with spherical ascospores (indicated by arrows). **r–t** *Ascoidea rubescens* (*Ascoideaceae*, *Ascoideales*, *Saccharomycetes*). **r** Asexual cells and cluster of ascospores (indicated by arrow) **s** Asexual cells and septate hyphae, **t** Ascus with spores in different states of nascendi. **u** *Sporopachydermia lactativora* (*Sporopachydermiaceae*, *Sporopachydermiales*, *Sporopachydermiomycetes*) budding cells. **v** *Trigonopsis variabilis* (*Trigonopsidaceae, Trigonopsidales*, *Trigonopsidomycetes*). Budding cells with ellipsoidal and triangular morphology. Triangular cells produce ellipsoidal and triangular buds. Scale bar: **a** = 5 µm, **b–q**, **u**, **v** = 10 µm, **r–t** = 30 µm

from its closest relative, *Sporopachydermia*, due to their long branches into two sister classes.

According to Groenewald et al. (2023), currently, the class comprises one order *Alloascoideales*, one family *Alloascoideaceae*, and one genus *Alloascoidea*.

Type order: ***Alloascoideales*** M. Groenew., Hittinger, Opulente & A. Rokas. Stud. Mycol. 105: 7 (2023).
Type family: ***Alloascoideaceae*** Kurtzman & Robnett, FEMS Yeast Res. 13: 429 (2013).
Type genus: ***Alloascoidea*** Kurtzman & Robnett, FEMS Yeast Res. 13: 426 (2013).
Type species: ***Alloascoidea hylecoeti*** (L.R. Batra & Francke-Grosm.) Kurtzman & Robnett, FEMS Yeast Res. 13: 427 (2013).

Dipodascomycetes M. Groenew., Hittinger, Opulente & A. Rokas, Stud. Mycol. 105: 10 (2023).

Index Fungorum Registration Identifier 847281; Fig. 16e,f

Sexual reproduction: *Ascomata* absent. *Asci* free or attached to hyphae, unconjugated or formed by isogamous or heterogamous conjugation of yeast cells or conjugation of gametangia, one- to many-spored, subspheroid ovoid, clavate, ellipsoid, cylindrical, tubular or acicular, an apical cell may be attached to it. Asci persistent, deliquescent or ascospores are liberating following rupture of the tip of the ascus. *Ascospores* hyaline or brown, spheroid, subspheroid, hemispheroid, ellipsoid, cylindrical, bacilliform, hat- or helmet-shaped, aseptate, smooth or rough, may be embedded in transparent coating material, ledge is present or absent. Species are homothallic or heterothallic. **Asexual reproduction:** White to cream coloured yeast-like or filamentous colonies. Spherical, ellipsoid, ovoid, elongated or apiculate budding cells present or absent. Two layered cell wall, holoblastic, multilateral budding or bipolar bud-fission, solitary or catenate, aseptate blastoconidia present or absent. Pseudohyphae and true hyphae present or absent. Arthroconidia present or absent. Chlamydospores rarely present. Sympodial or anneleidic conidiogenesis on undifferentiated conidiogenous cells rarely present. **Physiology/biochemistry:** Fermentation is present or absent. Nitrate assimilation is variable. The diazonium blue B reaction is negative, urease is not produced. The major ubiquinone, where known, is coenzyme Q-6 or Q-9. **Molecular analyses:** The class can be distinguished by the following molecular characteristics. Class-specific protein families OG0005588, OG0005810, and OG0006132 (Groenewald et al. 2023) as well as phylogenetic analyses using DNAsequences encoding LSU rDNA, SSU rDNA, *tef1-α*, *rpb1*, and *rpb2* (Kurtzman and Robnett 2013b).

Life mode and distribution: While some species have a restricted distribution, others occur worldwide in different terrestrial and aquatic ecosystems. Several species are associated in varying degrees with flowers, tree exudates, fruits, insects, and humans, or are saprobes in soil, rotten wood and other decaying plant materials. *Trichomonascus mycophagus* is a mycoparasite. *Magnusiomyces capitatus* is often recovered from the materials of patients (Kurtzman et al. 2011; de Hoog et al. 2020).

Notes: The class *Dipodascomycetes* in the subphylum *Saccharomycotina* was introduced by Groenewald et al. (2023), who, based on the analysis of genomic data, proposed the distribution of the yeasts assigned to *Saccharomycotina* among seven classes. They provided a diagnosis of *Dipodascomycetes* with class-specific orthologous groups of proteins (OGs). For more details, see the entry on *Saccharomycetes*. ITS rDNA phylogeny combined with nDNA/DNA reassociation data and physiological characters of ascomycete yeasts reproducing mainly by arthric conidiogenesis were used for species delimitation in *Geotrichum* and related genera by de Hoog and Smith (2004). As a result, they classified the teleomorphs of *Geotrichum* under genera *Galactomyces* and *Dipodascus* while *Magnusiomyces* with *Saprochaete* anamorphs accommodated the related group of arthroconidium forming yeasts. Several yeast species currently assigned to *Dipodascomycetes* were studied by means of multigene phylogenetic analysis by Kurtzman and Robnett (2007), who also proposed *Sugiyamaella*. Recent genome-scale phylogenetic studies (Shen et al. 2016, 2018, 2020) also included several taxa from class *Dipodascomycetes*.

According to Groenewald et al. (2023) the class currently comprises one order, *Dipodascales*, two families *Dipodascaceae* and *Trichomonascaceae* and 17 genera. The members of the class have been reported as important taxa in medical and other industries (e.g. *Galactomyces candidus*, *Magnusiomyces capitatus* and *Yarrowia lipolytica* are reported as human pathogens *fide* Groenewald et al. (2014), de Hoog et al. (2020), *Yarrowia lipolytica* and *Starmerella bombicola* have been used in food and biotechnology industries *fide* Groenewald et al. (2014), Qazi et al. (2022)).

Type order: ***Dipodascales*** M. Groenew., Hittinger, Opulente & A. Rokas, Stud. Mycol. 105: 10 (2023).
Type family: ***Dipodascaceae*** Engl. & E. Gilg, Syllabus der Pflanzenfamilien: 59. (1924).
Type genus: ***Dipodascus*** Lagerh., Jahrb. Wiss. Bot. 24: 549. (1892).
Type species: ***Dipodascus albidus*** Lagerh., Jahrb. Wiss. Bot. 24: 549. (1892).

Lipomycetes M. Groenew., Hittinger, Opulente & A. Rokas, Stud. Mycol. 105: 10 (2023).

Index Fungorum Registration Identifier 847285; Fig. 16g

Sexual reproduction: *Ascomata* absent. *Asci* unconjugated or formed by isogamous or heterogamous conjugation, or by fusion of buds of the same cell, or a bud with another cell, or by fusion of hyphal tips or by terminal and penultimate hyphal cells, one- to many-spored, globose, ellipsoid, pear shaped, saccate, tubular, cylindrical or acicular, persistent or deliquescent. *Ascospores* light brown, amber coloured or hyaline, spheroid, ellipsoid, reniform, allantoid or cymbiform, smooth walled or warty, or ornamented with longitudinal ridges. **Asexual reproduction:** Hyaline, often mucoid yeast-like or filamentous colonies. Spherical, ovoid, ellipsoid or elongated budding cells usually present. Multilateral budding. Pseudohyphae and true hyphae present or absent. **Physiology/biochemistry:** production of intracellular lipids and extracellular starch-like compounds, fermentation is absent, nitrate is not assimilated. The major ubiquinone, where known, is coenzyme Q-8, Q-9 or Q-10. **Molecular analyses:** The class can be distinguished by the following molecular characteristics. Class-specific protein families OG0010973, OG0011052, OG0008472, and OG0009553 (Groenewald et al. 2023) as well as phylogenetic analyses using either LSU rDNA or DNA sequences encoding SSU rDNA, LSU rDNA, mtSSU rDNA, and *tef1-α* (Kurtzman et al. 2007).

Life mode and distribution: The majority of the species assigned to *Lipomyces* are most frequently recovered from soil, while some of them are insect-associated or are reported from tree fluxes, wood cutting and cacti (Kurtzman et al. 2011; Yamazaki et al. 2020).

Notes: The class *Lipomycetes* in the subphylum *Saccharomycotina* was introduced by Groenewald et al. (2023) based on genomic data and diagnosed with class-specific orthologous groups of proteins (OGs). For more details, see the entry *Saccharomycetes*. Currently, *Lipomyces* and its anamorphic counterpart *Myxozyma*, *Babjevia*, *Dipodascopsis* and *Kockiozyma* are assigned to a single order and single family within the class (Groenewald et al. 2023). Based on their multigene phylogenetic analyses, Kurtzman et al. (2007) reassigned the species of *Kawasakia*, *Smithiozyma*, *Waltomyces* and *Zygozyma* to the genus *Lipomyces* and transferred *Babjevia anomala*, the single species in the genus, to *Dipodascopsis*. The genus *Lipomyces* was interpreted in a narrower sense by Jindamorakot et al. (2011, 2012) and they proposed novel monotypic genera, *Limtongia* and *Kockiozyma* for *Lipomyces* (*Zygozyma*) *smithiae* and *Lipomyces* (*Zygozyma*) *suomiensis*, respectively. Yamazaki et al. (2020) used multigene studies to investigate the relationships among lipomycetaceous yeasts and included in their analysis 14 undescribed species isolated from soil. They reinstated the genus *Babjevia* and described two novel *Babjevia* species. In addition, they described twelve anamorphic *Lipomyces* species. *Lipomyces starkeyi* was regarded as a species that can be used in biotechnology (McNeil and Stuart 2018).

Type order: ***Lipomycetales*** M. Groenew., Hittinger, Opulente & A. Rokas, Stud. Mycol. 105: 11 (2023).
Type family: ***Lipomycetaceae*** E.K. Novák & Zsolt, Acta Bot. Acad. Sci. Hung. 7: 97. (1961).
Type genus: ***Lipomyces*** Lodder & Kreger-van Rij, The Yeasts: A Taxonomic Study: 669. (1952).
Type species: ***Lipomyces starkeyi*** Lodder & Kreger-van Rij, The Yeasts: A Taxonomic Study: 669. (1952).

Pichiomycetes M. Groenew., Hittinger, Opulente & A. Rokas, Stud. Mycol. 105: 11 (2023).

Index Fungorum Registration Identifier 847268; Fig. 16h-m

Sexual reproduction: *Ascomata* absent. *Asci* unconjugated or formed after conjugation between a cell and its bud, or between independent cells. Asci may arise from conjugating haploid or from diploid cells, be formed on hyphae or a tube and may show a variety of shapes, such as globose, subglobose, lenticular, allantoid, elongate, clavate, sphaeropedunculate, or ellipsoidopedunculate. Asci persistent or deliquescent, with quick or slow spore release, thick- or thin-walled, usually contain one to four, more infrequently up to 16 ascospores. *Cephaloascus* forms erect and *Pachysolen* short tubular ascophores. *Ascospores* are spheroid, globose, ovoid, ellipsoid, hemispheroid, elongate, flattened, tapering at the ends, coiled nematode-like, hat-shaped, helmet-shaped, cap-shaped, clavate, needle-shaped, attenuated at one or both ends, occasionally swollen along one half, may contain a small oil droplet. *Ascospore* surface may be smooth, rough, or warty, with spiral ridges and may be ornamented with brims, equatorial or subequatorial ledges, membranes, be surrounded by a sheath and may or may not tend to agglutinate when released. Species are homothallic or heterothallic. **Asexual reproduction:** Cells divide by holoblastic budding, mostly multilateral on a narrow base, or bipolar on a broad or narrow base, cells occur singly, in short chains, in clusters, or may be formed at the end of a short protuberance. Cell wall is two layered. Cells may be globose, subglobose, spherical, ovoid, ellipsoid, cylindrical, elongate, ogival, apiculate, pyriform, cylindroid, lunate, triangular, or irregular and cells of *Pachysolen* may have apiculi. Pseudohyphae and branched septate or non-septate hyphae may be formed, *Metschnikowia* may form long aseptate germ tubes reminiscent of true hyphae. Hyphae of *Danielozyma* may form endoconidia, hyphal septa of *Ambrosiozyma* may have a central, plugged pore surrounded by a thickening of the wall (dolipore-like). Blastoconidia on denticles present or absent, and rarely arthroconidia may be formed. Colonies white to cream coloured, tannish-white, butyrous to hyphal, in *Kuraishia* and *Nakazawae* often mucoid due to the production of extracellular polysaccharides, with a smooth, glistening, or farinose surface. Pellicles may be formed on the surface of liquid media. *Brettanomyces*/*Dekkera* cultures grow slowly and are usually short-lived because of acetic acid production. **Physiology/biochemistry:** Fermentation of glucose and other sugars is present, weak, or absent. Xylose may be fermented, which is important for biofuel production. In *Brettanomyces/Dekkera* fermentation may be stimulated by molecular oxygen (negative Pasteur effect or Custers effect). Assimilative growth may occur with several carbohydrates, including pentoses, hexoses, disaccharides, alcohols, polyols, hexadecane, and organic acids. *Babjeviella inositovora* can utilize myo-inositol as a sole source of carbon. Nitrate assimilation is variable. Growth may require extraneous vitamins such as thiamine and biotin. Some *Ogataea* species grow at temperatures as high as 45–50 °C. The major ubiquinone, where known, is coenzyme Q-7, Q-8, and Q-9. **Molecular analyses:** The class can be distinguished by the following molecular characteristics. Class-specific protein family OG0000547 (Groenewald et al. 2023) as well as phylogenetic analyses using DNA sequences encoding LSU rDNA, SSU rDNA, *tef1-α*, *rpb1*, and *rpb2*, *ACT1*, *tef2*, Mcm7 (Kurtzman and Robnett 2013b; Daniel et al. 2014).

Life mode and distribution: Saprobic in terrestrial and aquatic habitats, may be associated with plants, animals, particularly insects, but also warm-blooded animals including humans. Few species may be pathogenic in animals, including immune-compromised humans. While some species have a restricted distribution, *Pichiomycetes* taxa are cosmopolitan in different terrestrial and aquatic ecosystems. Some species are widespread in natural and anthropogenic environments, while others are specialised (Kurtzman et al. 2011; Buzzini et al. 2017). Sugar or starch-rich environments are particularly favourable substrates. Many species are associated in varying degrees with different plant structures such as flowers, fruits, tree fluxes, phylloplane, and animals ranging from insects to humans, or are saprophytes in soil, rotten wood, and other decaying materials, while some are reported from fruiting bodies of mushrooms. They are also reported from fermented substrates with low pH, like acid beers, wine, cocoa, and coffee. Species of the genera *Komagataella, Kuraishia, Ogataea* and *Ascoidea* show an uncommon property among yeasts: the ability to grow on methanol as a sole carbon source. *Scheffersomyces*, *Spathaspora*, and *Pachysolen* ferment xylose, the major pentose of hemicellulosic plant residues, which is a possible ecological indicator of wood decomposition. Endemic species have been recognized through extensive studies on beetle associated *Metschnikowia* species, e.g. *M. borealis* in eastern North America, *M. santaceciliae* in Central America, *M. ipomoeae*, *M. lochheadii* in the Neotropics with modern introduction to Hawaii, *M. hawaiiensis* in Hawaii, *M. continentalis* and *M. cerradonensis* in South America, *M. aberdeeniae* in Africa, and *M. hibisci* in Australia. Some species are commensals in warm-blooded animals, and may have potential as opportunistic human pathogens (Inácio and Daniel 2017). *Candida albicans* is more frequently found in humans with and without signs of disease compared to other niches.

Notes: *Pichiomycetes* was introduced as one of six new classes to classify yeasts of the subphylum *Saccharomycotina* according to evolutionary divergence based on the analysis of genomic data (Groenewald et al. 2023). The diagnosis of *Pichiomycetes* was provided as a class-specific orthologous group of proteins. For more details, see the entry on *Saccharomycetes*. Following the nomenclatural requirement to use a single name for a single taxon, the genus *Candida,* originally used to group morphologically indistinguishable anascosporogenous yeast species, is to be reduced to a group typified by *C. tropicalis* and situated in the *Pichiomycetes* (Daniel et al. 2014). However, in the understanding that conclusive phylogenetic inference necessitates complete taxon sampling and genomic data, *Candida* species outside the *C. tropicalis* group and outside of *Pichiomycetes* still await their reclassification.

Members of *Pichiomycetes* are significant economically and ecologically, clinically and industrially (see Tables 12, 13, and 14 respectively for examples).

According to Groenewald et al. (2023) the class comprises the three orders *Alaninales*, *Pichiales*, *Serinales*, accommodating five families and 41 genera. The genus *Babjeviella* represents a highly divergent lineage in the class and was not assigned to a family.

Type order: ***Pichiales*** M. Groenew., Hittinger, Opulente & A. Rokas, Stud. Mycol. 105: 12 (2023).
Type family: ***Pichiaceae*** M. Groenew., Hittinger, Opulente & A. Rokas, Stud. Mycol. 105: 12 (2023).
Type genus: ***Pichia*** E.C. Hansen, Centralbl. Bakteriol. Parasitenk., 2. Abth. 12: 538. (1904).
Type species: ***Pichia membranifaciens*** (E.C. Hansen) E.C. Hansen, Centralbl. Bakteriol. Parasitenk., 2. Abth. 12: 538. (1904).

Saccharomycetes G. Winter, Rabenh. Krypt.-Fl. Ed. 2, 1(1): 32, 68. (1884) emend. M. Groenew., Hittinger, Opulente & A. Rokas, Stud. Mycol. 105: 13 (2023); Fig. 16n-t
Index Fungorum Registration Identifier 90791.

Sexual reproduction: *Ascomata* absent. *Asci* unconjugated or formed by isogamous or heterogamous conjugation, one- to many-spored, spheroid ovoid or ellipsoid, persistent or deliquescent. *Ascospores* spheroid, subspheroid, ovoid, ellipsoid, cylindroid, hat-shaped, reniform, saturn-shaped, fusiform, bacilliform or acicular, aseptate or rarely 1-septate; smooth or rough; ledges, appendages, brims and terminal extensions are present or absent. Species are homothallic or

Table 12 Economical and ecological significances of *Pichiomycetes*, examples:

Species name	Host	References
Metschnikowia spp., large-spored clade	Feces of floricolous nitidulid beetles of the genera *Conotelus* and *Prosopeus*	Lachance et al. (2011a)
Metschnikowia spp., some aquatic species	Potential pathogens in certain crustaceans	Lachance et al. (2011a)
Ogataea pini	*Dendroctonus brevicomis* (western pine beetle)	Six (2013)
Scheffersomyces (*Pichia*) *stipitis*	Beetles	Suh et al. (2003), Nardi et al. (2006)
Suhomyces spp.	Beetles including the genus *Pallodes* (*Nitidulidae*) from basidiomycete fruiting bodies	Suh et al. (2005, 2006)
Teunomyces spp.	Beetles including the genus *Pallodes* (*Nitidulidae*) from basidiomycete fruiting bodies	Suh et al. (2005, 2006)
Yamadazyma scolyti	Attraction of parasitoids and dipteran predators to their bark beetle prey	Boone et al. (2008)

Table 13 Medicinal/clinical significance of *Pichiomycetes,* examples

Species name	Human/animal	References
Candia auris	Human, soil, seawater, estuary, coastal wetlands, aquatic animals, birds, insects, plants	Du et al. (2020), Akinbobola et al. (2023), Irinyi et al. (2023)
Candida albicans	Human, soil, freshwater, seawater, plants, fruit, bird droppings, decaying organic matter	Opulente et al. (2019), Jacobsen (2023)
Candida haemulonii	Human, seawater, arthropods, plants, soft corals	Akinbobola et al. (2023), Francisco et al. (2023)
Candida parapsilosis	Human, soil, freshwater, seawater, estuary, marine invertebrates, woody debris, fruits, bird droppings	Opulente et al. (2019), Sharma and Chakrabarti (2023)
Candida tropicalis	Human, soil, freshwater, seawater, marine invertebrates, fruits, wood	Ann Chai et al. (2010), Opulente et al. (2019)
Clavispora lusitaniae (*Candida lusitaniae*)	Human, bird droppings, plants, insects	Akinbobola et al. (2023), Sharma and Chakrabarti (2023)
Pichia kudriavzevii (*Candida krusei, Issatchenkia orientalis*)	Human, soil, plants, fruits, freshwater	Douglass et al. (2018), Opulente et al. (2019)

Table 14 Industrial applications of *Pichiomycetes*

Species name	Industry	References
Brettanomyces/Dekkera spp.	Food spoilage, aroma production, kombucha, ethanol production from xylose	Steensels et al. (2015), Ojo and de Smidt (2023)
Candida maltosa	Decontamination of petroleum polluted soil	Kuznetsov and Avchieva (2002)
Candida oleophila	Postharvest biocontrol	Freimoser et al. (2019)
Candida tropicalis	Xylitol production, phenol degradation	Dias et al. (2021), Kumar et al. (2022), Umai et al. (2022)
Debaryomyces hansenii (*Candida famata*)	Cheese and meat ripening, riboflavin production	Stahmann et al. (2000), Breuer and Harms (2006)
Diutina (*Candida*) *rugosa*	Lipase production	Dave and Madamwar (2010)
Komagataella phaffii, *Komagataella* (*Pichia*) *pastoris*	Heterologous protein production	Vijayakumar and Venkataraman (2023)
Meyerozyma guilliermondii (*Candida guilliermondii, Pichia guilliermondii*)	Production of organic acids, polyalcohols, enzymes and other compounds, biocontrol	Yan et al. (2021)
Metschnikowia fructicola	Postharvest biocontrol	Freimoser et al. (2019)
Ogataea methanolica	Heterologous protein production	Cai et al. (2021)
Ogataea (*Hansenula*) *polymorpha*	Heterologous protein production	Manfrão-Netto et al. (2019)
Wickerhamomyces anomalus (*Pichia anomala*)	Biopreservation, biocontrol, sourdough	Daniel et al. (2011), Haïssam (2011), Borling Welin et al. (2015)
Pichia kluyveri	Fermented foods such as coffee beans, wine	Vicente et al. (2021)
Pichia kudriavzevii (*Candida krusei, Issatchenkia orientalis*)	Fermented foods such as cocoa, sourdough and bioethanol	Bourdichon et al. (2012), De Vuyst et al. (2016), Mukherjee et al. (2017)

heterothallic. **Asexual reproduction:** White to cream coloured, greyish or yellow yeast-like or filamentous colonies. Spherical, ellipsoid, ovoid, elongated or apiculate budding cells usually present. Two layered cell wall, holoblastic, multilateral or bipolar budding. Solitary or catenate, aseptate blastoconidia present or absent. Pseudohyphae and true hyphae present or absent. Arthroconidia rarely present. **Physiology/biochemistry**: Fermentation is present or absent. Nitrate assimilation is variable. The diazonium blue B reaction is negative, urease is not produced. The major ubiquinone, where known, is coenzyme Q-5, Q-6, Q-7, Q-8 or Q-9. **Molecular analyses**: The class can be distinguished by the class-specific protein families OG0004556 and OG0004235 (Groenewald et al. 2023).

Life mode and distribution: While some species have restricted distribution, the taxa assigned to *Saccharomycetes* are spread worldwide in different terrestrial and aquatic ecosystems (Kurtzman et al. 2011; Buzzini et al. 2017). Many species are associated with plants and inhabit, e.g. flowers and fruits, or are saprobes on decaying plant material, while some are reported from the fruiting bodies of mushrooms. *Eremothecium* species are phytopathogenic causing diseases on cotton, flax, coffee, soybean, mustard, and many other plants. They are often vectored by insects (Kurtzman and de Hoog 2011). Numerous species are saprobic in soil or dwelling in freshwater or in marine habitats. *Saccharomyces* species take an essential role in baking, brewing and winemaking. Various species are known from fermented substrates (e.g., sauerkraut and silage) thus, important in industries (Table 15). Several species, e.g. *Zygosaccharomyces* spp., may cause spoilage of foods and beverages. Some species are associated with warm-blooded animals, and a few, like *Nakazawaea glabratus* (*Candida glabrata*) are opportunistic human pathogens (Kurtzman et al. 2011). Three mycoparasitic genera *Endomyces*, *Helicogonium*, *Phialoascus* and an endoparasite of *Drosophila*, *Coccidiascus*, are tentatively assigned to *Saccharomycetes* as *Saccharomycetes incertae sedis* (Groenewald et al. 2023). Most of the species assigned to these genera have not been cultivated and sequenced yet, or if cultivated (*E. scopularum*), the identity of the strains remains to be confirmed (Suh et al. 2001).

Notes: The class *Saccharomycetes* was introduced by Winter (1884) for single-celled "plants" that multiply by budding and form endogen spores. Eriksson and Winka (1997) also proposed *Saccharomycetes* to accommodate the order *Saccharomycetales*, but it is a later homonym of Winter's class. Until recently *Saccharomycetes* has comprised all (more than 1,200) species assigned to *Saccharomycotina*. Detailed treatments of the species assigned to *Saccharomycetes* were presented in the subsequent editions of The Yeasts: A Taxonomic Study (Lodder and Kreger-van Rij 1952; Lodder 1970; Kreger-van Rij 1984; Kurtzman and Fell 1998; Kurtzman et al. 2011). Kurtzman was among the first to apply DNA sequence-based classification for *Saccharomycetes*.

Table 15 Industrial applications of *Saccharomycetes*

Species name	Industry	References
Saccharomyces cerevisiae	Baking	Lahue et al. (2020)
Saccharomyces cerevisiae	Wine	Gonzalez and Morales (2022)
Saccharomyces cerevisiae	Beverage	Niego et al. (2023)
Saccharomyces pastorianus	Brewing	Gibson et al. (2017)
Saccharomyces eubayanus	Brewing	Gibson et al. (2017)
Saccharomyces cerevisiae	Biotechnology	McCarty and Ledesma-Amaro (2019)
Kluyveromyces marxianus	Food, biotechnology	Karim et al. (2020), Karaalioğlu and Yüceer (2021)
Zygosaccharomyces spp.	Food, biotechnology	Solieri (2021)
Wickerhamomyces anomalus	Food	Karaalioğlu and Yüceer (2021), Comitini et al. (2023)
Cyberlindnera jadinii (*Candida utilis*)	Feed, SCP	Salazar-López et al. (2022)
Eremothecium spp.	Biotechnology	Zhang et al. (2022a)

Initially, he utilized rRNA coding gene sequences (Kurtzman and Robnett 1997, 1998), and later conducted multigene phylogenetic studies (Kurtzman 2003; Kurtzman and Robnett 2003, 2007, 2010; Kurtzman et al. 2007, 2008; Kurtzman and Suzuki 2010; Kurtzman and Robnett 2013a, b). In the latest decade, the classification of yeasts, including ascomycete, especially at higher ranks, has increasingly relied on genome-scale phylogenetic reconstructions (Hittinger et al. 2015; Shen et al. 2016, 2018, 2020). Based on relative evolutionary divergence (RED) analyses, Li et al. (2021a) pointed out that the subphylum *Saccharomycotina* is under-classified. Groenewald et al. (2023) proposed a new genome-informed higher-rank classification for *Saccharomycotina*. They emended the diagnosis of class *Saccharomycetes*, and reassigned numerous taxa from *Saccharomycetes* to six newly erected classes; *Alloascoideomycetes*, *Dipodascomycetes*, *Lipomycetes*, *Pichiomycetes*, *Sporopachydermiomycetes* and *Trigonopsidomycetes*. They also introduced new order(s) in each class. All classes and orders were supported by taxon-specific orthologous groups of proteins (OGs), used as diagnoses of the taxa. As summarised by Daniel et al. (2014), according to phylogenetic studies, numerous *Candida* species outside the *Lodderomyces*/*Candida* clade are affiliated with the class *Saccharomycetes* (sensu Groenewald et al. 2023). Some of them, (e.g. *C. glabrata*) have already been transferred to the corresponding teleomorph genera (Takashima and Sugita 2022), while others, (e.g. *C. adriatica*) are still awaiting reassignment.

According to Groenewald et al. (2023), the class currently comprises four orders; *Ascoideales*, *Phaffomycetales*, *Saccharomycetales* and *Saccharomycodales*, accommodating six families and 31 genera. The order *Ascoideales* comprises taxa forming expanding mycelia, while budding cells are present or absent. *Phaffomycetales* and *Saccharomycetales* are characterised by yeast cells multiplying by multilateral budding, while *Saccharomycodales* cells multiply by bipolar budding.

Type order: ***Saccharomycetales*** C. Luerssen, Grundz. Bot.: 156. 1877, emend. M. Groenew., Hittinger, Opulente & A. Rokas, Stud. Mycol. 105: 14(2023).
Type family: ***Saccharomycetaceae*** C. Luerssen, Grundz. Bot.: 160. (1877).
Type genus: ***Saccharomyces*** Meyen, Arch. Naturgesch. 4 (2): 100. (1838).
Type species: ***Saccharomyces cerevisiae*** (Desm.) Meyen, Arch. Naturgesch. 4 (2): 100. (1838).

Sporopachydermiomycetes M. Groenew., Hittinger, Opulente & A. Rokas Stud. Mycol. 105: 15 (2023); Fig. 16u

Index Fungorum Registration Identifier 847275.

Sexual reproduction: Conjugation may or may not precede ascus formation. Ascospores are spheroid, subglobose, ellipsoid, or bacilliform. One to four ascospores are formed per ascus. The ascospores usually have a thick coat of refractile material that keep them together after release from the ascus at maturity. They tend to agglutinate. **Asexual reproduction:** Cell division is by multilateral budding on a narrow base. Cells are ovoid, ellipsoid or elongate, occasionally curved and occur singly, in pairs or even in small groups. Pseudohyphae and true hyphae are not formed. **Physiology/biochemistry:** Glucose fermentation is absent or weak. Nitrate is not assimilated, myo-inositol as sole carbon source is assimilated. The major ubiquinone is coenzyme Q-9. The diazonium blue B reaction can be negative or positive. **Molecular analyses:** The class can be distinguished by the following molecular characteristics. Class-specific protein families OG0028621, OG0028581, OG0028722, and OG0028736 (Groenewald et al. 2023) as well as phylogenetic analyses using DNA sequences encoding LSU rDNA, mtSSU rDNA, and *COX II* sequences (Kurtzman and Robnett 2007).

Life mode and distribution: Cosmopolitan in distribution, on (decaying) cacti, non-cactus plant–insect interface, slimy exudates of red oaks (*Quercus rubra*, Fagaceae). A small number of *Sporopachydermiomycetes* members have primarily been reported from necrotic tissues of cacti, wood, and (sea) water (Lachance 2011b). High levels of 2-propanol and acetone are present in decaying cactus tissues. *Sporopachydermia* species can metabolise 2-propanol and acetone as carbon sources, making cactus tissues an ideal substrate.

Notes: The class *Sporopachydermiomycetes* was introduced by Groenewald et al. (2023) based on the analysis of genomic data, proposed the distribution of yeasts, assigned to *Saccharomycotina,* among seven classes. They provided a diagnosis of *Sporopachydermiomycetes,* with class specific orthologous groups of proteins (OGs). For more details see the entry *Saccharomycetes*. *Sporopachydermia* representatives form a strongly supported monophyletic clade as per LSU, MtSm and COXII analyses (Kurtzman and Robnett 2007). Although the number of species validly described in this class is limited, Lachance (2011b) has listed a fair number of species with strong affinity to the genus *Sporopachydermia,* that are awaiting formal descriptions. The distribution of those phylotypes is highly influenced by geography and less so by host-plant association (Lachance 2011b). Groenewald et al. (2023) is the latest study that provides a comprehensive background on the taxonomy of the higher-level classification of *Sporopachydermiomycetes*. Several phylogenetic studies found that the *Sporopachydermia* clade is situated on a long branch as a sister clade to *Alloascoidea*, indicating substantial evolutionary divergence (Lachance 2011b; Kurtzman and Robnett 2013a,b; Groenewald et al. 2023). Although a limited number of *Sporopachydermia* species are presented by the class *Sporopachydermiomycetes*, Groenewald et al. (2023) propose the separation of *Sporopachydermia* and its sister genus into two sister classes, *Sporopachydermiomycetes* and *Alloascoideomycetes*, respectively, due to their long branches.

Type order: ***Sporopachydermiales*** M. Groenew., Hittinger, Opulente & A. Rokas. Stud. Mycol. 105: 15 (2023).
Type family: ***Sporopachydermiaceae*** M. Groenew., Hittinger, Opulente & A. Rokas. Stud. Mycol. 105: 15 (2023).
Type genus: ***Sporopachydermia*** Rodr. Mir., Antonie van Leeuwenhoek 44: 440 (1978).
Type species: ***Sporopachydermia lactativora*** Rodr. Mir., Antonie van Leeuwenhoek 44: 440 (1978).

Trigonopsidomycetes M. Groenew., Hittinger, Opulente & A. Rokas Stud. Mycol. 105: 16 (2023).

Index Fungorum Registration Identifier 847283; Fig. 16v

Sexual reproduction: *Ascospores* are helical or lunate with tapering ends and arise in a bud formed by cells following isogamous conjugation. One to four *ascospores* are formed per *ascus*. Conjugation may or may not precede ascus formation. **Asexual reproduction:** The cells are either relatively small, ovoid to short cylindroid occur singly, in pairs and sometimes in short chains, or they can be arranged in thalli with a T-shaped cell. No *pseudohyphae* or *true hyphae* are produced. **Physiology/biochemistry:** Usually a narrow range of sugars are assimilated, absence of growth on nitrate as sole nitrogen source. Most simple carboxylic acids commonly tested are utilized. Only glucose can be fermented and only by some members. The major ubiquinone, where known, is coenzyme Q-9. The diazonium blue B reaction is negative. Some members can utilize 1-butanol as sole carbon source and produce extracellular proteases. **Molecular analyses:** The class can be distinguished by the following molecular characteristics. Class-specific protein families OG0008190 and OG0008482 (Groenewald et al. 2023) as well as phylogenetic analyses using DNA sequences encoding LSU rDNA, mtSSU-rDNA, and *COX II* (Kurtzman and Robnett 2007, 2013b; Lachance and Kurtzman 2013).

Life mode and distribution: Members of *Trigonopsidomycetes* have a relatively wide host range (Kerrigan and Smith 2001; Kurtzman 2011; Lachance and Kurtzman 2013). They can be found in alcoholic beverages such as wine and beer, grapes and vineyards, necrotic tissue of cactus and other plants, trees, from free-living nematodes, and wood-boring beetle galleries. Many are associated with grape must, especially the *Trigonopsis* members, suggesting that *Trigonopsis* may have a distinct ecological niche that is linked to grapes. It is frequently associated with necrotic tissue of primarily cactus, although the genus *Tortisopra* has been identified in other plants as well, most likely due to its ability to produce extracellular proteases that solubilize casein. Members of this class, particularly *Botryozyma*, have the ability to adhere to the cuticle of nematodes due to the presence of distinct T-shaped cells. Some members of this class are found in nematodes associated with beetles, and the yeast appears to have a commensal relationship, taking nutrition from the nematodes (Kerrigan and Smith 2001).

Notes: The class *Trigonopsidomycetes* in the subphylum *Saccharomycotina* was introduced by Groenewald et al. (2023), who, based on the analysis of genomic data, proposed the distribution of the yeasts assigned to *Saccharomycotina* among seven classes. They provided a diagnosis of *Trigonopsidomycetes* with class-specific orthologous groups of proteins (OGs) (for more details see the entry

Saccharomycetes). Members of the *Trigonopsidales* form a mildly supported monophyletic clade as per LSU, MtSm and COXII sequence analyses (Kurtzman and Robnett 2007, 2013b; Lachance and Kurtzman 2013) and the phylogenomic analyses done by Shen et al. (2018). Groenewald et al. (2023) is the latest study that provides a comprehensive background on the taxonomy of the higher-level classification of *Trigonopsidales*. Phylogenetic analysis of D1/D2 LSU rRNA gene sequences demonstrated that the two described species of *Botryozyma* are quite closely related to one another as well as to the two known species of *Ascobotryozyma* (Kerrigan and Smith 2001), and thus represent a single genus in the new single nomenclature system. The Melbourne Code assigns equal weight to anamorphic and teleomorphic genus names. Because the genus *Botryozyma* (1992) has priority of date over *Ascobotryozyma* (2001), Lachance and Kurtzman (2013) propose assigning the species of this clade to the genus *Botryozyma*. Considering the exceptional early divergence of the basal branching point marking this order, additional data may eventually support the division of this new order. However, due to the lack of additional species, Groenewald et al. (2023) have decided to combine the genera *Trigonopsis*, *Tortispora*, and *Botryozyma* into one order, while acknowledging that future descriptions of more species in this group may lead to the split of *Tortispora* and *Botryozyma* from *Trigonopsis* into a separate class.

The economic and ecological significance of members of this class is unknown, as is whether they have any application in the medical/clinical field. However, the ability of *Trigonopsis variabilis* to produce D-amino acid oxidases that catalyse the oxidative deamination of α-amino acids to α-keto acids and ammonia (Kurtzman 2011) is of great importance to the pharmaceutical industry. Other uses for this enzyme include the synthesis of chiral intermediates to produce antihypertensive drugs (Patel 2001) and the conversion of cephalosporin C to 7-amino cephalosporanic acid, which is a key intermediate for cephem antibiotics (Dib and Nidetzky 2008).

According to Groenewald et al. (2023), currently, the class comprises one order *Trigonopsidales*, one family *Trigonopsidaceae* and three genera (*Botryozyma*, *Tortispora* and *Trigonopsis*).

Type order: ***Trigonopsidales*** M. Groenew., Hittinger, Opulente & A. Rokas. Stud. Mycol. 105: 16 (2023).
Type family: ***Trigonopsidaceae*** Lachance & Kurtzman, Int. J. Syst. Evol. Microbiol. 63: 3113 (2013).
Type genus: ***Trigonopsis*** Schachner, Z. Ges. Brauwesen 52: 137 (1929).
Type species: ***Trigonopsis variabilis*** Schachner, Z. Ges. Brauwesen 52: 137 (1929).

Subphylum *Taphrinomycotina* O.E. Erikss. & Winka, Myconet 1(1): 11 (1997).

Index Fungorum Registration Identifier 501471.

Notes: Eriksson and Winka (1997) introduced *Taphrinomycotina* to accommodate *Neolectomycetes*, *Pneumocystomycetes* (as *Pneumocystidomycetes*), *Schizosaccharomycetes* and *Taphrinomycetes*. Rosling et al. (2011) and Čadež et al. (2021) introduced *Archaeorhizomycetes* and *Novakomycetes* respectively thus *Taphrinomycotina* comprises six classes.

Archaeorhizomycetes Rosling & T.Y. James, Science, N.Y. 333(no. 876): 879 (2011).

Index Fungorum Registration Identifier 561762.

Morphology: The life cycle of *Archaeorhizomycetes* is still poorly understood, and no sexual reproductive structures have yet been observed. In culture on MMN medium, the growth edges in both *Archaeorhizomyces borealis* and *A. finlayi* are characterised by thin (0.2–2 µm in diameter) hyphae. Pale aerial hyphae are produced in the older parts of the colonies (Fig. 17) (Rosling et al. 2011; Menkis et al. 2014). *Archaeorhizomyces finlayi* grows faster in culture than *A. borealis* (Menkis et al. 2014). In *A. finlayi*, the grouping of thin hyphae into chord-like bundles is common, a growth that is not observed in *A. borealis* (Fig. 17b). Based on TEM, both species form simple septa lacking pores, and some of the hyphal cell-walls are double layered and ca. 150–200 nm thick (Rosling et al. 2011; Menkis et al. 2014; Fig. 17c,e,f). In culture, *A. finlayi* hyphae are extensively coated by extracellular materials (Rosling et al. 2011), and the hyphal surface appears rough both in SEM and TEM (Fig. 17c). The hyphal cells have one or two nuclei (Fig. 18). Both species produce chlamydospore-like swellings in the older parts of the colony (Fig. 17). The swellings are larger and more numerous in *A. borealis* than in *A. finlayi* (Rosling et al. 2011; Menkis et al. 2014; Fig. 17). The large and old swellings are thick-walled, and the cell-wall is multi-layered (Fig. 17). They can contain multiple nuclei (Menkis et al. 2014) (Fig. 18j-l). In addition to the large swellings, smaller terminal and intercalary swellings are produced in both species, delimited by septa (Fig. 17,18). *A. borealis* has more swellings and a broader variation in colony morphology than *A. finlayi*. In addition, these swollen cells can be devoid of nuclei (Fig. 18b-c). Menkis et al. (2014) observed that *A. borealis* grows as yeast on b-cyclodextrin amended medium.

Life modes and distribution: Environmental DNA (eDNA) sequences taxonomically assigned to *Archaeorhizomycetes* are frequently observed in samples of soil from forest and woodland habitats. Interestingly, the class was underrepresented across root and rhizosphere samples suggesting a weak association with plants at the class level. Individual

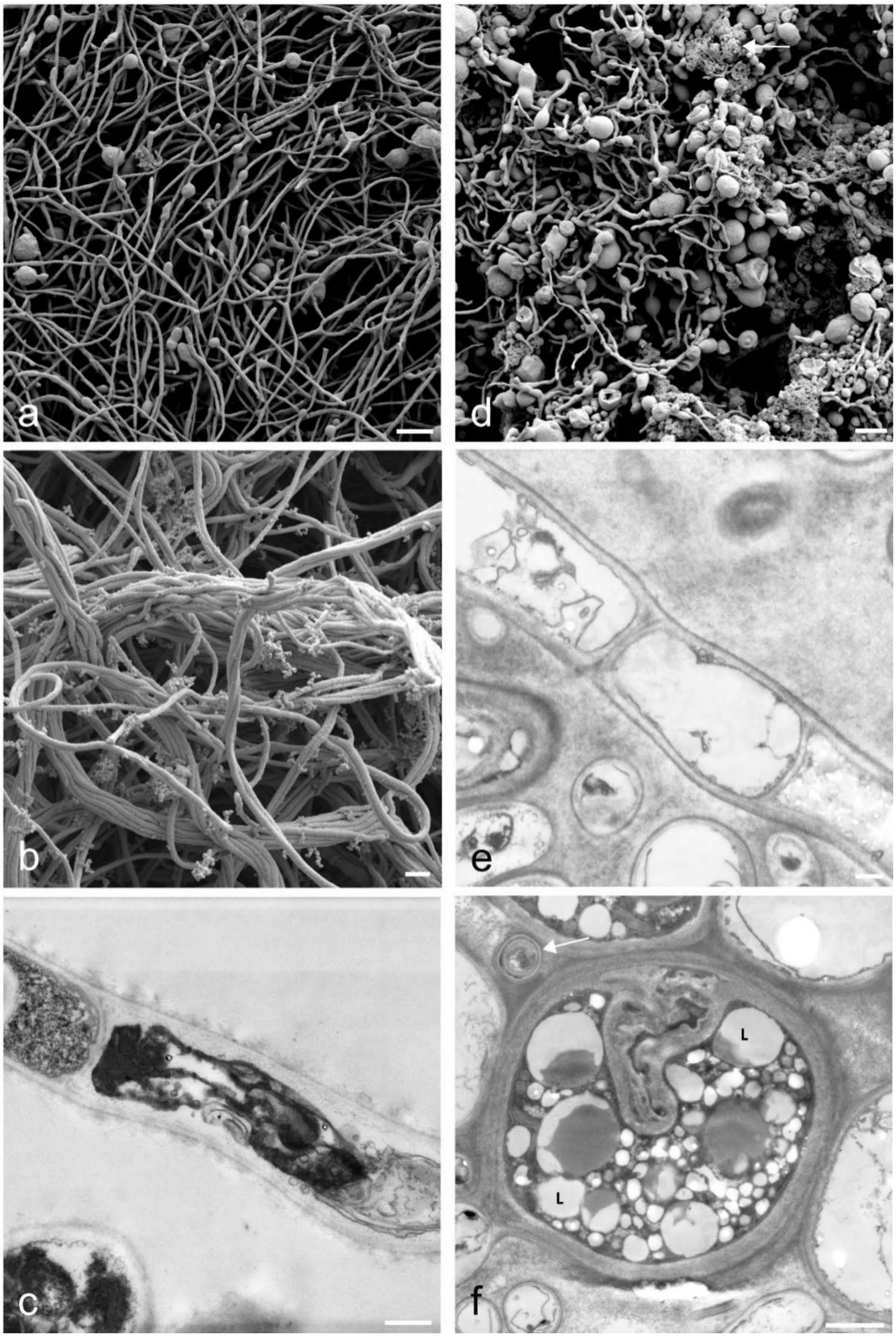
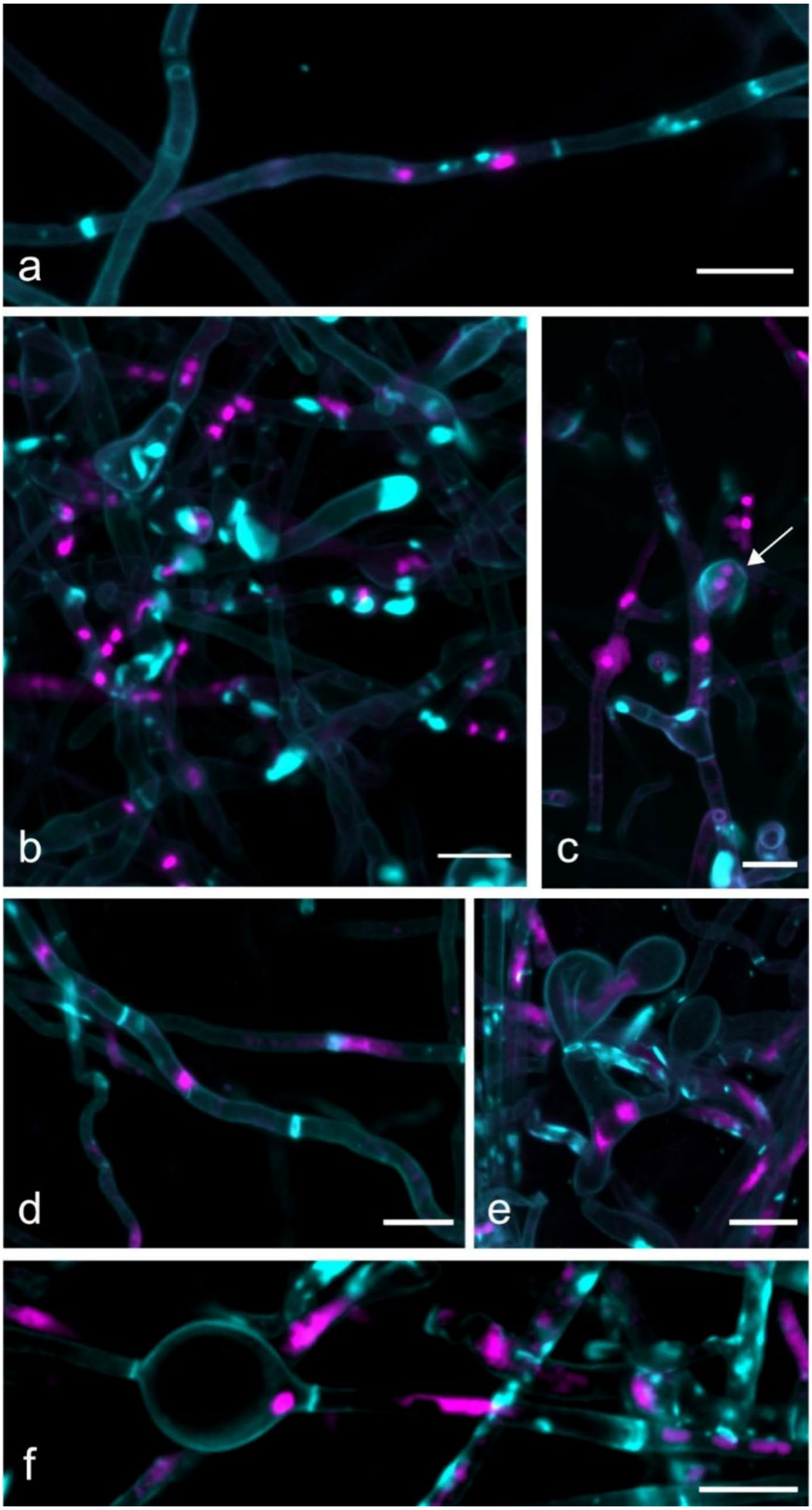


Fig. 17 SEM and TEM images of *Archaeorhizomyces finlayi* and *A. borealis* grown on MMN. **a** Terminal and intercalary swellings and hyphae of *Archaeorhizomyces finlayi*. **b** Chordlike hyphal bundles typical for *Archaeorhizomyces finlayi*. **c** *Archaeorhizomyces finlayi* hyphae with simple septa and uneven hyphal surface. **d** Terminal and intercalary swellings in *Archaeorhizomyces borealis* covered by the extracellular material (arrow). **e** *Archaeorhizomyces borealis* hyphae with simple septa without pores. **f** *Archaeorhizomyces borealis* hyphae with double cell-wall (arrow) and swellings with lipid-like bodies (L). Scale 1 µm. Scale bars **a**, **d**= 10 µm, b=3 µm, **d**, **e**= 300 nm

taxa in the class may, of course, respond differently, as suggested by the two described species that were both cultured from roots. Further, an eDNA metabarcoding of pot cultures with *Arabidopsis* found that three *Archaeorhizomycetes* OTUs had the highest relative abundance in the rhizosphere compared to endosphere and bulk soil samples (Urbina et al. 2018). Based on the two described species that have been studied in culture it is known that while associated with roots these fungi do not form characteristic mycorrhizal structures but can colonize roots without causing harm to the roots (Rosling et al. 2011). Further, the two described species have broad saprotrophic potential, as indicated by their ability to grow on a range of complex carbon sources, with a predominant occurrence in the rhizosphere soil (Menkis et al. 2014). These growth patterns are consistent with sequences from the class being more frequently observed in soil samples

Fig. 18 Confocal laser scanning images of *Archaeorhizomyces finlayi* and *A. borealis*. Calcofluor white stained septa and cell walls (cyan) and propidium iodine stained of nuclei (magenta) (**a** *A. finlayi* hyphae with two nuclei per cell. **b** Swollen hyphae of *A. finlayi* with often two nuclei per cell. Notice that some of the swollen cells are empty of nuclei. **c** Swollen hyphae of *A. finlayi* with a small intercalary swelling (arrow) with two nuclei. **d** *A. borealis* hyphae with one nucleus. **e** Multiple consecutive swellings in *A. borealis* hyphae with one or two nuclei. **f** Intercalary *A. borealis* swelling with one nucleus). Scale bars **a**–**f** = 5 µm



compared to other types of samples. It is likely that many taxa in *Archaeorhizomycetes* are free-living soil fungi and that species display different degrees of root association.

Archaeorhizomycetes is globally distributed, i.e., sequences taxonomically assigned to the class have been detected in 18% of all samples currently contained in the globalfungi.com database and include records from all continents (Větrovský et al. 2020) and sequences of *Archaeorhizomycetes* are frequently observed in environmental soil and root samples (Schadt et al. 2003; Porter et al. 2008; Rosling et al. 2011, 2013). Based on sequence similarity and clustering of published eDNA amplicon sequences, the class has been estimated to comprise at least 500 species (Menkis et al. 2014). However, estimating species richness from eDNA metabarcoding data is not trivial and global richness estimates based on clustering at 98.5% of environmental sequences available as Short Read Archive data has suggested that *Archaeorhizomycetes* may encompass as many as 16,231 taxa (Hawksworth and Lücking 2017). The authors emphasise that the latter number is likely inflated by a combination of sequencing errors and artifacts of the clustering method. More moderate estimates include the gbif.org database, which currently includes 17,131 occurrences and 767 species hypotheses for *Archaeorhizomycetes*. The curated fungal sequence database UNITE (version 9.0, Nilsson et al. 2018) currently has 765 species hypotheses classified in the class *Archaeorhizomycetes*, based on its 1.5% sequence dissimilarity threshold. Of these, 126 are also recovered in the globalfungi.com database, which currently includes fungal eDNA amplicon data from 515 studies (Větrovský et al. 2020). Local species richness can be high, with records of 278 *Archaeorhizomyces* hypothesised species in an alpine habitat (Pinto-Figueroa et al. 2019), 80 species recovered in a subtropical evergreen shrub bog (Tian et al. 2021) and 68 hypothesised species detected in a Swedish boreal forest site (Kalsoom Khan et al. 2020). Irrespective of the actual species richness, the two species that have been cultured, formally described, and named, *Archaeorhizomyces borealis* Menkis et al. and *Archaeorhizomyces finlayi* Rosling & T. James, certainly represent only a fraction of the true diversity in the class. Despite repeated efforts, no additional species have been successfully captured in pure culture, but two additional species, *A. secundus* and *A. victor*, have been proposed based on phylogenetic and ecological evidence from eDNA amplicon data (Kalsoom Khan et al. 2020).

Type order: ***Archaeorhizomycetales*** Rosling & T.Y. James, Science, N.Y. 333(no. 876): 879 (2011).
Type family: ***Archaeorhizomycetaceae*** Rosling & T.Y. James, Science, N.Y. 333(no. 876): 879 (2011).
Type genus: ***Archaeorhizomyces*** Rosling & T.Y. James, Science, N.Y. 333(no. 876): 879 (2011).
Type species: ***Archaeorhizomyces finlayi*** Rosling & T.Y. James, Science, N.Y. 333(no. 876): 879 (2011).

Neolectomycetes O.E. Erikss. & Winka, Myconet 1(1): 8 (1997).

Index Fungorum Registration Identifier 90270; Fig. 19

Ascomata long, irregularly clavate, lanceolate or spathulate and consisting of a sterile zone at the bottom and a fertile zone (hymenium) on the top, yellow to bright yellowish, smooth, irregularly lobate. *Asci* cylindrical to cylindrical-clavate, 8-spored. *Paraphyses* absent. *Ascospores* uniseriate, unicellular, 5.5–8 × 3–4 µm, reniform, ellipsoid or ovoid, hyaline, smooth (Claudiu Chinan and Hewitt 2012).

Life mode and distribution: Associated with rootlets of conifers. Distribution is cosmopolitan.

Notes: Eriksson and Winka (1997) introduced this class to accommodate *Neolecta* Speg., typified by *Neolecta flavovirescens* Speg. Currently, the class comprises a single order, a family and a genus. Index Fungorum (2023) has listed four epithets (accession date: 29.06. 2023). However, Landvik et al. (2001) have accepted only two species (viz*., N. vitellina* (Bres.) Korf & J.K. Rogers 1971 and *N. irregularis* (Peck) Korf & J.K. Rogers 1971) except the type species.

The placement of *Neolecta* has been problematic for the last three decades. Based on *RPB2* sequence data, Liu et al. (1999) showed that *Neolecta vitellina* can be accommodated in the basal lineage of the *Ascomycota,* sister to *Schizosaccharomyces pombe* Lindner. Furthermore, Liu et al. (1999) stated that ‘the ancestral ascomycetes may have been filamentous fungi with a sexual phase that produced a fruiting body’. The clade in which both taxa resided was named ‘Archiascomycetes’ but this was not a proper rank (See editorial comment in the Index Fungorum 2023). Landvick et al. (2001), however, showed that *Neolecta* is phylogenetically close to yeast taxa in *Saccharomycotina* and *Taphrinomycotina*. Schoch et al. (2009) confirmed the placement of *Neolecta* in *Taphrinomycotina.*

Type order: ***Neolectales*** Landvik, O.E. Erikss., Gargas & P. Gust., Syst. Ascom. 11: 107–118 (1993).
Type family: ***Neolectaceae*** Redhead, Can. J. Bot. 55: 305 (1977).
Type genus: ***Neolecta*** Speg., Anal. Soc. cient. argent. 12(5): 218 (1881).
Type species: ***Neolecta flavovirescens*** Speg. [as ‘flavo-virescens’], Anal. Soc. cient. argent. 12(5): 218 (1881).

Novakomycetes Dlauchy, G. Péter & Čadež, Microorganisms 9 (2, no. 301): 14 (2021).

Index Fungorum Registration Identifier 838640; Fig. 20

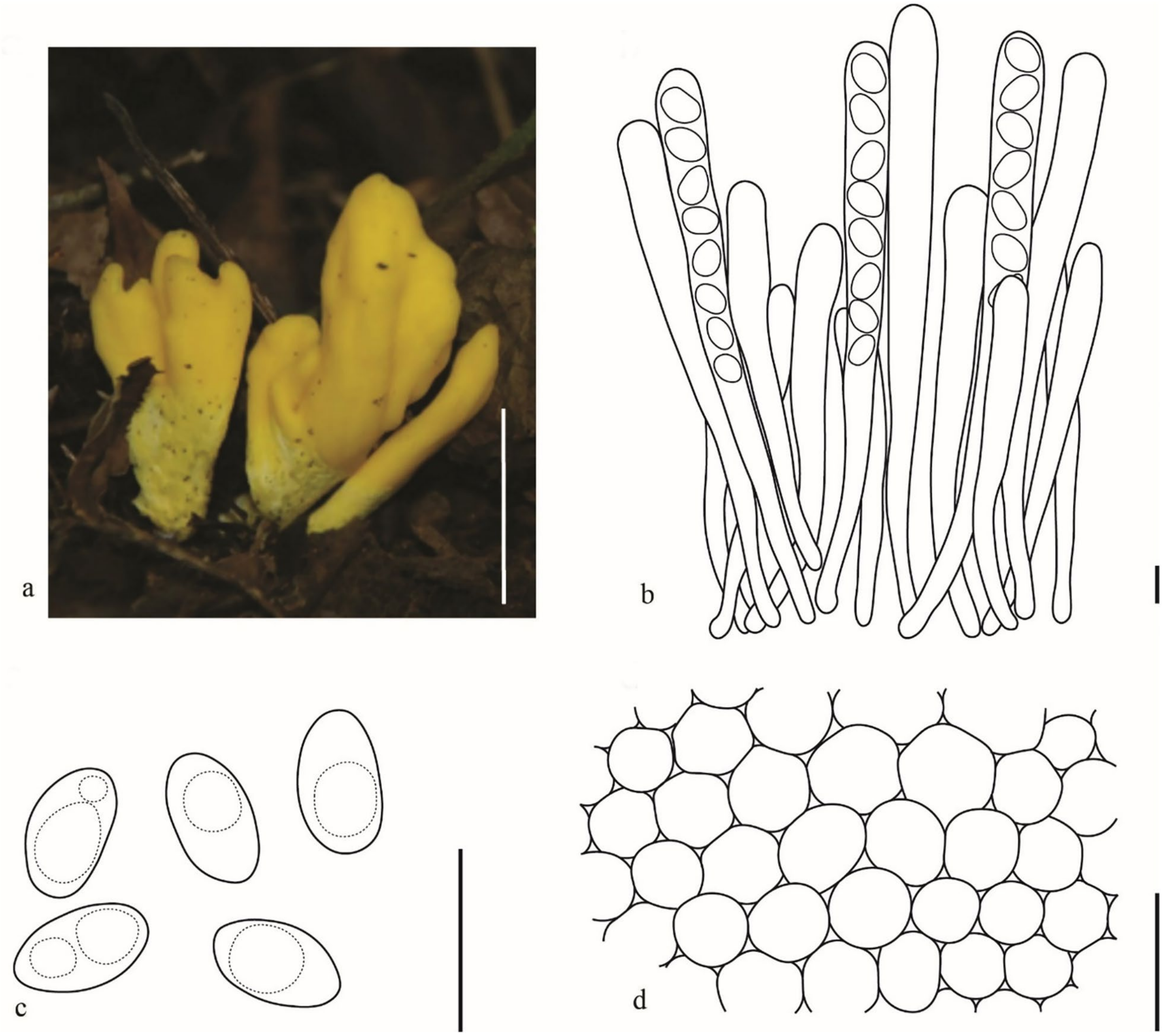


Fig. 19 *Neolecta irregularis*: **a** Ascomata. **b** Asci. **c** Ascospores. **d** Cells of stipe. Scale bars: **A** = 10 mm; **B** = 20 µm; **C**–**D** = 10 µm. (Photograph 'a' with the courtesy of Bau Tolgor. b-d was redrawn from Jin-Zhao and Tolgor 2009)

Sexual reproduction: *Ascomata* absent. *Asci* unconjugated or formed by heterogamous conjugation, one- or two-spored, ellipsoid, deliquescent. *Ascospores* subspheroid or ellipsoid, aseptate. **Asexual reproduction:** White to cream coloured yeast colonies formed by budding cells. Two layered cell walls, enteroblastic budding, solitary, aseptate blastoconidia. Pseudohyphae and true hyphae absent.

Life mode and distribution: Budding yeast originating from olive oil in Spain.

Notes: The class *Novakomycetes* was introduced by Čadež et al. (2021). Currently, it is the smallest among the six classes assigned to the subphylum *Taphrinomycotina* (Wijayawardene et al. 2022a). According to phylogenomic analyses, *Novakomycetes* is closely related to *Schizosaccharomycetes* comprising fission yeasts (Čadež et al. 2021). The class includes a hierarchic chain of monotypic taxa: *Novakomycetales*, *Novakomycetaceae* and *Novakomyces* erected to accommodate the species *Novakomyces olei* (Čadež et al. 2021).

The single species assigned to *Novakomycetes* is budding yeast originating from olive oil; however, it may be allochthonous in this habitat, as no additional report of its occurrence has been published (Čadež et al. 2021; Zullo and Ciafardini 2022).

Type order: ***Novakomycetales*** Dlauchy, G. Péter & Čadež, in Čadež, Dlauchy, Tome & Péter, Microorganisms 9(2, no. 301): 14 (2021).

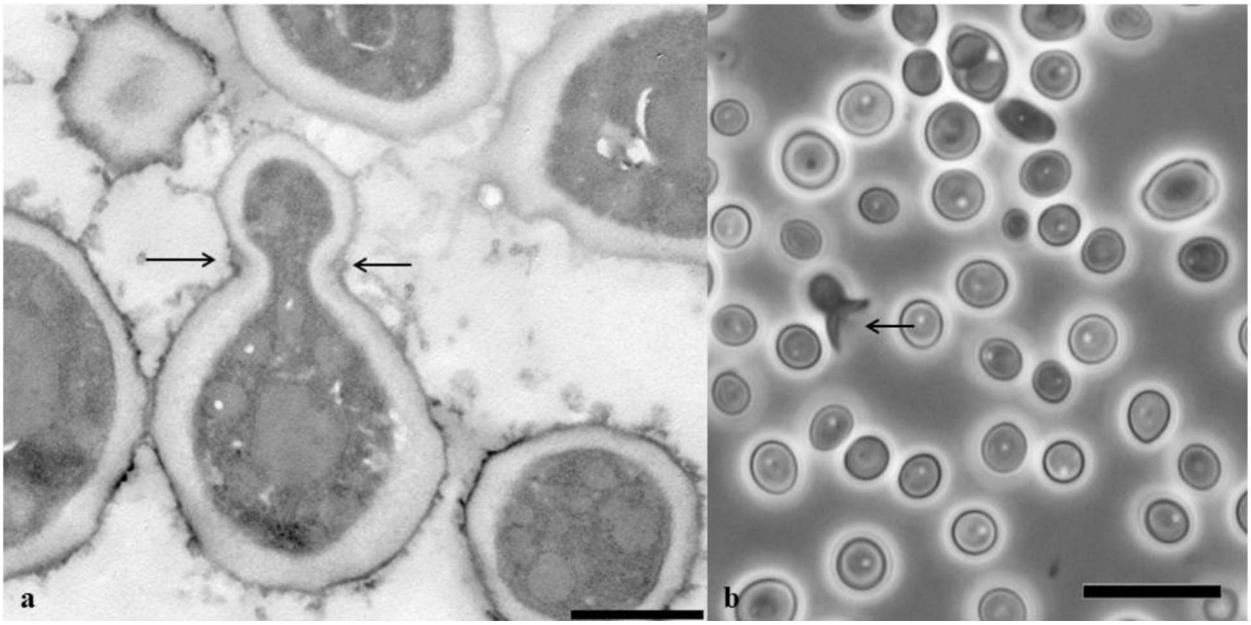


Fig. 20 Micromorphological characters of *Novakomyces olei* (from Čadež et al. 2021). **a** Budding cell of *Novakomyces olei*. Collarette surrounding the forming bud is indicated by arrows. **b** Ascosporulating culture of *Novakomyces olei*. The remnant of an ascus formed by heterogamous conjugation is indicated by arrow. Scale bars: **a** = 1 µm, **b** = 10 µm (The image 'a' was taken by Bence Rácz)

Type family: ***Novakomycetaceae*** Dlauchy, G. Péter & Čadež, in Čadež, Dlauchy, Tome & Péter, Microorganisms 9(2, no. 301): 14 (2021).
Type genus: ***Novakomyces*** Dlauchy, G. Péter & Čadež, Microorganisms 9 (2, no. 301): 14 (2021).
Type species: ***Novakomyces olei*** Dlauchy, G. Péter & Čadež, in Čadež, Dlauchy, Tome & Péter, Microorganisms 9(2, no. 301): 14 (2021).

Pneumocystomycetes O.E. Erikss. & Winka [as 'Pneumocystidomycetes'], Myconet 1(1): 9 (1997).

Index Fungorum Registration Identifier 91007.

Non-filamentous yeast-like organisms, aggregated and parasitic cells in mammalian alveoli, thin-coated, uninucleate, divided by fission. *Asci* crassitunicate, tetra- or octosporum. *Ascospores* globose or round, 8-spored, thick-walled (Eriksson and Winka 1997; Cushion et al. 2004).

Life mode and distribution: Parasitic on mammals as they aggregate in mammalian alveoli and *P. carinii* causes pneumonia (PCP) in immunocompromised (esp. AIDS) patients (Mills 1986; Kirk et al. 2008) and cancer patients (Sepkowitz et al. 1992; Sepkowitz 1993).

Notes: The genus *Pneumocystis* P. Delanoë & Delanoë was introduced by Delanoë and Delanoë (1912). For almost eight decades, *Pneumocystis* was regarded as a protozoan taxon (Stringer 2002) but Edman et al. (1988) confirmed that *Pneumocystis* is related to *Saccharomyces cerevisiae* using rRNA. Later, Stringer et al. (1989) confirmed that the members of *Pneumocystis* are related to *Candida albicans*, *Neurospora crassa*, and *Cryptococcus neoformans* as well.

Eriksson (1994) introduced the family *Pneumocystaceae* O.E. Erikss. and the order *Pneumocystales* O.E. Erikss. to accommodate *Pneumocystis*. Later, Eriksson and Winka (1997) introduced the class *Pneumocystomycetes*.

Pneumocystomycetidae P.M. Kirk, P.F. Cannon, Stalpers & J.C. David.

Index Fungorum Registration Identifier IF 558745.

= *Pneumocystomycetidae* P.M. Kirk, P.F. Cannon, Stalpers & J.C. David, Ainsworth & Bisby's Dictionary of the Fungi, Edn 9 (Wallingford): 417 (2001); Nom. inval., Art. 38.1(a) (Shenzhen).

Index Fungorum Registration Identifier 91006.

Description: The description is identical to the Class description.

Notes: *Pneumocystomycetidae* P.M. Kirk et al. 2001 was invalidly published (Art. 38.1(a) (Shenzhen)). Here we validate *Pneumocystomycetidae*.

Type order: ***Pneumocystales*** O.E. Erikss. [as 'Pneumocystidales'], Syst. Ascom. 13(2): 170 (1994).
Type family: ***Pneumocystaceae*** O.E. Erikss. [as 'Pneumocystidaceae'], Syst. Ascom. 13(2): 170 (1994).
Type genus: ***Pneumocystis*** P. Delanoë & Delanoë, C. r. hebd. Séanc. Acad. Sci., Paris 155: 660 (1912).

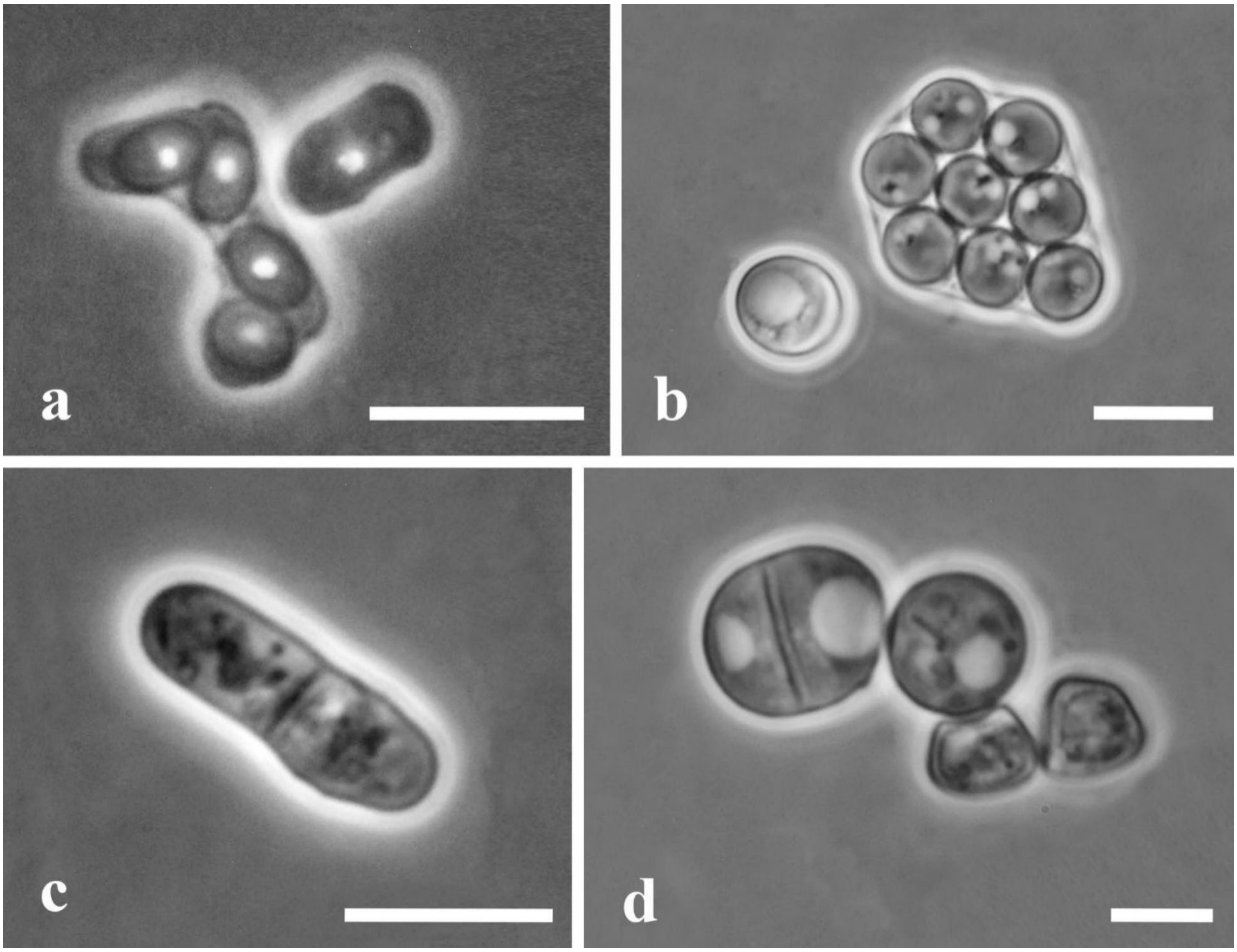


Fig. 21 Microphotographs of different *Schizosaccharomyces* species. **a** Ascus of *S. pombe* with 4 ascospores (nuclei stained with dapi). **b** Ascus of *S. lindneri* with 8 ascospores. **c** Dividing cell of *S. pombe*. **d** Dividing cell of *S. lindneri.* Cell division instead of budding is one of the characteristic features that differentiates the *Schizosaccharomycetes* from the *Saccharomycetes*

Type species: ***Pneumocystis carinii*** P. Delanoë & Delanoë, C. r. hebd. Séanc. Acad. Sci., Paris 155: 660 (1912).

Schizosaccharomycetes O.E. Erikss. & Winka, Myconet 1(1): 10 (1997).

Index Fungorum Registration Identifier 90345; Fig. 21

All species are haplontic and homothallic. After mating type switching, clonal haploid cells of opposite mating type may conjugate and form a zygote. The diploid phase is restricted to the zygote, which promptly undergoes meiosis upon its formation. Asci of *Schizosaccharomyces pombe* contain 4 spores whereas the asci of all other species contain usually contain 8 spores. *S. cryophilus* is described as being very variable in the number of spores per ascus, which ranges from 1 to 8. Spores are round, ovoid, drop-shaped or reniform.

Other characteristics: Asexual reproduction is by polar growth and fission. While all other species solely live as unicellular organisms *Schizosaccharomyces japonicus* and *S. versatilis* may switch to hyphal growth. Cell walls mainly consists of (1 → 3)-α-glucan with some (1 → 4) linkages, (1 → 3)-β-glucan with some (1 → 6)-β-linkages and galactomannans (Bush et al. 1974; Sietsma and Wessels 1990). Additionally, a small amount (0.5%) of glucosamine was detected (Sietsma and Wessels 1990). In the glycoprotein the sugars are predominantly O-linked to the peptide moiety (de Mora et al. 1990).

The major ubiquinone is either coenzyme Q9 or Q10 (Yamada et al. 1973; Yamada and Banno 1987). In *Schizosaccharomyces japonicus* in a certain proportion of the strains no coenzyme was detected.

Glucose and other sugars are fermented. Urease is produced. Nitrate is not assimilated. Diazonium Blue B reaction is negative. Starch and acetic acid are not produced.

Life modes and distribution: All *Schizosaccharomyces* species live saprobic in terrestrial habitats. Pathogenicity was not observed. *Schizosaccharomyces japonicus* and *S. versatilis* are most frequently isolated from forest materials while the rest of the species seem to depend on honey bees and/or solitary bees. Occasionally, *S. pombe, S. japonicus* and *S. versatilis* are present on fresh and rotting fruit. On dried fruit like raisins or dried mango pieces or dried pineapple pieces *S. octosporus* and *S. pombe* were frequently detected. In some manmade fermentative environments (kombucha, rum production or cacao bean fermentation), *S. pombe* plays an important role. *S. octosporus* seem to occur more frequently in the tropical and subtropical zones while others like *S. osmophilus* seem to be well adapted to cold climatic conditions (Brysch-Herzberg et al. 2022). The ecology of *S. cryophilus* is unknown as just one strain was isolated by now and its origin is rather unclear.

Schizosaccharomyces japonicus and *S. versatilis* do not exhibit a special osmotolerance while *S. octosporus, S. osmophilus* and *S. lindneri* are among the most osmotolerant yeast species. In terms of osmotolerance, *S. pombe* has an intermediate position.

Notes: Eriksson et al. (1993) introduced the order *Schizosaccharomycetales* O.E. Erikss. et al. to accommodate the family *Schizosaccharomycetaceae* Beij. ex Klöcker. Eriksson and Winka (1997) introduced the class *Schizosaccharomycetes.* The phylogenetic placement was subject to a longlasting discourse. Although it was early concluded that the fission yeasts diverged early from a common ancestor of the eukaryotes it could not be answered unambiguously if they are archaic ascomycetes which diverged early from the *Ascomycota* or if they diverged later after the *Ascomycota* from the lineage that leads to the Metazoa (Sipiczki 1989; Sipiczki 1995). Only after whole genome data were available open questions concerning the phylogeny of the fission yeast could be answered with higher confidence. Liu et al. (2009) confirmed the placement of *Schizosaccharomyces* (the representative genus of *Schizosaccharomycetes*) in the subphylum *Taphrinomycotina*. Currently, the class comprises one order, one family which only contains the genus *Schizosaccharomyces*. It was proposed to divide the genus *Schizosaccharomyces* in three genera: *Schizosaccharomyces*, *Octosporomyces* (Kudrjawzew 1960) and *Hasegawaea* (Yamada and Banno 1987). This proposal was never broadly accepted by later authors. The genus *Schizosaccharomyces* currently comprises seven species (i.e. *S. japonicus, S. versatilis, S. cryophilus, S. pombe, S. octosporus, S. lindneri* and *S. osmophilus*).

Type order: ***Schizosaccharomycetales*** O.E. Erikss., Syst. Ascom. 11: 146 (1994).
Type family: ***Schizosaccharomycetaceae*** Beij. ex Klöcker, Lafar's Handb. Techn. Mykol., Edn 2 4: 189 (1905).

Type genus: ***Schizosaccharomyces*** Lindner, Wochenschr. Brau. 10: 1298 (1893).
Type species: ***Schizosaccharomyces pombe*** Lindner, Wochenschr. Brau. 10: 1298 (1893).

Taphrinomycetes O.E. Erikss. & Winka, Myconet 1(1): 11 (1997).

Index Fungorum Registration Identifier 90366; Fig. 22

Sexual morph: *Mycelium* enlarged, multinucleate. *Ascogenous cells* intercalarily as a bulge on the cell of the intercellular mycelium, spherical to roughly spherical (lemon and globose form). *Exosporium and mesosporium* smoothwalled. *Endosporium* thickness, three layers, with short pedicle-like basal appendages. **Asexual morph**: *Cells* ovoid to ellipsoidal or cylindrical, with few globose cells. *Budding* unipolar or bipolar budding cells. No hyphae and pseudohyphae (Bacigálová 2008).

Life modes and distribution: The members of *Taphrinomycetes* can be saprobic or pathogenic on plants, soil, insect frass broad range of terrestrial and distributed in a broad range of ecosystems (worldwide) and are reported as different life modes. Phytopathogenic members of the class are responsible for causing galls on stems or inflorescences, leaf curls and witches' brooms (Mix 1949; Fonseca and Rodrigues 2011). Some members of *Taphrinomycetes* are detected as endophytic fungi in ITS rDNA libraries (Jumpponen and Jones 2009, 2010; Cordier et al. 2012).

Notes: The class *Taphrinomycetes* was introduced by Eriksson and Winka (1997), with *Taphrinales* as the type order. *Taphrinales* comprises two families viz., *Taphrinaceae* and *Protomycetaceae*. *Protomycetaceae* has five genera (i.e. *Protomyces, Protomycopsis, Saitoella, Taphridium,* and *Volkartia*) while *Taphrinaceae* has only one genus (*Taphrina*) (Wijayawardene et al. 2022a). The type genus of *Protomycetaceae* (*Protomyces*) was first established by Unger (Kurtzman 1833), and *P. macrosporus* as a type species. This genus has been strictly defined previously, based on morphology and the host range (*Compositae* and *Umbelliferae*) (Reddy and Kramer 1975;). Later, Wang et al. (2016a, b) found out that *Protomyces* species can be detected in other host plant families. The type genus of *Taphrinaceae* (*Taphrina*) was introduced by Fries (1815) to accommodate *T. populina* as a type species of the genus, which has a dimorphic lifestyle. The parasitic counterparts on plants are known as teleomorphs, and the anamorphic yeast state is known as the saprotrophic state and is classified in the genus *Lalaria* (Mix 1949; Nutaratat et al. 2022). In 2003, Rodrigues and Fonseca (2003) studied the *Taphrina* species based on DNA sequence by using the LSU rRNA gene (D1/D2 domains) and ITS regions to confirm the placement of the genus *Taphrina* and

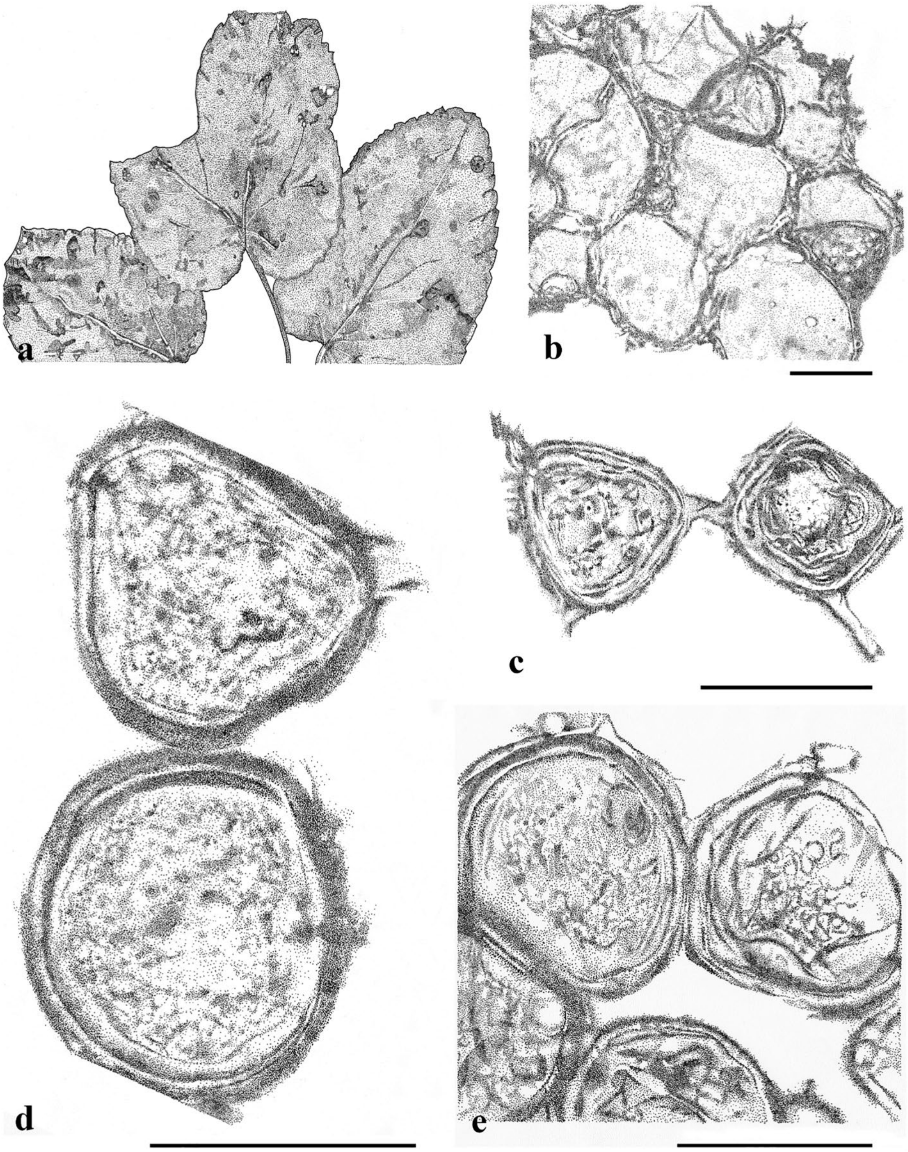


Fig. 22 **a** Leaf spots and galls on *Laserpitium latifolium* caused by *Protomycesmacrosporus*. **b**, **c**Young stage of ascogenous cells. **d**, **e** Mature ascogenous cells. Scale bar: **b**–**e** = 50 µm (Redraw from Bacigálová et al. 2008)

found that *Taphrina* is closely related to the genus *Protomyces*. Later, the reclassification of four *Lalaria* species (*L. arrabidae, L. inositophila, L. kurtzmanii,* and *L. veronaerambellii*) was proposed and synonymized under *Taphrina*, according to the International Code of Nomenclature for Algae, Fungi, and Plants.

Type order: ***Taphrinales*** Haeckel, Systemat. Phylogen. Protist. Pflanzen, Entwurf natürl. Syst. Organism. Grund ihrer Stammesg. 1: 316 (1894).
Type family: ***Taphrinaceae*** Gäum., in Gäumann & Dodge, Comp. Morph. Fungi (London): 161 (1928).
Type genus: ***Taphrina*** Fr., Observ. mycol. (Havniae) 1: 217 (1815).
Type species: ***Taphrina populina*** Fr., Observ. mycol. (Havniae) 1: 217 (1815).

BASIDIOBOLOMYCOTA Doweld, Prosyllabus Tracheophytorum, Tentamen Systematis Plantarum Vascularium (Tracheophyta) (Moscow): LXXVII (2001).

Index Fungorum Registration Identifier 90741.

Mycelium is widely distributed, thick, highly branched, and soon becomes divided by septa. Conidiophores are erect, undivided, and swollen in the upper part into a thick elliptical club (basidium), on the top of which the conidium is formed. At maturity, the basidium cytoplasm forms the fruiting body at its lower part and is propelled by the ejecting plasma together with the still-attached conidium. Later, the conidium is separated from the basidium by the protrusion of a sharp column. Resting spores are formed on the mycelium by the copulation of two adjacent cells that initially grow up into beak-like projections on the common septum. The resting spores are crowned by these beaks.

Life modes and distribution: Saprobic and pathogenic widespread.

Note: The phylum *Basidiobolomycota* was proposed by Doweld (2001). *Basidiobolomycota* encompasses certain fungi that were traditionally classified within the phylum '*Zygomycota*' but were reclassified due to molecular and phylogenetic evidence (Doweld 2001). The classification was revised to account for monophyly and divergence time, as presented in studies conducted by Tedersoo et al. (2018) and Wijayawardene et al. (2018b). Members of *Basidiobolomycota* are characterized by their unique features, particularly in their reproductive structures. They produce spores on specialized structures called basidia, which are club-shaped cells that typically bear four spores at their tips. This mode of spore production is one of the defining characteristics of the phylum and distinguishes it from other fungal groups. One of the remarkable traits of *Basidiobolomycota* is the production of multinucleate cells, known as coenocytic hyphae. Unlike most fungi, which have septate hyphae with distinct cell walls separating individual compartments, the hyphae of *Basidiobolomycota* lack septa, and multiple nuclei can exist within a single hyphal compartment (Tedersoo et al. 2018; Wijayawardene et al. 2018b).

Controversial opinions: Humber (2012) established *Entomophthoromycota*, to accommodate *Basidiobolomycetes*, *Neozygitomycetes* and *Entomophthoramycetes*. This placement was accepted by Gryganskyi et al. (2013). In the phylogenomic analyses of Galindo et al. (2021), the representative taxa of *Basidiobolomycota* clustered in *Zoopagomycota*. Strassert and Monaghan (2022a, b) also confirmed the results of Galindo et al. (2021) and regarded *Basidiobolomycota* as a subphylum of *Zoopagomycota*, i.e. *Basidiobolomycotina*.

Basidiobolomycota comprises one subphylum (*Basidiobolomycotina*) and one class (*Basidiobolomycetes*).

Basidiobolomycetes Doweld, Prosyllabus Tracheophytorum, Tentamen Systematis Plantarum Vascularium (Tracheophyta) (Moscow): LXXVII (2001); Fig. 23

Index Fungorum Registration Identifier 90740.

Cells in their vegetative state possess a single nucleus and can manifest either as a septate mycelium or as yeast-like cells that originate from the insides of preceding cells, exemplified by the 'Darmform' growth pattern. During mitosis, the nuclear membrane starts by breaking into pieces. These fragments, alongside other membranes, accumulate around a specific nuclear area. The chromosomes, which are numerous and minuscule, get compacted and position themselves on a central metaphase plate. This plate typically embeds within the nucleolus, working in conjunction with a barrel-shaped spindle. During the interphase, these chromosomes relax and expand. The cell responsible for producing conidia, known as the conidiophore, is straightforward but showcases a distinct bulbous enlargement at its tip, directly below the emerging conidium. Conidia are spherical, with a single nucleus, and have a tiny conical outgrowth at their base. This outgrowth juts into the spore body but flips out during release. The wall layers of the conidia are indistinguishable. The release of these conidia is quite forceful, resembling a rocket's propulsion, which is triggered by a rupture in the central frail region of the sub-conidial enlargement. The upper part of this enlargement is released with the conidium and can occasionally separate during its movement. If secondary conidia are produced, they are typically elongated, sometimes bent, and may have a mucous drop at their tip. These are formed at the top of a slender, long conidiophore and are dispersed passively. Resting spores, generally zygospores, are developed within the axis of preceding cells. The nuclei of the gametangial cells divide before merging, but only a single nucleus from each cell becomes part of the zygospore. Once matured, zygospores exhibit robust, double-layered walls. Their germination directly results in a germ conidium, typically resembling the secondary type, which is elongated and passively released from a thin conidiophore (modified description from Humber 2012).

Life modes and distribution: Although *Basidiobolomycetes* are mostly known for their saprophytic lifestyle, there are a few species that can cause rare infections in humans and animals. *Basidiobolus ranarum* is the most well-known species responsible for infections, which are known as basidiobolomycosis. These infections often affect the subcutaneous tissue, gastrointestinal tract, or rhinofacial regions (Eidam 1886; Benjamin 1979).

Notes: Similar to notes in the phylum.

Type order: *Basidiobolales* Jacz. & P.A. Jacz. (1931), Opredelitel' Gribov, I Ficomiţeti (Leningrad)**:** 8 (1931).

Type family: *Basidiobolaceae* Engler & Gilg (1924), Syllabus, Edn 9 & 10 (Berlin): 45 (1924).

Type genus: *Basidiobolus* Eidam 1886 [Amphoromorpha Thaxter 1914], Krypt.-Fl. Schlesien (Breslau) 3.1(9–16): 224 (1886) [1889].

Type species: *Basidiobolus ranarum*, Krypt.-Fl. Schlesien (Breslau) 3.1(9–16): 225 (1886) [1889].

BASIDIOMYCOTA R.T. Moore, Bot. Mar. 23(6): 371 (1980).

Index Fungorum Registration Identifier 90050.

Basidiomycota is a very large and diverse phylum of fungi, second to *Ascomycota* in species number (He et al. 2019). Many species produce macroscopic sexual

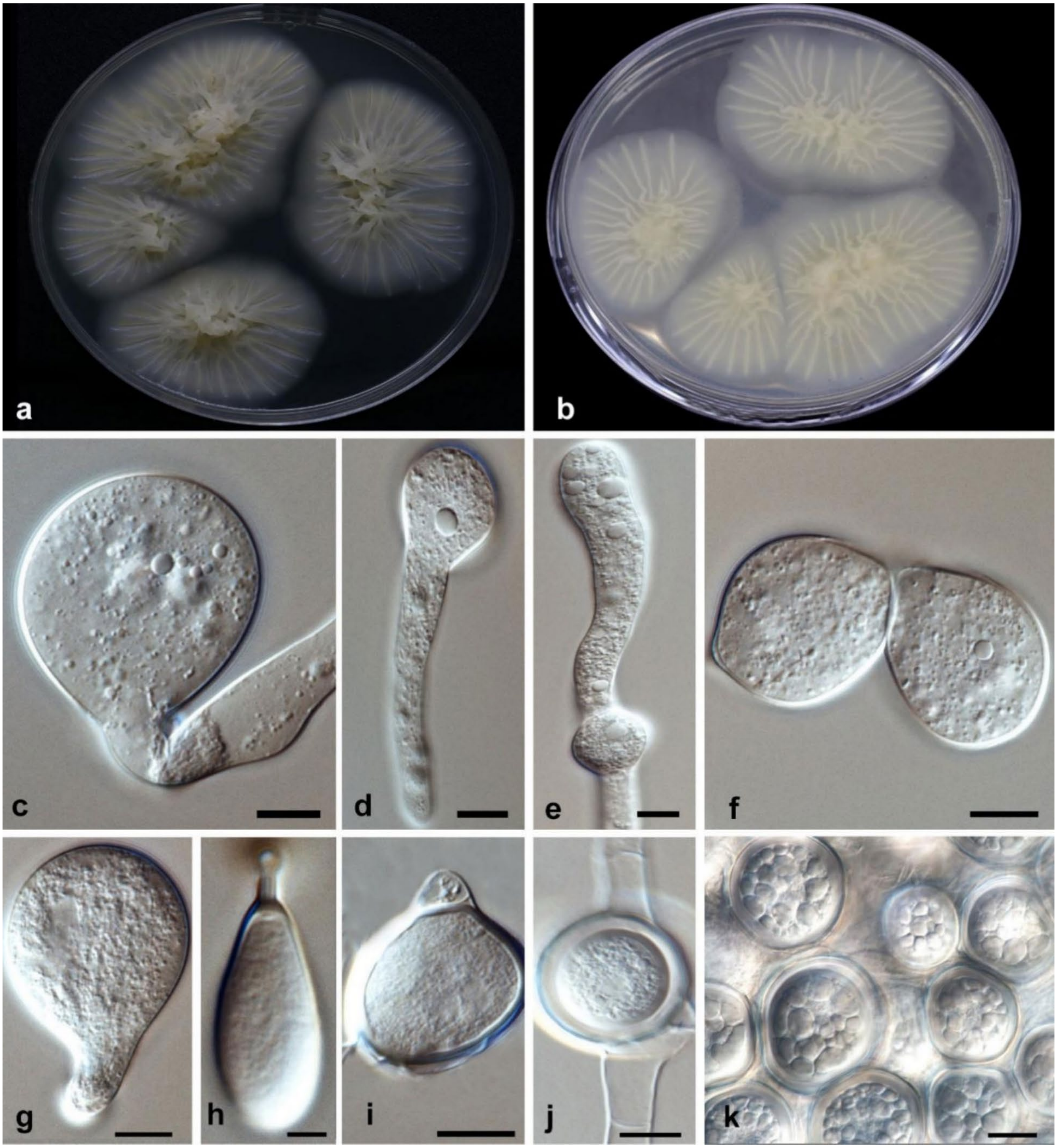


Fig. 23 Culture and micromorphological characteristics of *Basidiobolus omanensis* (CBS 146282). **a**, **b** Colony after 7 days of incubation at 28 °C. **a** MEA front. **b** PDA front. **c** Primary conidia. **d** Primary conidia arising from mycelia. **e** Young zygospore. **f** Zygospores. **g** Mature conidia. **h** Capilloconidium. **i** Conidia with sharp-pointed papillae projection with beak. **j** Smooth mature sexual zygospore. **k** Numerous primary conidia. Scale bars **c**–**k** = 10 µm

reproductive organs known as fruiting bodies, basidiocarps, or basidiomata. Karyogamy and meiosis occur in specialized structures (basidia), resulting in mostly four (one to twelve) haploid basidiospores. Basidia are aseptate or may be longitudinally, oblique, or transversely (partially) septate. Other important diagnostic characteristics include dolipore septa in several lineages such as *Agaricomycetes* (a barrel-shaped cell wall swelling) between hyphal cells, and the presence of clamp connections at hyphal septa (although not all representatives produce clamp connections). The phylum includes mushroom-forming fungi, bracket fungi, puffballs, earthstars, stinkhorns, false truffles, and jelly fungi, but also a number of microscopic fungi, such as rusts, smuts, and yeasts (Zhao et al. 2017). Some species with fleshy fruiting bodies are traditionally used for culinary purposes and/or contain diverse bioactive compounds with medicinal or health-promoting properties (Sandargo et al. 2019; Sum et al. 2023). *Basidiomycota* yeasts are sometimes dimorphic, switching between anamorph (unicellular yeast) and teleomorph (dikaryotic hyphal) stages (Boekhout et al. 2011).

Life modes and distribution: Saprobes, ectomycorrhizal, parasites (on plants, animals, humans, or fungi including lichens), lichen-forming, insect symbionts, endophytes, filamentous or yeast-like, widespread.

Notes: *Basidiomycota* was introduced at the phylum rank by Moore (1980). It is the second largest phylum in the kingdom, *Fungi*, which includes 2,106 genera belonging to 297 families (He et al. 2024). The first taxonomic review of *Basidiomycota* (and *Entorrhizomycota*) of genera and higher ranks was published by Begerow et al. (2018). Subsequently, He et al. (2019) provided a complete outline, phylogenetic dating and notes for all genera and higher ranks of *Basidiomycota*.

Basidiomycota comprises four subphyla: *Agaricomycotina*, *Pucciniomycotina*, *Ustilaginomycotina*, and *Wallemiomycotina* (Tables 2, 16).

Subphylum *Agaricomycotina* Doweld, Prosyllabus Tracheophytorum, Tentamen Systematis Plantarum Vascularium (Tracheophyta) (Moscow): LXXVIII (2001).

Notes: Doweld (2001) introduced *Agaricomycotina,* which currently comprises four classes (He et al. 2024), **1. *Agaricomycetes*; 2. *Bartheletiomycetes*; 3. *Dacrymycetes*** and **4. *Tremellomycetes***.

Agaricomycetes Doweld, Prosyllabus Tracheophytorum, Tentamen Systematis Plantarum Vascularium (Tracheophyta) (Moscow): LXXVIII (2001).

Index Fungorum Registration Identifier 501297; Fig. 24a

The morphological diversity of fruiting bodies in *Agaricomycetes* is unparalleled in any other clade of *Fungi*. In *Agaricomycetes*, the pileate-stipitate morphotype is dominant, along with the coralloid, polyporoid, corticioid, gasteroid, and other forms (Hibbett et al. 2014). Size variation of their fruiting bodies encompasses at least four orders of magnitudes ranging from tiny cyphelloid forms, such as *Henningsomyces candidus* (Pers.) Kuntze (in the order of 1 mm) (Wei et al. 2007), to giant polypores (*Phellinus ellipsoideus* (B.K. Cui & Y.C. Dai) B.K. Cui, Y.C. Dai & Decock), which can measure up to 1,085 cm long (Dai and Cui 2011). Sánchez-García et al. (2020) highlighted that morphological transitions, not nutritional modes, are the most important drivers of diversification across *Agaricomycetes* and that lineages with pileate-stipitate basidiomata have strongly increased diversification rates across all clades.

Life modes and distribution: *Agaricomycetes* are saprobes (e.g., *Agaricaceae*, *Polyporaceae*), and form mutualistic symbioses with a great variety of vascular plants (e.g., *Amanitaceae*, *Boletaceae*, *Russulaceae*) or insects (e.g., *Termitomyces*). Others are plant pathogens (e.g., *Heterobasidion*, *Armillaria*) (Weiß et al. 2004), human pathogens (e.g., *Schizophyllum commune* Fr.), mycophilous fungi and mycoparasites (e.g., *Squamanita*) (Liu et al. 2021; Schoutteten et al. 2024), and predators on nematodes (e.g., *Hohenbuehelia*, *Pleurotus*). Although less common, some *Agaricomycetes* species are lichenized (e.g. *Omphalina licheniformis* X.L. Wei, Z.H. Cao & R.L. Zhao) (Zhang et al. 2022d). Members of the class are widespread.

Notes: *Agaricomycetes* with about 30,000 species encompasses the majority of described species in *Basidiomycota,* including 22 orders, 128 families, and 1,434 genera (He et al. 2019). As a result of the complexity of morphological and ecological diversity, there are many difficulties in the delimitation of *Agaricomycetes* species. Given this, the best practice is to delimit species and publish new taxa based on as many independent lines of evidence as available, that is, by applying a so-called integrative (or polyphasic)

Table 16 Subphyla and classes of *Basidiomycota*

Phylum	*Basidiomycota*			
Subphyla	*Agaricomycotina*	*Pucciniomycotina*	*Ustilaginomycotina*	*Wallemiomycotina*
Classes	*Agaricomycetes* *Bartheletiomycetes* *Dacrymycetes* *Tremellomycetes*	*Agaricostilbomycetes* *Atractiellomycetes* *Classiculomycetes* *Cryptomycocolacomycetes* *Cystobasidiomycetes* *Microbotryomycetes* *Mixiomycetes* *Pucciniomycetes* *Spiculogloeomycetes* *Tritirachiomycetes*	*Exobasidiomycetes* *Malasseziomycetes* *Moniliellomycetes* *Peribolosporomycetes* *Ustilaginomycetes*	*Wallemiomycetes*

Fig. 24 Different taxa of *Basidiomycota*. **a** *Agaricomycetes* (*Amanita hemibapha*). **b** *Bartheletiomycetes* (*Bartheletia paradoxa*). **c** *Cystobasidiomycetes* (*Cyphobasidium*), white arrow shows the fruiting bodies. **d** Dacrymycetes (*Dacryomyces spathularia*). **e** *Exobasidiomycetes* (*Exobasidium ferrugineae*). **f** *Malasseziomycetes* (*Malassezia*). **g** *Microbotryomycetes* (*Microbotrium*). **h** *Physodermatomycetes* (*Physoderma menyanthis*). **i** *Pucciniomycetes* (*Puccinia*). **j** *Tremellomycetes* (*Tremella fusiformis*). **k** *Tritirachiomycetes* (*Tritirachium oryzae*). **l** *Ustilaginomycetes* (*Mycosystema maydis*). **m** *Wallemiomycetes* (*Wallemia sebi*). Photo credits: Figure a: Stephen Axford, Figures B-M: iNaturalist (The photos have been used under the CC BY-NC 4.0 non-commercial use license)

taxonomic approach (Cao et al. 2021). The most comprehensive phylogenetic analyses of *Agaricomycetes* so far were a multilocus and genomic-scale data-based phylogeny of 5,284 taxa (Varga et al. 2019) and a five-locus analysis of 8,472 taxa (Sánchez-García et al. 2020).

The vast majority of wild or cultivated edible fungi include *Agaricus bisporus* (J.E. Lange) Imbach, *Tricholoma matsutake* (S. Ito & S. Imai) Singer, and *Lentinula edodes* (Berk.) Pegler, all of which are *Agaricomycetes* (Niego et al. 2023). Similarly, a significant proportion of medicinal mushrooms, including *Ganoderma lucidum* (Curtis) P. Karst., and *Hericium erinaceus* (Bull.) Pers., also belong to the *Agaricomycetes* (Thongbai et al. 2015; Dai et al. 2021). However, there also are many poisonous mushrooms threatening public health. The lethal species are mainly from *Agaricales*, such as *Amanita exitialis* Zhu L. Yang & T.H. Li, *A. phalloides* (Vaill. ex Fr.) Link, and *Galerina marginata* (Batsch) Kühner (He et al. 2022b).

Type order: ***Agaricales*** Underw., Moulds, mildews, and mushrooms. A guide to the systematic study of the Fungi and Mycetozoa and their literature (New York): 97 (1899).
Type family: ***Agaricaceae*** Chevall., Fl. gén. env. Paris (Paris) 1: 121 (1826).
Type genus: ***Agaricus*** L., Sp. pl. 2: 1171 (1753).
Type species: ***Agaricus campestris*** L. [as 'campester'], Sp. pl. 2: 1173 (1753).

Bartheletiomycetes Thines, Mycological Progress 17 (3): 340 (2017).
Index Fungorum Registration Identifier 815512; Fig. 24b

Asexual morph: *The sori* produce copious conidia (slimy, hyaline 1-celled), which germinate readily to infect other newly fallen leaves. *Conidiophores* branched, hyaline, finely verruculose in the apical parts, originating from a ± compact base of irregularly interwoven, hyaline to pale brown intramatrical hyphae. *Conidiogenesis* holoblastic. *Conidiogenous cells* are mostly long, terminal, or intercalary with one or two conidiogenous branches, unilocal with percurrent proliferation and rather dense annellations, and/or multilocal with distichous sympodial proliferation and densely stacked secession scars. *Conidia* hyaline, one-celled, straight, cylindrical-bacilliform or sometimes slightly broader below the middle with a short attenuate base and minutely truncate scar, uninucleate with the nuclear area in the middle, with minute guttules, finely verruculose. The *conidiophores* are soon replaced by teliospores originating from the same basal cushion of intramatrical hyphae (Scheuer et al. 2008).

Sexual morph: thick-walled, dark brown teliospores either single, immersed in the leaf tissues and ± evenly dispersed (most conspicuous in the epidermis), or conglutinated in compact, erumpent, and finally ± superficial telia. *Telia* (similar to those of rust fungi) are single or arranged in ± circular groups. Telia often develop from conidial sori, hemispherical or cushion-like to ± spherical. After a year of dormancy, teliospores germinate with stipitate, longitudinally septate, statismosporic phragmobasidia and produce basidiospores on each sporogenous locus (Scheuer et al. 2008).

Life modes and distribution: *Bartheletia paradoxa* is apparently saprotrophic rather than endophyte, strictly host-specific and widely distributed fungal companion of *Ginkgo biloba*. Most probably, just like its host plant, the fungus is also a living fossil (Scheuer et al. 2008). Its biology is unclear. Kirschner and Okuda (2013) showed that the fungus is a pioneer colonizer in the initial stage of decomposition of *Ginkgo* litter. According to available information, although *Ginkgo* is grown worldwide, the global distribution of *B. paradoxa* is uneven. The species are generally distributed in Europe (Austria, Czech Republic, Denmark, France, Germany, Sweden, Netherlands, and the United Kingdom), Russia, Ukraine, and Asia (Japan and Korea) (Hayova and Tykhonenko 2017).

Note: The family *Bartheletiaceae* was proposed to accommodate *B. paradoxa,* which was discovered on ginkgo leaf litter and remained unknown for a long time (Scheuer et al. 2008). The first valid information on this fungus was included only by Scheuer et al. 2008 (Hayova and Tykhonenko 2017). The position of *B. paradoxa* was not resolved in the initial nrSSU DNA sequence analysis, but Mishra et al. (2018) took a more phylogenetic approach using a large set of conserved genes and offered a perfect solution. The new study used 67 highly conserved orthologous loci for network analysis. New data excluding negative genes strongly (but not conclusively) support that this organism is at the base of the *Agaricomycetes* and is the sister of all other members of the sub-phylum and separate from the *Ustilaginomycotina* and *Pucciniomycotina*, which together create a sister group to the whole of the *Agaricomycotina*. The new class and order *Bartheletiomycetes* and *Bartheletiales*, were introduced by Mishra et al. (2018).

According to Wijayawardene et al. (2020a), the class *Bartheletiomycetes* consists of a single order *Bartheletiales*, single family *Bartheletiaceae*, and single genus *Bartheletia. B. paradoxa* is the only species within this genus (Scheuer et al. 2008). *Bartheletiomycetes paradoxa* reproduces sexually only on ginkgo leaves and can survive in some tissues of ginkgo trees as an asymptomatic disease (Scheuer et al. 2008).

Type order: ***Bartheletiales*** Thines, Mycological Progress 17 (3): 340 (2017).

Type family: ***Bartheletiaceae*** R. Bauer, Scheuer, M. Lutz & Grube, in Scheuer, Bauer, Lutz, Stabentheiner, Melnik & Grube, Mycol. Res. 111(11): 1269 (2008).

Type genus: ***Bartheletia*** G. Arnaud ex Scheuer, R. Bauer, M. Lutz, Stabenth., Melnik & Grube, Mycol. Res. 111(11): 1269 (2008).

Type species: ***Bartheletia paradoxa*** G. Arnaud ex Scheuer, R. Bauer, M. Lutz, Stabenth., Melnik & Grube, Mycol. Res. 112(11): 1269 (2008).

Dacrymycetes Doweld, Prosyllabus Tracheophytorum, Tentamen Systematis Plantarum Vascularium (Tracheophyta) (Moscow): LXXVIII (2001).

Index Fungorum Registration Identifier 501296; Fig. 25 & 26

Sexual morph: *Basidiomata* scattered or gregarious, coalesced, displaying a wide variation in size and shape, pustulate to pulvinate or subglobose, cylindrical, subulate, rugose pilei, palmate, stipitate-pileate or sessile, strikingly long bisterigmate (forked) holobasidia, pale yellow to yellow, orange, olive, reddish brown to dark reddish brown, firm-gelatinous or soft-cartilaginous (Hibbett et al. 2007), except *Unilacryma unispora* (Shirouzu et al. 2013). *Hymenium* amphigenous, producing numerous basidia. *Basidia* 1–3-spored, bearing a loop-like basal clamp connection; apex frequently U-shaped, sometimes Y-shaped dacrymycete, and more rarely with an apical protuberance, bearing elliptical aseptate spores at the apices of these basidia (Zamora and Ekman 2020). *Basidiospores* 0–1-septate (exceptionally 3-septate), thin-walled, hyaline, cylindric-allantoid. Spore prints whitish. Basidia and basidiospores with or without conspicuous lipid drops when old. *Hyphae* densely branching and frequently anastomoses, with a

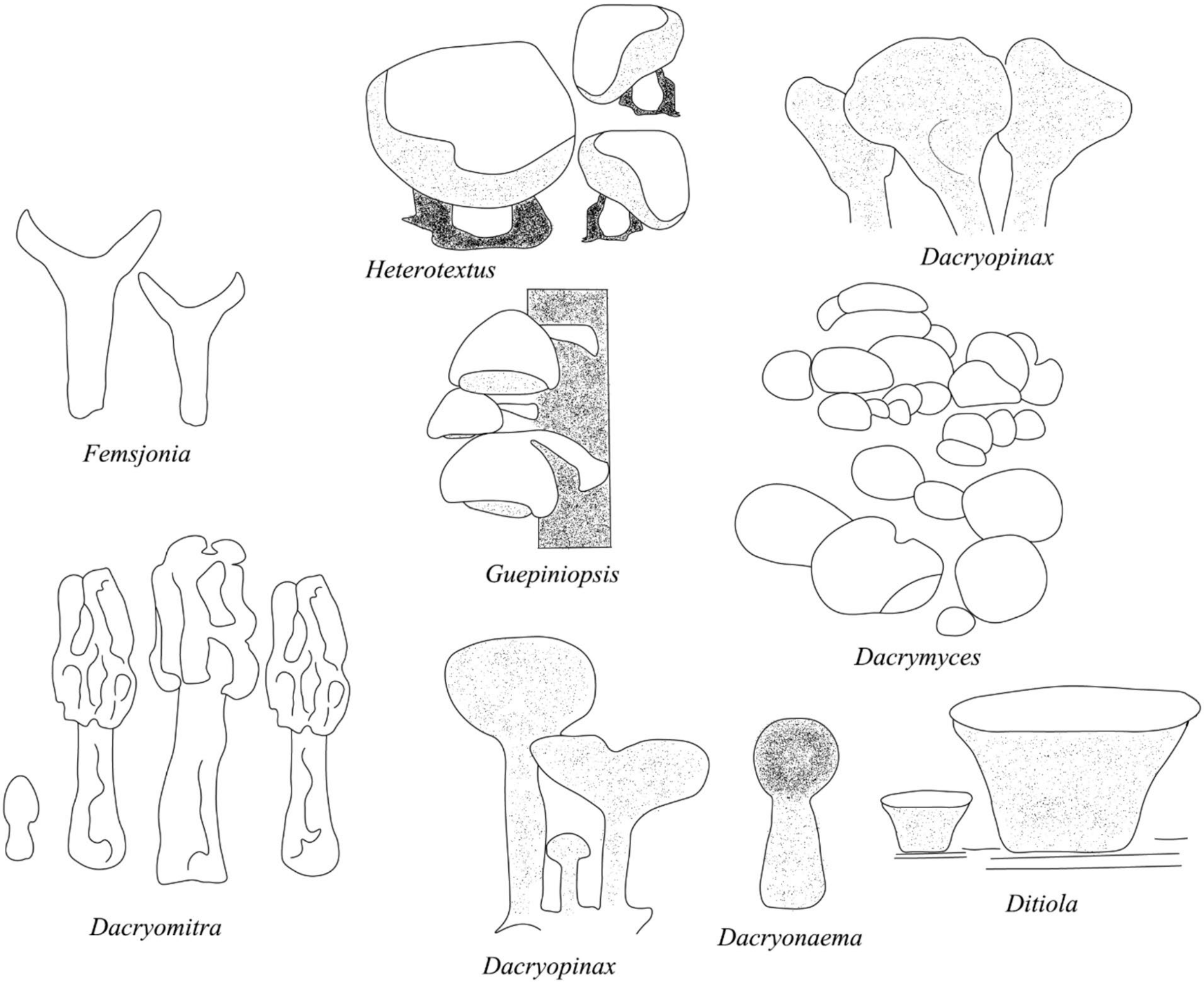


Fig. 25 Basidiocarps of *Dacrymycetales*. No scale bar, modified from Oberwinkler (2012), and Oberwinkler et al. (2014)

loop-like basal clamp attachment. Brownish intracellular and diffuse parietal pigments often visible in some cortical/marginal hyphae. **Asexual morph:** Asexual fructifications are prevalent in *Dacrymyces stillatus*; however, infrequent or absent in other members of the *Dacrymycetes*. Fragmenting hyphae typically manifest in asexual fructifications but may also occur sporadically in basidiocarps (Oberwinkler 2014).

Life modes and distribution: The members of *Dacrymycetes* occur worldwide (Brasfield 1938; Shirouzu et al. 2016, 2017), and are reported as brown-rot fungi (Worrall et al. 1997), and some have been reported to degrade considerable amounts of lignin (Seifert 1983). Gene contents from two *Calocera* genomes also suggest a brown-rotting lifestyle (Nagy et al. 2016), and *Dacrymycetes* are the clade with the oldest stem age among *Basidiomycota* wood decomposers (e.g. *Pseudotsuga* spp., *Pinus* spp., *Juniperus* spp., Fagaceae, Nothofagaceae, Myrtaceae, Podocarpaceae, and Araucariaceae). The ancestors of this class and the *Agaricomycetes* appear to have separated during the upper Devonian or Carboniferous periods (Garnica et al. 2016; Varga et al. 2019).

Notes: Doweld (2001) introduced the class *Dacrymycetes*, one of the three widely accepted classes of phylum *Basidiomycota*. Worrall et al. (1997) provided a comprehensive background of the classification of these typically brown-rot fungi, and *Dacrymycetes* are the clade with the oldest stem age among *Basidiomycota* wood decomposers (Oberwinkler 1994; Kirk et al. 2008; Floudas et al. 2012). According to Wijayawardene et al. (2022a), the class comprises two orders, four families, and twelve genera.

About 400 published species names, but many of these names are synonyms, at least 120 reported species have been identified (Savchenko et al. 2021). However, predicting from recent studies that the real number of species is

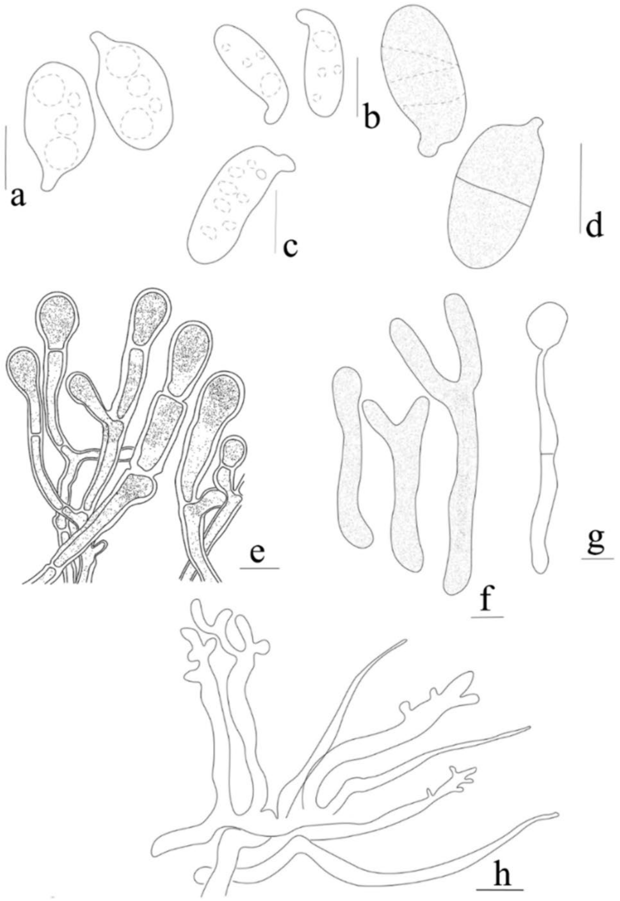


Fig. 26 Micromorphological characters of *Dacrymycetales*. **a**–**d** Basidiospores. e Terminal cells of cortical/marginal hyphae, branched and gelatinised in *Dacryonaema macnabbii*. **f** Bisterigmate basidia in *Dacrymyces estonicus*. **g** Unisterigmate basidium in *Unilacryma unispora*. **h** Hyphidia, simple in *Dacrymyces ovisporus*. Modified from Zamora and Ekman (2020). Scale bars: **a**, **c** = 5 µm, **b**, **d**–**h** = 10 µm

certainly larger, probably over 200 (Savchenko et al. 2021). Except *Unilacryma unispora*, which contains unisterigmate basidia, members of the class may be easily differentiated from other basidiomycetes by their bisterigmate Y-shaped basidia (Wells 1994; Shirouzu et al. 2013). *Dacrymycetes* are distinguished by dolipore septa with imperforate parenthesomes, or rarely with a single pore on an ultrastructural level (Maekawa 1987; Oberwinkler 1994; Shirouzu et al. 2013). In terms of macromorphology, the class is dominated by "jelly fungi" with pustulate-pulvinate, cupulate, dendroid, and spathulate basidiocarps coloured with carotenoids in various yellow and orange colours (Goodwin 1953; Czeczuga 1980; Zamora and Ekman 2020). As a result, they have been used as taxonomic characters both in *Ascomycota* (Eckblad 1968; Schumacher 1990; Baral 2004) and *Basidiomycota* (Arpin and Fiasson 1971; Olariaga et al. 2015; Zamora and Ekman 2020). Shirouzu et al. (2017) provided the most complete phylogeny in terms of included vouchers with both DNA data and morphological data from fruitbodies. Some of the provisionally recognized species were found to be polyphyletic or to have extremely lengthy branches within their clade, indicating that there is significant sequence variation. Zamora and Ekman (2020) provided multi loci phylogeny of the class *Dacrymycetes* and revealed five lineages that putatively represent five different families, four of which were previously accepted and named.

He et al. (2024) recognized only one order *Dacrymycetales* in *Dacrymycetes.*

Type Order: *Dacrymycetales* Henn., in Engler & Prantl, Nat. Pflanzenfam., Teil. I (Leipzig) 1(1**): 96 (1897) [1900].
Type family: *Dacrymycetaceae* J. Schröt. [as 'Dacrymycetini'], in Cohn, Krypt.—Fl. Schlesien (Breslau) 3.1(25–32): 399 (1888).
Type genus: *Dacrymyces* Nees [as 'Dacryomyces'], Syst. Pilze (Würzburg): 89 (1816) [1816–17].
Type species: *Dacrymyces stillatus* Nees, Syst. Pilze (Würzburg): 89 (1816) [1816–17].

Tremellomycetes Doweld, Prosyllabus Tracheophytorum, Tentamen Systematis Plantarum Vascularium (Tracheophyta) (Moscow):73 (2001).

Index Fungorum Registration Identifier: 90764; Fig. 24k

Dimorphic fungi, yeasts, hyphae and/or complex fruiting bodies. Fruiting bodies are gelatinous or absent, parenthesomes sacculate or absent, basidia septate or nonseptate (Hibbett et al. 2007).

Life modes and distribution: The members of *Tremellomycetes* are a nutritionally heterogeneous group comprising saprobes, human and animal parasites, mycoparasites and lichen-inhabiting species and distributed worldwide (Sampaio 2004; Boekhout et al. 2011; Cooper 2011; Millanes et al. 2011; Weiss et al. 2014; Schoutteten et al. 2024). Species from the genera *Cryptococcus*, *Naganishia*, *Papiliotrema*, and *Trichosporon* have been reports as human and animal pathogens (Kurtzman et al. 2011). Several *Tremella* and *Naematelia* species are mycoparasites and have been cultivated for food (Schmidt et al. 2011; Ma et al. 2021; Kuddus and Aguilar 2022; Linnakoski et al. 2023). Some taxa have been exclusively reported in agriculture and industrial applications (Sun et al. 2020; Palmieri et al. 2021; Yan et al. 2022).

Notes: The name *Tremellomycetes* was circumscribed by Hibbett et al. (2007). The members of *Tremellomycetes* dimorphic taxa, but the majority of species is only known from yeast morphs. Fruiting bodies of the hyphal morph in this class either develop intrahymenially or comprise complex fruiting bodies, often with a gelatinous texture (Millanes et al. 2011, Weiss et al. 2014). The anamorphic *Tremellomycetes* have been found in the yeast morph, including *Bullera*, *Cryptococcus*, *Dioszegia* and *Fellomyces* among others (Nakase 2000; Litvinseva et al. 2006; Boekhout et al. 2011; Kurtzman et al. 2011). Among the sexually typified taxa, the spore-producing basidia are often formed in gelatinous basidiocarps or gall deformations on other fungi (Chen et al. 2001; Sampaio 2004; Millanes et al. 2011). Phylogenetic analyses of rRNA gene (SSU, ITS, and LSU sequence data) of Hibbett et al. (1998, 2007), Matheny et al. (2006), and Millanes et al. (2011) accommodated this class in subphylum *Agaricomycotina.*

He et al. (2019) provided the divergence time estimates for the various orders and families in the class, which comprises five orders, 18 families, and 54 genera. According to Wijayawardene et al. (2022a), the class comprises six orders (*Chionasterales*, *Cystofilobasidiales*, *Filobasidiales*, *Holtermanniales*, *Tremellales*, and *Trichosporonales*), 20 families and 73 genera. Various genera have a presumed affinity to *Tremellomycetes* based on morphological and ultrastructural similarities, namely Anastomyces, Celatogloea, *Heteromycophaga*, Phragmoxenidium, Sigmogloea, Sirotrema, Tremellina, *Trichosporonoides*, and *Xenolachne*. *Since viable cultures and/or DNA sequence data are lacking for these genera, they are currently classified as Tremellomycetes incertae sedis.*

The members of *Tremellomycetes* are widely used in different applications (Table 17) while some are medicinally important taxa, either as source of pharmacological compounds or as infectious agents (Table 18).

Type order: ***Tremellales*** Fr. [as 'Tremellinae'], Syst. mycol. (Lundae) 1: 2 (1821).
Type family: ***Tremellaceae*** Fr. [as 'Tremellini'], Syst. mycol. (Lundae) 1: lv (1821).
Type genus: ***Tremella*** Pers., Syn. meth. fung. (Göttingen) 2: 622 (1801).
Type species: ***Tremella mesenterica*** Retz., K. svenska Vetensk-Akad. Handl., ser. 1 30: 249 (1769).

Subphylum ***Pucciniomycotina*** R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw., Mycol. Prog. 5(1): 45 (2006).

Notes: Based on multilocus phylogenetic reconstructions and ultrastructural markers, Bauer et al. (2006) introduced *Pucciniomycotina* to accommodate *Agaricostilbomycetes*, *Atractiellomycetes*, *Classiculomycetes*, *Cryptomycocolacomycetes*, *Cystobasidiomycetes*, *Microbotryomycetes*, *Mixiomycetes* and

Table 17 *Tremellomycetes* taxa used in different industries

Species	Industry	References
Mrakia gelida	Brewing of beer	Linnakoski et al. (2023)
Phaffia rhodozyma	Astaxanthin production for the feed industry and dietary supplement	Schmidt et al. (2011)
Tausonia pullulans	Enzyme production for the food industry	Kuddus and Aguilar (2022)
Tremella fuciformis	Cosmetic, daily chemical, and food industries	Ma et al. (2021), Yuan et al. (2022)
Naematelia aurantialba	Food industries, source of bioactive polysaccharides, and medicinal purposes	Sun et al. (2020), Yan et al. (2022)
Papiliotrema terrestris	Biocontrol agent used in the field and postharvest	Palmieri et al. (2021)

Table 18 Clinically important members of *Tremellomycetes*

Species	Disease	References
Cryptococcus neoformans	Cryptococcosis in human	Maziarz and Perfect (2016)
Cryptococcus gattii	Cryptococcosis in human	Maziarz and Perfect (2016)
Cryptococcus uniguttulatus	Meningitis in human	Pan et al. (2012)
Naganishia albida	Superficial infections of human skin	Aghaei et al. (2017)
Naganishia diffluens	Superficial infections in human skin	Kim et al. (2022)
Papiliotrema laurentii	Emerging opportunistic pathogen in human	Londero et al. (2019)
Papiliotrema flavescens	Subcutaneous infection in human and dog	Zhang et al. (2022c)
Trichosporon asahii	Trichosporonosis in human (superficial and invasive infections)	Kourti and Roilides (2022)
Trichosporon asteroides	Superficial and disseminated infections in human	Mehta et al. (2021)
Trichosporon cutaneum	Superficial and disseminated infections in human	Mehta et al. (2021)
Trichosporon inkin	Superficial and disseminated infections in human	Mehta et al. (2021)
Trichosporon mucoides	Superficial and disseminated infections in human	Mehta et al. (2021)
Trichosporon ovoides	Superficial and disseminated infections in human	Mehta et al. (2021)

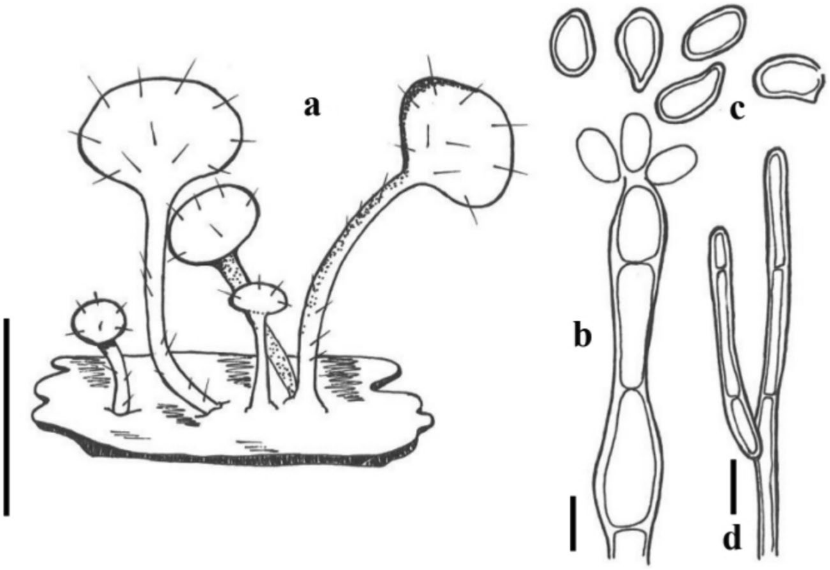


Fig. 27 *Agaricostilbum palmicola.* **a** Habit. **b** Conidiophore tip showing the emergence of conidia, and **c** Conidia × 2800. **d** Branching of young conidiophore × 850. Scale bars: **a** = 1 mm, **b**, **c** = 5 µm (redrawn from Wright 1970)

Pucciniomycetes. Subsequent studies by Schell et al. (2011) and Wang et al. (2015b) introduced *Tritirachiomycetes* and *Spiculogloeomycetes* respectively. Currently, *Pucciniomycotina* consists of ten classes comprising organisms with a diverse range of morphological features and ecological strategies. Members of Pucciniomycotina have a type A structure of the 5.8S rDNA, mannose as the major sugar component of the cell wall, and are characterised by septal pores without membrane caps, often referred to as simple septal pores.

Agaricostilbomycetes R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw., Mycol. Progr. 5(1): 45 (2006).

Index Fungorum Registration Identifier 501474; Fig. 27

Agaricostilbomycetes are a highly diverse class of fungi in terms of morphology and ecology. Currently, the class comprises one order, five families, and more than 70 species distributed over 13 genera (Aime et al. 2014; Wang et al. 2015b; Oberwinkler 2017; Begerow et al. 2018; He et al. 2019; Li et al. 2020; Cao et al. 2021). The monophyly of the class was recognised by various phylogenetic studies (Bauer et al. 2006; Aime et al. 2006; Wang et al. 2015b). These studies often recovered long terminal branches in this class, indicating large phylogenetic distances between the representatives. At the ulturastructural level, the class is characterised by septal pores with simple morphology and without associated microbodies, separation of nucleoplasmic spindle pole bodies, and metaphasic spindle pole bodies that occur intranuclearly (Bauer et al. 2006; Begerow et al. 2018). Most species are exclusively known as asexually reproducing yeast morphs, whereas a few species are characterised by a dimorphic lifecycle, alternating between a unicellular yeast morph and a multicellular filamentous morph in which sexual structures are developed. It is likely that all *Agaricostilbomycetes* are dimorphic organisms, and that the hyphal morph for most species remains to be discovered in natural or laboratory conditions. For example, Fonseca et al. (2000) reported the development of a hyphal morph with transversally septate basidia in *Kondoa aeria* and *K. malvinella* in culture conditions after several months of inoculation. Basidiomata are usually small and comprise stilboid (*Chionosphaera*, *Crittendenia*, *Sterigmatomyces* and *Stilbum*) and pustulate forms (*Mycogloea* spp.). The studied dimorphic species in this class display a large diversity in the structures for sexual reproduction. *Stilbum* spp. develop transversally septate basidia producing statismospores. *Chionosphaera* spp. and *Crittendenia* spp. produce holobasidia with statismospores (Kirschner et al. 2001). *Kondoa* spp. produce transversally septate basidia producing ballistospores (Fonseca et al. 2000). *Mycogloea* spp. produce transversally septate basidia that become detached from the basidiogenous cell, after which sterigmata and ballistospores are formed (Bandoni 1998; Kirschner et al. 2003).

Life modes and distribution: *Agaricostilbomycetes* have been isolated from a large diversity of substrates in marine and terrestrial habitats. Yeast morphs are often considered to act as saprobes. Hyphal morphs were isolates from soil (*Cystobasidiopsis nirenbergiae*), palm litter (*Sterigmatomyces* spp.), lichens (*Crittendenia* spp.), and fruitbodies of other fungi (*Bensingtonia* spp. and *Kondoa* spp.). Whether the fungicolous and lichenicolous species are parasites of their respective hosts remains unknown (Millanes et al. 2021). Haustorial cells are often seen as an indication of mycoparasitism and were reported from *Stilbum vulgare* and *Kondoa myxariophila*, but only in laboratory conditions (Seifert et al. 1992; Li et al. 2020; Schoutteten et al. 2024).

Notes: Bauer et al. (2006) introduced the class *Agaricostilbomycetes* to accommodate two orders, *Agaricostilbales*

Oberw. & R. Bauer and *Spiculogloeales* R. Bauer et al. However, *Spiculogloeales* was only represented by two representatives (*Mycogloea* sp. and *Spiculogloea* sp.), and the authors already suggested that in the future the clade should be separated into its own class (Bauer et al. 2006). Wang et al. (2015b) showed that the *Sporobolomyces subbruneus* clade clustered with *Spiculogloea* sp., and introduced the class *Spiculogloeomycetes* for this lineage.

Agaricostilbum species are presumed saprobic fungi on palm leaves that were isolated from various palm hosts. Oberwinkler (2017) critically discussed the suggested synonymy of *Agaricostilbum palmicola* and *A. pulcherrimum* that was proposed by Brady et al. (1984) without providing details to support the synonymy. Based on DNA sequence data, Wang et al. (2015b) combined *A. pulcherrimum* in the genus *Sterigmatomyces*. Oberwinkler (2017) emphasised that this genus is in need of reinvestigation, combining phylogenetic and morphological markers from a broad sampling of various palm hosts.

Mycogloea nipponica was shown to be the filamentous morph of *Kurtzmannomyces* sp. (Kirschner et al. 2003). Several other *Kurtzmannomyces* yeast species are known, as well as various *Mycogloea* species (Bandoni 1998). However, the overlap in data derived from these fungi is minimal, and many teleomorph-anamorph links remain to be discovered. Because of the lack of DNA sequence data, it remains unclear if all known *Mycogloea* species belong to *Agaricostilbomycetes*.

Type order: ***Agaricostilbales*** Oberw. & R. Bauer, Sydowia 41: 240 (1989).
Type family: ***Agaricostilbaceae*** Oberw. & R. Bauer, Sydowia 41: 240 (1989).
Type genus: ***Agaricostilbum*** J.E. Wright, Mycologia 62(4): 679 (1970).
Type species: ***Agaricostilbum palmicola*** J.E. Wright, Mycologia 62(4): 680 (1970).

Atractiellomycetes R. Bauer, Begerow, J.P. Samp., M. Weiß & Oberw., Mycol. Progr. 5(1): 45 (2006)

Index Fungorum Registration Identifier 501476

Atractiellomycetes is a heterogenous class of which the representatives are only known from filamentous morphs, yeast budding is not known from this class. At the ultrastructural level, *Atractiellomycetes* are characterised by the presence of symplechosomes. These structures were described as stacked plate-like cisternae derived from the endoplasmatic reticulum, interconnected by hexagonally arranged filaments, and connected to mitochondria, but their origin and function remain unknown (Bauer and Oberwinkler 1991a). Symplechosomes are synapomorphic for this class, but only a few species were investigated for their ultrastructural properties. Septal pores are complex and are associated with either microbodies or atractosomes (Bauer et al. 2006).

Atractiellomycetes comprise the order *Atractiellales*, the families *Atractogloeaceae*, *Hoehnelomycetaceae* and *Phleogenaceae*, ten genera, and more than 60 known species (Aime et al. 2018a; Begerow et al. 2018; Schoutteten et al. 2018; Spirin et al. 2018; Cao et al. 2021).

The documented diversity of basidiomata in this class is high, with resupinate (*Bourdotigloea*, *Helicogloea*, *Saccosoma*), stilboid (*Atractiella*, *Phleogena*) and pycnidioid (*Basidiopycnis*, *Proceropycnis*) structrures. Basidia are transversally septate, contain laterally attached probasidia for karyogamy (*Bourdotigloea*, *Helicogloea*, and *Saccosoma*), and usually produce ballistospores (Baker 1936). The formation of statismospores is known from *Atractogloea* and *Phleogena* (Oberwinkler and Bandoni 1982a, b, c). Some *Atractiellomycetes* are known from a teleomorphic and an anamorphic morph, of which the anamorps were formerly assigned to the genera *Hobsonia*, *Infundibura*, *Leucogloea*, and *Pleurocolla* (Kirschner 2004; Spirin et al. 2018). Some species are known exclusively from the anamorph, e.g. *Proceropycnis pinicola* (Oberwinkler et al. 2006a, b).

Life modes and distribution: *Atractiellomycetes* have a worldwide distribution, covering Northern temperate and tropical /sub-tropical regions. Members of the class usually produce inconspicuous basidiomata or conidiomata, often on woody or herbaceous materials, sometimes overgrowing other fungi (Bauer et al. 2006; Aime et al. 2018a; Spirin et al. 2018). Most *Atractiellomycetes* are considered saprobic, associated withdecaying vegetation, or with bark beetle galleries in decaying conifer logs (Bauer et al. 2006; Oberwinkler et al. 2006a, b). However, recent studies indicated that members of this class might be associated with plant roots and may be mycorrhizal or endorrhizal (Kottke et al. 2010; Bonito et al. 2017). One species is reportedly involved in in orchid mycorrhiza (Kottke et al. 2010), *Atractiella rhizophila* and *Proceropycnis hameedii* were found to be endophytes of *Populus* roots, and *Atractidochium hillariae* was recovered as an endophyte of *Pinus taeda* needles (Bonito et al. 2017; Aime et al. 2018a).

Note: Most species in *Atractiellomycetes* are known from one or a few collections only, and DNA sequence data is often limited to ribosomal markers, or completely lacking (Schoutteten et al. 2018; Cao et al. 2021). Also, only a few cultures are available of *Artactiellymycetes*, and spore germination often occurs through the formation of microconidia (Bauer et al. 2006). Spirin et al. (2018) performed a taxonomic study on the resupinate, corticioid members of the *Atractiellomycetes*, focussing on the species formerly assigned to *Helicogloea* and *Saccoblastia*. He delineated three genera based on combined phylogenetic and morphological characters. *Helicogloea* spp. are characterised by efibulate hyphae and the absence of cystidia, *Bourdotigloea* spp. are characterised by efibulate hyphae and the presence of cystidia, and *Saccosoma* spp. are characterised by clamped hyphae and the absence of cystidia. However, the current sampling remains low, and sequencing of more well-studied material is necessary to further test and refine the proposed species delimitation in this group (Malysheva et al. 2020).

Type order: ***Atractiellales*** Oberw. & Bandoni, Can. J. Bot. 60(9): 1740 (1982).
Type family: ***Atractiellaceae*** R.T. Moore, Mycotaxon 59: 8 (1996).
Type genus: ***Atractiella*** Sacc., Syll. fung. (Abellini) 4: 578 (1886).
Type species: ***Atractiella brunaudiana*** (Sacc.) Sacc., Syll. fung. (Abellini) 4: 579 (1886).

Classiculomycetes R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw., Mycol. Prog. 5(1): 46 (2006).

Index Fungorum Registration Identifier 501479.

Classiculomycetes were introduced by Bauer et al. (2006) to accommodate a clade with two species isolated from aquatic habitats, namely *Classicula fluitans* and *Jaculispora submersa*. More recently, Qiao et al. (2018) described a second *Classicula* species from China. The class comprises one order (*Classiculales*), one family (*Classiculaceae*), two genera and three species (Bauer et al. 2006; Begerow et al. 2018; He et al. 2019). At the ultrastructural level, the septal pores have a simple morphology, and are associated with microbodies (Bauer et al. 2003, 2006). All species were originally isolated and described as anamorphic fungi, with typical navicular conidia characterised by three or four setose appendages, clamped hyphae, and the presence of basally clamped haustorial cells. All three species are known from filamentous morphs only, no yeast budding is known. *Naiadella fluitans* was originally isolated as an anamorphic fungus from leaf litter in a freshwater stream in Canada (Marvanová and Bandoni 1987). Bauer et al. (2003) reported the production of the sexual state of *Naiadella fluitans*, which is characterised by transversally septate basidia producing ballistospores and for which the name *Classicula fluitans* was introduced. These basidia were only observed in pure culture after soaking the fungus in water. No basidiospore germination was observed (Bauer et al. 2003). Aime et al. (2018b) called for the protection of the name *Classicula*, based on which the nomenclature of the higher taxa in the class is based.

Life modes and distribution: *Classicula* and *Jaculispora* were isolated from aquatic environments and are especially associated with leaf litter in freshwater habitats (Bauer et al. 2003). The conidia with broadly diverging setose branches in the three known species resemble those of other aquatic hyphomycetes and may be an adaptation to survival and dispersal in such environments (Ingold 1979). Also, the long and small basidiospores produced by *Classicula fluitans* could be an adaptation to water dispersal (Bauer et al. 2003). Plant host preferences have been tested for *Jaculispora submersa*, and suggest an affinity for oak leaves (Prokhorov and Bodyagin 2007). There are indications that *Classicula* and *Jaculispora* species are mycoparasites because of the presence of basally clamped haustorial cells. Such haustorial cells are known from many basidiomycetous mycoparasites, and along the contact surface between the haustorial cell and host cell one or more fusion pores are produced (Bauer 2004; Bauer et al. 2006; Schoutteten et al. 2024). However, the haustorial cells in *C. fluitans* were only observed to attach to hyphae of their own mycelium, which was interpreted as self-parasitism, but no fusion pores were observed (Bauer et al. 2003). It remains unclear if these structures are also formed in natural conditions, and if, and with which other fungi mycoparasitic associations are established.

Notes: The species diversity of this class may be higher than currently known because freshwater ecosystems have always been under-sampled niches for fungi (Cao et al. 2021). Generally, *Jaculispora submersa* is distributed in aquatic environments in Jamaica (Hudson and Ingold 1960) and is also found in Europe, Great Britain, Canada, North America (Cole and Kendrick 1981), and India (Borse et al. 2015). *Classicula fluitans* found in Canada, Czechia, and India (Borse et al. 2015). *Classicula sinensis* was only recorded in China (Qiao et al. 2018).

Type order: ***Classiculales*** R. Bauer, Begerow, Oberw. & Marvanová, Mycologia 95(4): 763 (2003).
Type family: ***Classiculaceae*** R. Bauer, Begerow, Oberw. & Marvanová, Mycologia 95(4): 763 (2003).
Type genus: ***Classicula*** R. Bauer, Begerow, Oberw. & Marvanová, Mycologia 95(4): 757 (2003).
Type species: ***Classiculafluitans*** R. Bauer, Begerow, Oberw. & Marvanová, Mycologia 95(4): 757 (2003).

Cryptomycocolacomycetes R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw., Mycol. Prog. 5(1): 46 (2006).

Index Fungorum Registration Identifier 90612; Fig. 28

Cryptomycocolacomycetes is comprising the order *Cryptomycocolacales*, family *Cryoptomycocolacaceae*, and the two monotypic genera *Cryptomycocolax* and *Colacosiphon* (Oberwinkler and Bauer 1990a, b; Kirschner et al. 2001; Bauer et al. 2006; Begerow et al. 2018). The class was introduced by Bauer et al. (2006) based on molecular phylogenetic reconstructions combined with ultrastructural and morphological observations. Both *Cryptomycocolax abnormis* and *Colacosiphon filiformis* are colacosome-interacting mycoparasites associated with ascomycetous hosts. At the

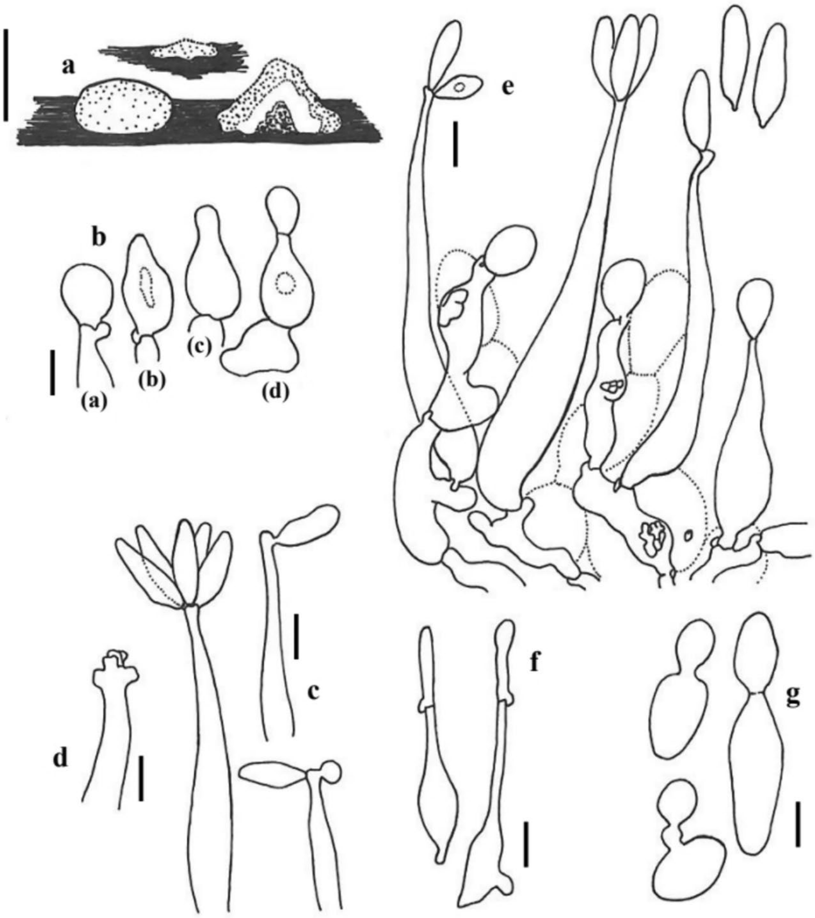


Fig. 28 *Cryptomycocolax abnorme*. **a** Habit sketch of fructification growing in and on sclerotia of the host; one sclerotium longitudinally sectioned. **b** Basidial development (**a**); globose probasidium (**b**, **c**); apical elongation of young basidium (**d**); two celled-basidium (phragmobasidial stage). **c** Basidial apices of mature, one-celled holobasidia with sessile basidiospores at different development stages. **d** Old apex of basidium with bases of spore attachments. **e** Sectional view of sclerotium with hyphae of the host, unclamped and hyphae and basidia of the parasite with clamps; note botryose structures of cellular interactions. The basidia are in different development stages. **f** Germination of basidiospores by hyphae. **g** Yeast-like budding of basidiospores. Scale bars: a = 1 mm; b-g = 10 µm (re-drawn from Oberwinkler and Bauer 1990a, b)

ultrastructural level, both species are characterised by simple septal pores surrounded by woronin-like bodies, which are reminiscent of the woronin bodies found in *Ascomycota*. *Colacosiphon abnormis* was found to contain two distinct types of colacosomes with differences in their morphology and spatial organisation. In *C. filiformis* on the other hand, only one type of colacosomes was reported, which is presumably the same as one of the types found in *C. abnormis*, and in mycoparasites of *Microbotryomycetes*. The colacosomes are mostly organised in vesicular cells, which are invaginate by host hyphae. Along the contact surface, a dense formation of colacosomes is observed, resulting in botryose structures in these cells. Reproductive structures in these two species are considerably different from each other and from other *Basidiomycota*. The sporogenous cells are elongated and produce a variable number of sessile spores. Oberwinkler and Bauer (1990a, b) performed an excellent study of the lifecycle of *C. abnormis* by using transmission electron microscopy (TEM), and observed meiosis in the elongated cells, which they interpreted as basidia. During basidium development, a short phragmobasidial stage is present in which the basidium is transversally one-septate. Later in the development, the top cell is abscised and the basal cell elongates, eventually producing sessil spores apically. The nature of the sporogenous cells in *Colacosiphon* was not studied in such detail by TEM and remains unclear (Kirschner et al. 2001). Therefore, these structures are tentatively interpreted as conidiogenous cells for asexual reproduction. Yeast budding was microscopically observed in *C. abnormis*, but not in *C. filiformis* (Oberwinkler 2017).

Life modes and distribution: Both species in this class are colacosome-interacting mycoparasites, associated with ascomycetous hosts. *Cryptomycocolax abnormis* was isolated as a slimy layer overgrowing pyrenomycetes on a decaying branch of *Circium subcoriaceum* in Costa Rica (Oberwinkler and Bauer 1990a, b). *Colacosiphon filiformis* was isolated from bark beetles (*Ips sexdentatus*) retrieved from decaying *Pinus sylvestris* logs in Germany. This species was obtained in co-culture with other fungi, in which it was found in a parasitic interaction with an ascomycetous host (Kirschner et al. 2001).

Notes: Currently, only DNA sequence data from the D1/D2 region of the LSU ribosomal nuclear DNA are available for these two species. Weiß et al. (2004) discussed the possibility that *Cryptomycocolacomycetes* is a sister to all other *Basidiomycota*, but the phylogenetic analyses rendered low bootstrap support for this scenario. Also in later studies, the phylogenetic position of this class was unresolved (e.g. Bauer et al. 2006). It can be expected that more diversity within this class remains to be discovered, and genome-scale data will help to determine the evolutionary relationships of this class and the species it comprises.

Type order: ***Cryptomycocolacales*** Oberw. & R. Bauer, Mycologia 82(6): 672 (1990).
Type family: ***Cryptomycocolacaceae*** Oberw. & R. Bauer, Mycologia 82(6): 672 (1990).
Type genus: ***Cryptomycocolax*** Oberw. & R. Bauer, Mycologia 82(6): 672 (1990).
Type species: ***Cryptomycocolax abnormis*** Oberw. & R. Bauer [as 'abnorme'], Mycologia 82(6)**:** 672 (1990).

Cystobasidiomycetes R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw., Mycol. Prog. 5(1): 46 (2006).

Index Fungorum Registration Identifier 501480.

The class *Cystobasidiomycetes* was proposed by Bauer et al. (2006) and comprises six orders (*Buckleyzymales*, *Cyphobasidiales*, *Cystobasidiales*, *Erythrobasidiales*, *Naohideales*, and *Sakagushiales*), eight families (*Buckleyzymaceae*, *Cyphobasidiaceae*, *Cystobasidiaceae*, *Erythrobasidiaceae*, *Microsporomycetaceae*, *Naohideaceae*, *Sakaguchiaceae*, and *Symmetrosporaceae*), 16 genera, and over 100 species (Wang et al. 2015b; Begerow et al. 2018; He et al. 2019; Li et al. 2020). At the ultrastructural level, *Cystobasidiomycetes* have simple septal pores which are surrounded by cylindrical organelles with a reticulate surface, called cystosomes.

The cystosome seems to be synapomorphic for this class, but they were only reported from a few dimorphic representatives. However, the cystosome was not found in the septal pores of *Naohideales*. Cell walls of *Cystobasidiomycetes* lack fucose in the sugar composition (Takashima et al. 2000; Bauer et al. 2006). The vast majority of *Cystobasidiomycetes* is exclusively known from a yeast morph, although it is likely that most of them have dimorphic life cycles. The filamentous morphs of *Cystobasidiomycetes* are usually characterised by transversally septate basidia, often subtended by a thin- or thick-walled probasidium. Reproductive structures in *Bannoa* and *Erythrobasidium* are single-celled, but it remains unclear whether it concerns conidiophores or real basidia (Bauer et al. 2006; Oberwinkler 2017; Begerow et al. 2018). Dimorphic species are found in *Bannoa*, *Cystobasidium*, *Naohidea*, *Occultifur*, and *Sakaguchia*. Several species were assigned to genera in *Cystobasidiomycetes* based on morphological resemblances, such as the (swollen) probasidium in combination with transversally septate basidia. However, their assignment to this class remains to be confirmed by molecular data. Basidiospore germination is either with hyphae, secondary spore formation, or yeast budding. Yeast colonies are usually orange-pinkish pigmented, except in *Nahoideale* which is characterised by whitish yeast colonies.

Life modes and distribution: *Cystobasidiomycetes* have been discovered and isolated from various substrates in terrestrial and marine habitats, including air, freshwater aquatic environments, soil, beetle guts, mammals, sea sponges, other fungi, and plants (Libkind et al. 2010; Oberwinkler 2017; Begerow et al. 2018; Jiang et al. 2024). Several species in this class are (intrahymenial) mycoparasites characterised by haustorial cells and interact with nanometer fusionpores, establishing cytoplasmic contact between host and mycoparasite (Bauer 2004; Bauer et al. 2006; Oberwinkler 2017). *Occultifur* and *Cyphobasidium* mycoparasites produce typical tremelloid haustorial cells, the haustoria of *Naohidea sebacea* invaginates host cells. *Cyphobasidium* species are found in association with lichen thalli, but the nature of this association is still unclear (Millanes et al. 2016; Diederich et al. 2022). Some species from the genera *Cyrenella* and *Microsporomyces* were isolated as endothallic species in *Cladonia* lichens (Kachalkin et al. 2024)

Notes: The class *Cystobasidiomycetes* was introduced by Bauer et al. (2006) to include fungi without fucose in their cell walls, and spindle pole bodies that are intranuclear during the metaphase.

Type order: ***Cystobasidiales*** R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw., Mycol. Progr. 5(1): 46 (2006).
Type family: ***Cystobasidiaceae*** Gäum., Vergl. Morph. Pilze (Jena): 411 (1926).
Type genus: ***Cystobasidium*** (Lagerh.) Neuhoff, Bot. Arch. 8: 272 (1924).
Type species: ***Cystobasidium lasioboli*** (Lagerh.) Neuhoff, Bot. Arch.: 273 (1924).

Microbotryomycetes R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw., Mycol. Progr. 5(1): 47 (2006).

Index Fungorum Registration Identifier 501489; Fig. 24g.

The class *Microbotryomycetes* was introduced by Bauer et al. (2006) as a highly supported clade in molecular phylogenetic reconstructions. It currently accommodates eight accepted orders (*Curvibasidiales*, *Heitmaniales*, *Heterogastridiales*, *Kriegeriales*, *Leucosporidiales*, *Microbotryales*, and *Sporidiobolales*), 13 families (*Camptobasidiaceae*, *Curvibasidiaceae*, *Chrysozymaceae*, *Colacogloeaceae*, *Heitmaniaceae*, *Heterogastridiaceae*, *Kriegeriaceae*, *Leucosporidiaceae*, *Microbotryaceae*, *Mycogloiocolacaceae*, *Rosettozymaceae*, *Sporidiobolaceae*, and *Ustilentylomataceae*), more than 46 genera, and more than 300 species (Begerow et al. 2018; He et al. 2019; Li et al. 2020; Schoutteten et al. 2024; Jiang et al. 2024). The class is mainly circumscribed by phylogenetic analyses, in which it forms a well-supported monophyletic clade (Aime et al. 2006; Bauer et al. 2006; Wang et al. 2015b; Li et al. 2020; Schoutteten et al. 2024).

Microbotryomycetes is a class with largely distinct ecological, morphological, and ultrastructural features, and currently, no synapomorphic characters are known that unify all members of this class. Basidiome morphology ranges from effused to pycnidioid, and many mycoparasites develop intrahymelially in the host basidiome and are barely visible or invisible to the naked eye (Toome and Aime 2014; Malysheva et al. 2021). At the ultrastructural level, Microbotryomycetes are characterised by simple septal pores, and intranuclear metaphasic spindle pole bodies (Bauer et al. 2006). Most organisms are known as dimorphic parasites of plants and fungi, but a large number of species are exclusively known as saprobic yeast morphs. These dimorphic fungi alternate between a dikaryotic parasitic filamentous stage, and a haploid saprobic yeast stage. Some exceptions are known, such as *Heterogastridium pycnidioideum* which is only known from a filamentous morph, and for which no yeast budding was observed (Oberwinkler et al. 1990). Many parasites in *Microbotryomycetes* do not produce basidiomata, but produce reproductive structures in the tissues of their host organisms (Schoutteten et al. 2024, 2024). Phytoparasites usually produce sori in specific plant tissues (Kemler et al. 2020), whereas mycoparasites often develop intrahymenially in the hymenium of their host fungus and are only visible as a slimy layer in fresh condition (Schoutteten et al. 2024). Several species produce peculiar structures, such as the stalked basidiophores in *Krieglsteinera*, the stilboid structures in *Pycnopulvinus*, and the pycnidioid basidiomata of *Heterogastridium*. Basidia are usually transversally septate (except in *Camptobasidium*), and arise from thick-walled diploid teliospores in Microbotryales. In various genera of mycoparasites, the basidia arise directly from hyphae (e.g. *Colacogloea* spp.), or thin-walled probasidia (e.g. *Slooffia micra*). Basidiospores germinate by hyphae, secondary spore formation, or yeast budding.

Life modes and distribution: The ecological diversity in this class is large. The largest group of currently known species belongs to the dimorphic phytoparasitic *Microbotryales*. Phytoparasitism occurs in *Kriegeriales* (*Kriegeria eriophori*) and *Microbotryales*. A second ecologically relevant group are the dimorphic mycoparasites. Schoutteten et al. (2024) showed that mycoparasitism is phylogenetically diverse in this class, with representatives occurring in various orders and families. Mycoparasites in *Microbotryomycetes* engage in colacosome interaction, which is a unique interaction mechanism only found in this class and *Cryptomycocolacomycetes* (Bauer et al. 2006; Schoutteten et al. 2024, 2024). Colacosomes, also known as lenticular bodies, are small structures (0.5 µm diam.) produced in mycoparasite hyphae that are adjacent to host hyphae, and comprise a membrane-bound electron dense core, and an electron transparent sheet engulfing the core (Bauer and Oberwinkler 1991b). A secondary cell wall layer is separating the colacosome from the mycoparasite cytoplasm. Colacosomes penetrate the outer cell wall, and the cell wall of the host, which eventually degrades. How the nutrient transfer from host to parasite takes place remains unknown. A third large group of organisms comprises the *Microbotryomycetes* that were isolated as yeasts from a multitude of habitats and substrates, but of which the ecological functions and trophic strategies remain largely unknown. Several of these yeasts are psychrophilic, and were isolated from extreme habitats such as glaciers and crater lakes in Patagonian, Arctic and Antarctic regions (de Garcia et al. 2020; Perini et al. 2021). It can be expected that many of the *Microbotryomycetes* only known from yeast morphs are in fact dimorphic fungi, and that the filamentous morphs remain to be discovered. Possibly these filamentous morphs are parasitic stages of plants, fungi, or other organisms, but this remains to be investigated.

Notes: The phylogenetic distances in *Microbotryomycetes* are usually large, and phylogenetic reconstructions are often characterised by long terminal tip lengths (Bauer et al. 2006; Wang et al. 2015b; Schoutteten et al. 2024). Due to the isolated position of various clades, several orders and families were introduced to accommodate a single genus. Although this causes some degree of taxonomic rank inflation, this highlights the phylogenetic distance to other known taxa (Schoutteten et al. 2024). This is likely reflecting the large morphological and ecological diversity, and it is to be expected that only a small fraction of the real diversity in this class is currently known. All previously published phylogenetic studies of this class failed to resolve the relationships between the different orders and families. More sampling and genome-scale datasets will be necessary to resolve the relationships within *Microbotryomycetes*. Based on currently known diversity, sampling strategies should focus on extreme habitats, soil, phylloplanes, and colacosome-interacting mycoparasites of other fungi.

Type order: ***Microbotryales*** R. Bauer & Oberw., in Bauer, Oberwinkler & Vánky, Can. J. Bot. 75: 1309 (1997).
Type family: ***Microbotryaceae*** R.T. Moore, Mycotaxon 59: 17 (1996).
Type genus: ***Microbotryum*** Lév., Annls Sci. Nat., Bot., sér. 3 8: 372 (1847).
Type species: ***Microbotryum antherarum*** (DC.) Lév. 1847 (Designated by Pfeiffer, Nomenclator Botanicus (Cassellis) 2: 303. 1873) (*fide* Index Fungorum 2023).

Mixiomycetes R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw., Mycol. Prog. 5(1): 47 (2006).

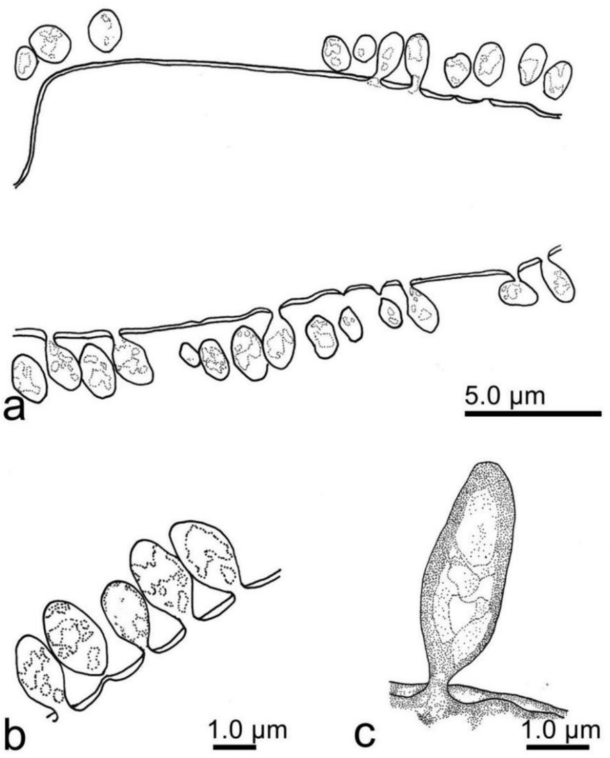


Fig. 29 *Mixia osmundae* on *Osmunda japonica*. **a–c** Ultrathin sections of showing the sporogenous cell from which spores are enteroblastically produced (redrawn from Nishida et al. 1995)

Index Fungorum Registration Identifier 501490; Fig. 29

Asexual morph: Sporogenous cells developing on the surface of the host epidermal cells, the host cell walls are thickened at the contact area with the hyphal cells; sporogenous cells fusiform, oblong, ellipsoid, pyriform, or bacilliform, without septa. Hyphal cells are multinucleate with electrontransparent, non-fibrillate cell walls; numerous spores are produced exogenously, enteroblastically and simultaneously from the sporogenous cells. The spores are hyaline and ellipsoidal. At the surface of the sporogenous cell, after the release of the spores, numerous tiny denticles were observed using light microscopy. The denticles are cuneiform, ca. 0.5 μm in diameter at the tip and were slightly sunken at the center **Sexual morph:** Unknown (Nishida et al. 1995; Bauer et al. 2006).

Life modes and Distribution: Parasitic on ferns *Osmunda regalis*, *O. japonica* and *Osmundastrum cinnamomeum* (Nishida et al. 1995; Sugiyama et al. 2018).

Notes: The class *Mixiomycetes* was introduced by Bauer et al. (2006). According to Wijayawardene et al. (2020a) and He et al. (2024), *Mixiomycetes* comprises one order, *Mixiales*, which include a single family *Mixiaceae* (type: *Mixia*).

Mixia osmundae is the sole known species in the *Mixiomycetes*. For more than 80 years, it was identified as an ascomycete called *Taphrina osmundae*, partly because the sporogenous cells of *Mixia* have some superficial resemblance to the asci produced by certain *Ascomycota* (Aime et al. 2014). However, subsequent revaluation based on examination of cell wall ultrastructure and the observation of enteroblastic budding led to its reclassification as a *Basidiomycetes* (Boekhout et al. 2011).

According to Wang et al. (2015a), *Mixiomycetes* is placed phylogenetically as a sister of *Spiculogloeales* which is an order of *Agaricostilbomycetes*. Other analyses by Wang et al. (2015a), Hibbett et al. (2007), and Aime et al. (2014) found various placements for *Mixiomycetes*, where it was not sister to *Spiculogloeales*. The identification of new taxa within the monotypic class *Mixiomycetes*, as well as the place of additional taxa and sequences from subphylum *Pucciniomycotina*, will be necessary to complete the phylogenetic placement of genus *Mixia*.

Type order: ***Mixiales*** R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw., Mycol. Progr. 5(1): 47 (2006).
Type family: ***Mixiaceae*** C.L. Kramer, Stud. Mycol. 30: 159 (1987).
Type genus: ***Mixia*** C.L. Kramer, Mycologia 50(6): 924 (1959) [1958].
Type species: ***Mixia osmundae*** (Nishida) C.L. Kramer, Mycologia 50(6): 924 (1959) [1958].

Pucciniomycetes R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw., Mycol. Prog. 5(1): 48 (2006).

Index Fungorum Registration Identifier 501494; Fig. 30

With over 8000 known species, *Pucciniomycetes* is the largest class of *Pucciniomycotina*. This class was introduced by Bauer et al. (2006), and currently comprises five orders: *Helicobasidiales Pachnocybales*, *Platygloeales*, *Pucciniales*, and *Septobasidiales*. There exists much ecological and morphological diversity, and no synapomorphic characters are known for this class (Aime et al. 2014; Begerow et al. 2018). At the ultrastructural level, *Pucciniomycetes* have septal pores which can be occluded by a plug, and are mostly associated with microbodies that delineate an organelle-free zone. Hyphae of *Pucciniomycetes* are clampless. Basidia of *Pucciniomycetes* are usually transversally septate. Basidiospores usually germinate by hyphae, yeast budding is known only from some *Septobasidiales* species (Oberwinkler 2017). The majority of the species belongs to the *Pucciniales*, which are the obligate phytoparasitic rust fungi (Aime et al. 2014). The order *Pachnocybales* is monotypic, and contains the presumably saprobic *Pachnocybe ferruginea*. This species is characterised by holobasidia producing

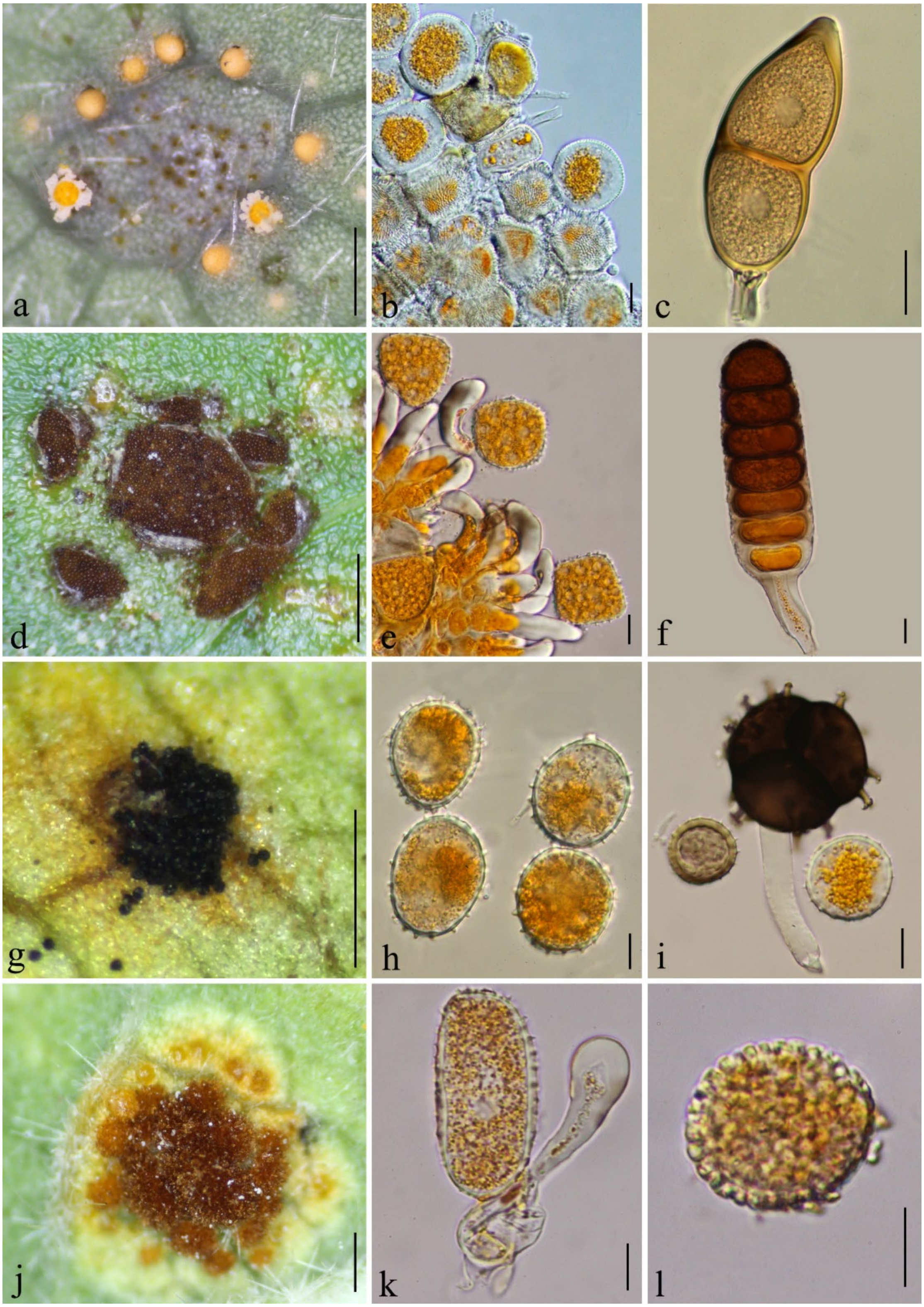


Fig. 30 Examples of the members of *Pucciniales*. **a** *Aecidium*-type aecia gathered on leaves. **b** Aeciospores of the family *Pucciniaceae*. **c** Teliospores of the family *Pucciniaceae*. **d**, **g** Telia on leaves. **e**, **h** Urediniospores of the family *Phragmidiaceae*. **f** Teliospores of the family *Phragmidiaceae*. **i** Teliospores of the *Uredinineae incertae sedis*. **j** Uredinia and telia on leaves. **k** Urediniospores of the family *Melampsoraceae*. **l** Urediniospores of the family *Coleosporiaceae*. Scale bars: **a**, **d**, **g**, **j** = 0.5 mm, **b**, **c**, **e**, **f**, **h**, **i**, **k**, **l** = 10 µm

sessile statismospores. *Septobasidiales* are entomopathogenic fungi producing dense hyphal mats covering scale insects on their plant hosts. It is generally believed that *Septobasidiales* species parasitize in the scale insects, but the nature of this association remains to be better understood (Aime et al. 2014). *Septobasidiales* produce transversally septate basidia, and the basidiospores can germinate by yeast budding. *Platygloeales* are all characterised by transversally septate basidia, and mainly comprise parasites of ferns and mosses (e.g. *Eocronartium*, *Herpobasidium*, *Jola*, *Insolibasidium*, *Platycarpa*, and *Ptechelitium*), but also some saprobic fungi such as *Platygloea disciformis*. *Helicobasidiales* species have a dual ecological strategy. The sexual morphs of these species are characterised by transversally septate basidia, and are known as the '*Helicobasidium* stage', in which they are phytoparasitic. The asexual morphs are mycoparasites of rusts (*Pucciniales*), and were previously classified in the genus *Tuberculina*. During the mycoparasitic stage, these fungi interact with their host fungus via micrometer fusion-pore interaction, in which migration of nuclei and mitochondria from the mycoparasite to the host cell was observed (Bauer 2004; Bauer et al. 2004; Lutz 2004).

Notes: Much diversity in the *Pucciniomycetes* remains to be discovered. The best-investigated group is the phytoparasitic *Pucciniales* because of their economic importance (Aime et al. 2014). The known diversity in the other orders is much smaller, and few taxonomic treatments are available covering the genera in these groups. The number of currently accepted *Helicobasidiales* species is low compared to the number of potential host species in the order *Pucciniales*. Many names are available for *Tuberculina*, and this complex genus is in urgent need of a taxonomic revision in which the host range of the different species is assessed (Table 19).

Type order: *Pucciniales* Caruel, Atti R. Accad. Naz. Lincei, Mem. Cl. Sci. Fis. Matem. Nat., sér. 5: 246 (1881).
Type family: *Pucciniaceae* Chevall. [as 'Puccinieae'], Fl. gén. env. Paris (Paris) 1: 413 (1826).
Type genus: *Puccinia* Pers., Neues Mag. Bot. 1: 118 (1794).
Type species: *Puccinia graminis* Pers. 1794 (Designated by Laundon, Mycol. Pap. 99: 15. 1965).

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

Index Fungorum Registration Identifier: 813101.

Spiculogloeomycetes belongs to the subphylum *Pucciniomycotina* (Bauer et al. 2006; Wang et al. 2015b; Oberwinkler 2017). The class comprises a single order, *Spiculogloeales*, accommodating the genera *Meniscomyces*, *Phyllozyma*, and *Spiculogloea* (Wang et al. 2015b; Oberwinkler 2017; Li et al. 2020). The majority of the species belonging to *Spiculogloeomycetes* are known only from a yeast morph and no filamentous morphs with sexual structures are known from the species in *Meniscomyces* and *Phyllozyma*, which were all isolated from plant surfaces. Yeast colonies are usually yellow to pale yellowish-brown, occasionally pinkish-orange, budding cells are present, and hyphae and pseudohyphae are present or not. Ballistoconidia are fusiform, ellipsoidal, or sometimes sickle-shaped in *Meniscomyces* spp.

Spiculogloea species on the other hand are intrahymenial mycoparasites known from filamentous morphs only and generate hyphae with clamp collections, three-septate auricularioid basidia that are spiculated at the surface producing ballistospores, and sometimes conidiophores with cyanophilous conidia (Roberts 1996, 1997; Langer and Oberwinkler 1998; Bauer et al. 2006; Oberwinkler 2017; Schoutteten et al. 2018, 2024). The basidiospores can germinate by hyphae, yeast budding, or secondary spore production. Furthermore, *Spiculogloea* species are characterised by the presence of clamped haustorial cells, of which the globular apex attaches to hyphae of the host fungus. Along the contact surface, one or more nanopores are produces, establishing a cytoplasmic bridge between the host and mycoparasite (Weiß et al. 2004; Bauer et al. 2006). Cultures and DNA sequence data are unavailable for most of the *Spiculogloea* species, and thus, their systematic placement remains to be investigated. Several phylogenetic reconstructions found the

Table 19 Examples of economically significant species

Species	Host	References
Helicobasidium mompa	Causes violet root rot in Africa and Asia	Bauer et al. (2004), Lutz et al. (2004a, b, c)
Helicobasidium purpureum	Causes cosmopolitan violet root rot	Bauer et al. (2004), Lutz et al. (2004a, b, c)
Phragmidium spp.	*Rosa, Rubus,* and *Potentilla,* with a few species on *Sanguisorba, Duchesnea,* and *Acaena*	Sun et al. (2022)

clustering of a *Mycogloea* isolate in *Spiculogloeomycetes*, although only LSU and SSU sequence data are available and the obtained support is usually low (Weiß et al. 2004; Bauer et al. 2006; Wang et al. 2015b). Hence, it is unclear whether this *Mycogloea* truly belongs to *Spiculogloeomycetes*, or is a member of a different class in *Pucciniomycotina*.

Life modes and distribution: *Spiculogloeomycetes* are comprised of teleomorphic members (*Spiculogloea* spp.) that produce basally clamped transversally three-septate basidia and clamped tremelloid haustorial cells. *Spiculogloea* spp. are intrahymenial mycoparasites of corticioid fungi and resupinate jelly fungi (*Agaricomycetes*), and interact with their host fungi by means of nanofusionpore interaction. These mycoparasites are mainly known from North-America and Europe, but it can be expected that these mycoparasites follow the distribution of their hosts (Bandoni et al. 2002; Spirin et al. 2016; Oberwinkler 2017; Schoutteten et al 2018, 2024). Some taxa are isolated as anamorphic yeast colonies from plant surfaces (mainly the phyllosphere), and their ecological role remains poorly understood (e.g. *Meniscomyces* spp. and *Phyllozyma* spp.). These species were isolated from various parts of the world, including South-America, Japan and China (Wang et al. 2015b; Oberwinkler 2017; Li et al. 2020).

Notes: The placement of *Spiculogloeomycetes* was confirmed by a phylogenetic analysis using seven genes in which it formed a well-supported lineage sister to *Mixiomycetes* within *Pucciniomycotina* (Bauer et al. 2006; Wang et al. 2015b). *Spiculogloeomycetes* are poorly studied, and the little overlap between the teleomorphic and anamorphic data allows for further studies.

Type order: ***Spiculogloeales*** R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw. 2006.
Type family: ***Spiculogloeaceae*** Denchev, Mycol. Balcanica 6: 87 (2009).
Type genus: ***Spiculogloea*** P. Roberts, Mycotaxon 60: 112 (1996).
Type species: ***Spiculogloea occulta*** P. Roberts, Mycotaxon 60: 113 (1996).

Tritirachiomycetes Aime & Schell, in Schell, Lee & Aime, Mycologia 103(6): 1339 (2011).

Index Fungorum Registration Identifier: 561067; Fig. 31

Asexual morph: Multinucleate hyphae, simple pore septa, conidiophores that are subhyaline to dematiaceous and subhyaline to dematiaceous sympodial conidiogenous cells that occur in whorls and bear conidia on an elongated rachis. **Sexual morph:** Unknown (Schell et al. 2011).

Life modes and distribution: The members of *Tritirachiomycetes* are worldwide in distribution and reported as saprophytes (Moraes et al. 2010; Schell et al. 2011; Naseri et al. 2013), biotrophic mycosymbionts (Beguin 2010), endophytes (Vieira et al. 2011; Bezerra et al. 2013; Qadri et al. 2014), and as human opportunistic pathogens (Martínez-Herrera et al. 2015; Vanam et al. 2018; Bezerra et al. 2020), e.g. *Tritirachium oryzae* is important species that causes human infections (Martínez-Herrera et al. 2015; Vanam et al. 2018).

Notes: The class *Tritirachiomycetes* was introduced by Schell et al. (2011). Multi-gene phylogenetic analyses (LSU, SSU, ITS, and *tef-1α*) and septal pore ultrastructure confirmed its placement in *Pucciniomycotina* (Schell et al. 2011). He et al. (2019) provided the divergence time estimates for *Tritirachiomycetes*. Wijayawardene et al. (2022a) and He et al. (2024) accepted the class *Tritirachiomycetes* comprises with one order (i.e. *Tritirachiales*), one family (*Tritirachiaceae*), two genera (*Paratritirachium* and *Tritirachium*), and six species.

Type order: ***Tritirachiales*** Aime & Schell, in Schell, Lee & Aime, Mycologia 103(6): 1339 (2011).
Type family: ***Tritirachiaceae*** Aime & Schell, in Schell, Lee & Aime, Mycologia 103(6): 1339 (2011).
= *Tritirachiaceae* Locq., Mycol. gén. struct. (Paris): 208 (1984).
Type genus: ***Tritirachium*** Limber, Mycologia 32(1): 24 (1940).
Type species: ***Tritirachium dependens*** Limber, Mycologia 32: 26 (1940).

Subphylum *Ustilaginomycotina* Doweld, Prosyllabus Tracheophytorum, Tentamen Systematis Plantarum Vascularium (Tracheophyta) (Moscow): LXXVIII (2001).

Notes: Doweld (2001) introduced *Ustilaginomycotina* that currently consists of five classes; 1. *Exobasidiomycetes*; 2. *Malasseziomycetes*; 3. *Moniliellomycetes*. 4. *Peribolosporomycetes* and 5. *Ustilaginomycetes* (He et al. 2024).

Exobasidiomycetes Begerow, M. Stoll & R. Bauer, Mycologia 98(6): 908 (2007) [2006].

Index Fungorum Registration Identifier 501484; Fig. 24e

Simple spores and interaction apparatus (Bauer et al. 1997; Begerow et al. 2006).

Life modes and distribution: Parasitic smut fungi (e.g. infecting Asparagaceae, Melanthiaceae, and Xanthorrhoeaceae), yeasts, widespread.

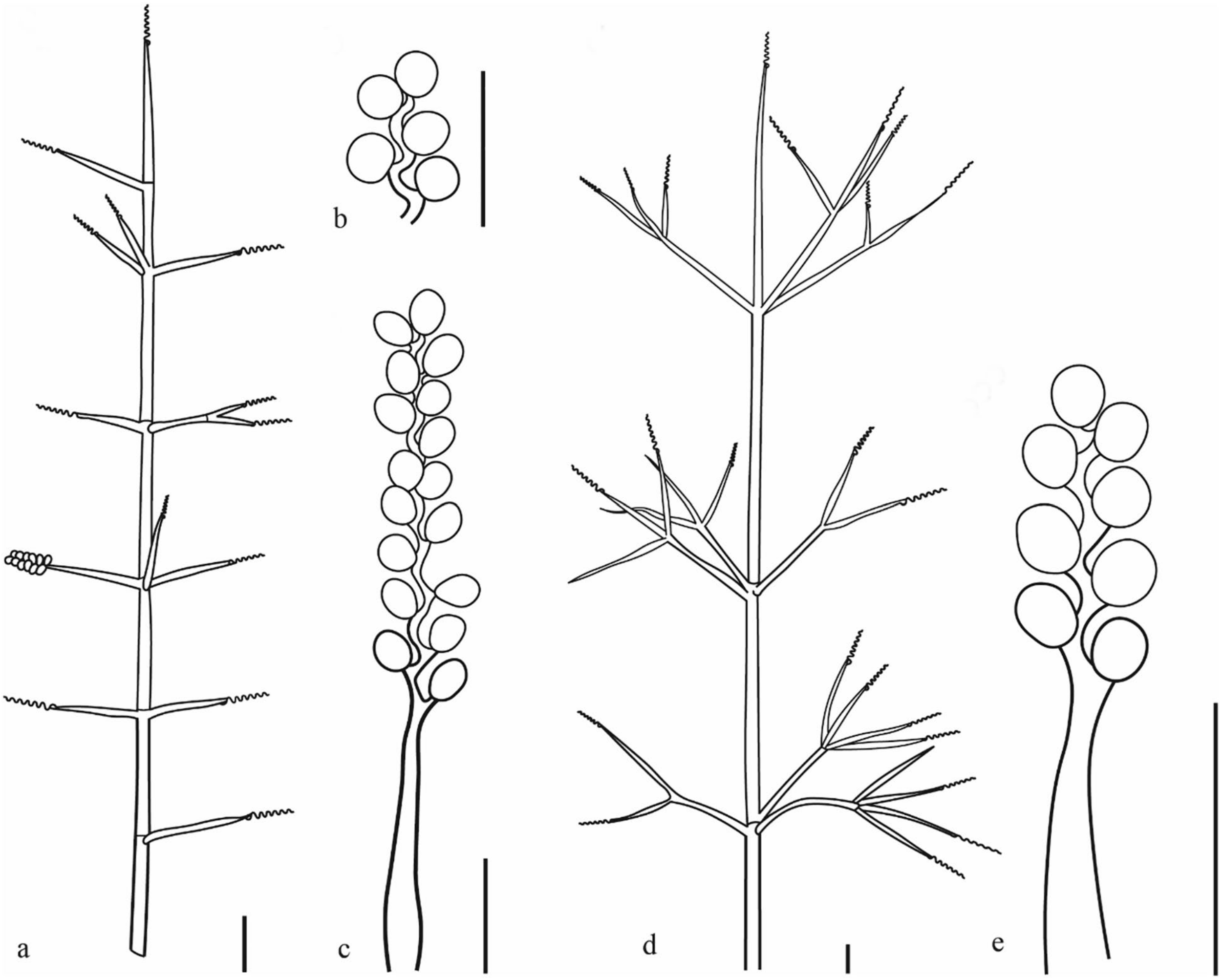


Fig. 31 *Tritirachium* sp. **a**–**c** *T. dependens*. **d**, **e** *T. album*. Scale bars: **a**–**e** = 10 μm (redrawn from Limber 1940)

Notes: Bauer et al. (1997) introduced *Exobasidiomycetidae* to accommodate *Doassansiales* R. Bauer & Oberw., *Entylomatales* R. Bauer & Oberw., *Exobasidiales* Henn., *Georgefischeriales* R. Bauer et al., *Graphiolales* Oberw., *Microstromatales* R. Bauer & Oberw., and *Tilletiales* Haeckel. However, Begerow et al. (2006) introduced *Exobasidiomycetes* and regarded *Exobasidiomycetidae* as a synonym of the former. Begerow et al. (2006) also introduced *Ceraceosorales* Begerow et al. as a new order in *Exobasidiomycetes*. Subsequent studies by Wang et al. (2015a) and Li et al. (2022) introduced *Golubeviales* Q.M. Wang et al. and *Franziozymales* Q.M. Wang et al. hence, currently, the class comprises ten orders.

Type order: ***Exobasidiales*** Henn., in Engler & Prantl, Nat. Pflanzenfam., Teil. I (Leipzig) 1(1**): 103 (1898) [1900].
Type family: ***Exobasidiaceae*** J. Schröt. [as 'Exobasidiacei'], in Cohn, Krypt.-Fl. Schlesien (Breslau) 3.1(25–32): 413 (1888) [1889].

Type genus: ***Exobasidium*** Woronin, Verh. Naturf. Ges. Freiburg 4(4): 397 (1867).
Type species: ***Exobasidium vaccinii*** (Fuckel) Woronin, Verh. Naturf. Ges. Freiburg 4(4): 397 (1867).

Malasseziomycetes Denchev & T. Denchev, Index Fungorum 145: 1 (2014).

Index Fungorum Registration Identifier 550570; Fig. 24f

Zoophilic members of the *Ustilaginomycotina* have a monopolar budding yeast phase showing percurrent or sympodial proliferation of the buds. Yeasts are lipid-dependent or lipophilic (excluding the case of *Malassezia pachydermatis*), with a multilayered cell wall and a helicoidal evagination of the plasma membrane. **Sexual morph:** Unknown (Denchev and Denchev 2014).

Life modes and distribution: Parasitic on the skin of warm-blooded animals (Gupta et al. 2004; Begerow et al. 2006) and widespread (Kirk et al. 2008).

Notes: Denchev and Denchev (2014) introduced *Malasseziomycetes* to accommodate the single-order *Malasseziales*. Currently, the class accommodates one order, one family, and one genus.

Type order: ***Malasseziales*** R.T. Moore [as 'Malesseziales'], Bot. Mar. 23(6): 371 (1980).
Type family: ***Malasseziaceae*** Denchev & R.T. Moore, Mycotaxon 110: 379 (2009).
Type genus: ***Malassezia*** Baill., Traité Bot. Méd. Crypt.: 234 (1889).
Type species: ***Malassezia furfur*** (C.P. Robin) Baill., Traité Bot. Méd. Crypt.: 234 (1889).

Moniliellomycetes Q.M. Wang, F.Y. Bai & Boekhout [as 'Monilielliomycetes'], in Wang, Theelen, Groenewald, Bai & Boekhout, Persoonia 33: 46 (2014).

Index Fungorum Registration Identifier 823105; Fig. 32

Asexual morph: Chlamydospore formation of *Moniliella* occurred when the yeast is transferred from nutrient-rich to poor media, or in nitrogen-depleted media (de Hoog et al. 2011; Thanh et al. 2013). Pseudohyphae and chlamydospores are sometime present, cell walls are multi-lamellar. Hyphal septa typically possess dolipores with an arch of endoplasmic reticulum, but 'micropore'-like structures may also be present (de Hoog et al. 2011). Sugars are fermented by most species. Nitrate is assimilated. Urease and diazonium blue B (DBB) reactions are positive. Coenzyme Q-9 is present. Xylose and fucose are absent from whole-cell hydrolysates (Wang et al. 2014). **Sexual morph:** Unknown. ***Colonies*** are restricted, smooth, velvety or cerebriform, cream then paleolivaceous or black-brown, yeast-like growth, budding cells are ellipsoidal and form terminally on true hyphae that disarticulate with arthroconidia (Wang et al. 2014).

Life modes and distribution: The members of *Moniliellomycetes* are distributed in a broad range of ecosystems in North and South America, Asia, and Europe in different life modes. Yeasts in *Moniliellomycetes* have been isolated from man-made products such as sweet fruit sauce, sweet pickles, acetic acid-containing products, honey, jam, leaf-cutting bees, honey bees, brood cells of the honey bees, pollen in honeycomb, buffalo milk, flowers (e.g. *Ipomoea pes-caprae* and *Calotropis gigantea*), fermented food, rotting wood, meat processing environments, and air (Rosa et al. 2009; de Hoog et al. 2011; Thanh et al. 2012, 2013; Lei et al. 2022; Pipiková et al. 2023), or pathogenetic on humans and cats (McKenzie 1984; Guarro et al. 1999). Species may be osmophilic and lipophilic, and are used to produce erythritol, a low-calorie sweetener (de Hoog et al. 2011).

Notes: The monotypic class *Moniliellomycetes* belongs to the subphylum *Ustilaginomycotina*, and has only one order (*Moniliellales*) and one family (*Moniliellaceae*), with *Moniliella* as the type genus (Wang et al. 2014). The phylogeny of *Moniliella*, was not well understood for a long time (de Hoog et al. 2011). The genus was initially thought to be closely related to *Tremellomycetes* in *Agaricomycotina* (de Hoog 1979; Guarro et al. 1999). *Moniliella* includes black, yeast-like fungi in the *Basidiomycota*, but morphologically similar black, yeast-like fungi also occur in *Ascomycota* (Yurlova et al. 2008). Despite their relative uniformity in morphological appearance and physiological properties, species of *Moniliella* exhibit a high degree of genetic divergence (Rosa et al. 2009).

Type order: ***Moniliellales*** Q.M. Wang, F.Y. Bai & Boekhout, in Wang, Theelen, Groenewald, Bai & Boekhout, Persoonia 33: 46 (2014).
Type family: ***Moniliellaceae*** Q.M. Wang, F.Y. Bai & Boekhout, in Wang, Theelen, Groenewald, Bai & Boekhout, Persoonia 33: 46 (2014).
Type genus: ***Moniliella*** Stolk & Dakin, Antonie van Leeuwenhoek 32: 399 (1966).
Type species: ***Moniliella acetoabutans*** Stolk & Dakin [as 'acetoabutens'], Antonie van Leeuwenhoek 32: 400 (1966).

Peribolosporomycetes Witfeld, M.A. Guerreiro, H.D.T. Ngyuen & Begerow, in Witfeld, Guerreiro, Nitsche, Wang, Ngyuen & Begerow, Mycol. Progr. 22(4, no. 30): 10 (2023).

Index Fungorum Registration Identifier 843630.

Class of mesophilic, heat resistant, and osmotolerant basidiomycetes with slow hyphal growth and high phenotypic variability. Characteristically, triangular-shaped chlamydospores are distally produced on coiled hyphae. Sympodial, ovoid conidia are produced. Relatively 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. Based on the analysis of 38 protein-coding genes, orthology analysis, and septal pore type analysis, this class is placed within the *Ustilaginomycotina* (Witfeld et al. 2023).

Life modes and distribution: From soil, associated with *Pinus resinosa*. Known from Nova Scotia (Witfeld et al. 2023).

Notes: Witfeld et al. (2023) introduced *Peribolospora* Witfeld et al. (type: *P. baueri* Witfeld et al.) and showed that this genus has a distinct phylogenetic lineage in *Ustilaginomycotina*. Hence, they introduced new family (*Peribolosporaceae*), order (*Peribolosporales*) and class (*Peribolosporomycetes*).

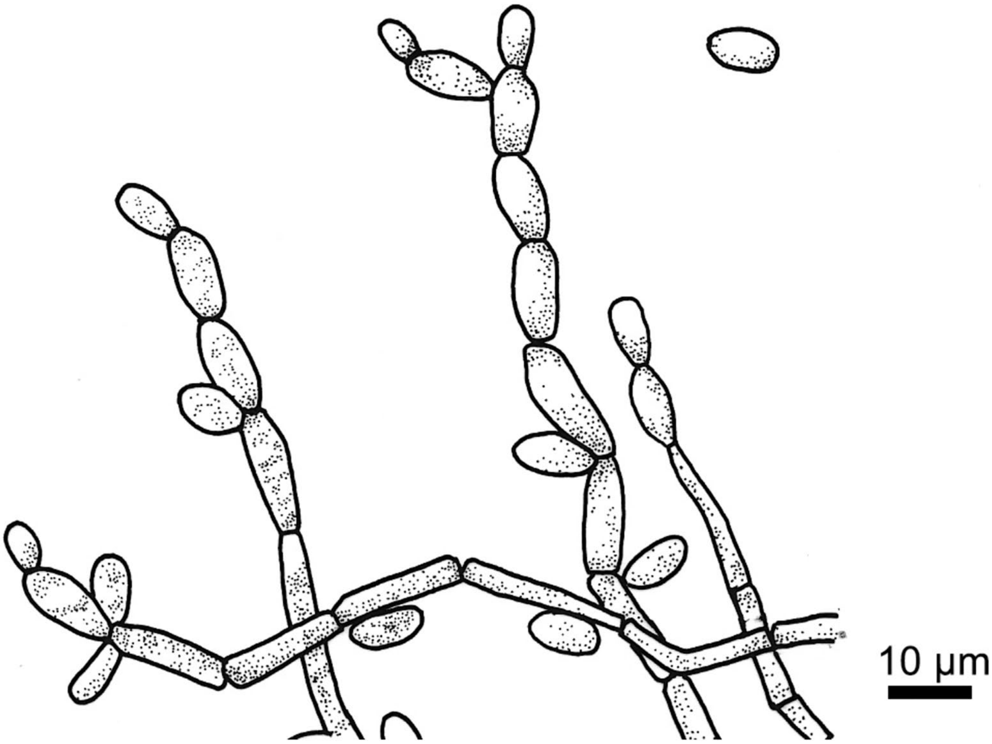


Fig. 32 Morphology of *Moniliella pyrgileucina* (redrawn from Thanh et al. 2018)

Type order: ***Peribolosporales*** Witfeld, M.A. Guerreiro, H.D.T. Ngyuen & Begerow, in Witfeld, Guerreiro, Nitsche, Wang, Ngyuen & Begerow, Mycol. Progr. 22(4, no. 30): 11 (2023).
Type family: ***Peribolosporaceae*** Witfeld, M.A. Guerreiro, H.D.T. Ngyuen & Begerow, in Witfeld, Guerreiro, Nitsche, Wang, Ngyuen & Begerow, Mycol. Progr. 22(4, no. 30): 10 (2023).
Type genus: ***Peribolospora*** Witfeld, M.A. Guerreiro, H.D.T. Ngyuen & Begerow, in Witfeld, Guerreiro, Nitsche, Wang, Ngyuen & Begerow, Mycol. Progr. 22(4, no. 30): 11 (2023).
Type species: ***Peribolospora baueri*** Witfeld, M.A. Guerreiro, H.D.T. Ngyuen & Begerow, in Witfeld, Guerreiro, Nitsche, Wang, Ngyuen & Begerow, Mycol. Progr. 22(4, no. 30): 11 (2023).

Ustilaginomycetes Warm., Haandb. syst. Bot., Edn 2 (Kjøbenhavn): 57 (1884).

Index Fungorum Registration Identifier: 816414.

Free-living saprobic phase with yeast and pathogenic on many plants, typically grasses of the family Poaceae, shrubs, some ferns, and conifers, or parasites on animals.

Sexual morph: *Sori* surrounding stems, inflorescence, ovaries, and organs, long-cylindrical, circular, subcircular, angular to tubular or curved, hypertrophied sometimes bearing small remnants of deformed glumes or as leaf spots, whitish to brown or yellow-green with or without peridium, peridium greyish to brown splitting longitudinally to expose powdery spore mass, sori not usually present in all organs, partitioning cells may be present or absent (Piepenbring 2001; Shivas et al. 2006; McTaggart et al. 2016). *Columellae* sometimes present or absent, stout or woody, flagelliform or filiform. *Spore balls* colourless to pigmented, irregular to globose to slightly flattened when connected to adjacent balls, composed of compacted masses of spores, friable or persistent with or without cortex, lobed, and with a central part consisting of parenchymatous sterile cells in the air canals of the mesophyll. *Teliospores* correspond to probasidia, thick-walled, dark-coloured, sometimes smooth-walled, usually ornamented with warts and ridges, arranged singly or in pairs, multicellular or in pairs, in groups or balls, elongate, globose, subglobose, sometimes broadly ellipsoidal, ovoid, subcuneiform, boomerang shaped, sometimes irregular, collapsed, hemispherically cupped, sub-angular, oblong, club-shaped to oval, three-layered (perisporium, episporium, endosporium), pale olivaceous brown to reddish brown in colour (Rattan et al. 1995; Vánky et al. 2009; Hu et al. 2018). Teliospores germinate into a cylindrical, four-celled basidium that buds as basidiospores. *Basidia* club-shaped, phragmobasidial, or holobasidial, with or without septa, respectively. *Basidiospores* numerous, filiform, uninucleate, mostly ballistosporic, and others are passively released (Bauer et al. 2001; Hu et al. 2018).

Asexual morph: hyphomycetous or yeast-like. **Hyphomycetous** *Conidiophores* solitary or aggregated, semi-macronematous to micronematous. *Conidiogenous cells* monoblastic, basally clamped, single conidia derived by completely transferring protoplasm. *Conidia* navicular, obclavate, or fusiform to ellipsoidal on short sterigmata-like structures with 3–4 branches, sometimes narrow at the base, along with many bristle-like distal branches. *Chlamydospores* present. (Marvanova and Bandoni 1987; Mekha et al. 2014). **Yeast** budding yeast-like phase, with the presence of hyphae and pseudohyphae, cells spherical, ellipsoidal to fusoid-shaped on short denticles, cream to light salmon in colour (Piątek et al. 2017).

Life modes and distribution: The members of *Ustilaginomycetes* are distributed in a wide range of habitats and are reported to follow different life modes (Boekhout 1995; Avis et al. 2001). They are mostly phytopathogenic, mostly infecting members of the grass families *Poaceae* and *Cyperaceae*, and are responsible for causing smut diseases and huge economic losses (e.g., *Ustilago maydis* and *U. nuda*) (Kruse et al. 2017) (Table 20). *Melanotaenium oreophilum* and *M. selaginellae* are two smuts found to be associated with *Selaginella* (Bauer et al. 1999). Rarely, some yeast morphs of the members have also been reported to infect humans (Teo and Tay 2006; McNeil and Palazzi 2012) (Table 21). Some of the members have been isolated from the leaves, fruits, and flowers of plants; there are also reports of isolation from human secretory fluid or blood (Sugita et al. 2003; Arendrup et al. 2014). *Moesziomyces antarcticus* has been isolated from soil and plants and rarely from human blood (Boekhout 2011). *Moesziomyces aphidis* was first isolated from an aphid and was later also isolated from water (Boekhout 2011). Rarely, a few species of *Ustilaginomycetes* parasitize ferns or conifers (Bauer et al. 1999, 2001). Riess et al. (2016) reported *Uleiella chilensis* to be parasitic on gymnosperms like *Araucaria araucana*.

Notes: Warming (1884) introduced the class *Ustilaginomycetes* of the phylum *Basidiomycota*. Bauer et al. (1997), on the basis of ultrastructural markers, revealed that *Ustilaginomycetes* form three lineages belonging to the phyto-parasitic members that lack dolipore with multilayered pore-bearing caps. Bauer et al. (2006) and Hibbett et al. (2007), in their phylogenetic classification of fungi, renamed the clade *Ustilaginomycetes* as in Kirk et al. (2008) as *Ustilaginomycotina* to minimize confusion between the names of the taxon and informal terms. Tedersoo et al. (2018), in their classification of the fungi, placed the class *Ustilaginomycetes* under the subphylum *Ustilaginomycotina*.

Hyde et al. (2011), in an initial attempt to compile asexually typified genera among the members of the Kingdom *Fungi*, incorporated anamorphic fungi in the class *Ustilaginomycetes* according to the natural system of classification. Later, Wijayawardene et al. (2012, 2017b, 2021b) published an updated checklist along with notes and entries on the pleomorphic genera in *Ustilaginomycetes*. Aime et al. (2018) recommend the use of generic names in place of synonymous alternate asexually typified morph generic names for several members of *Ustilaginomycetes*, such as *Anthracoidea* for *Crotalia*, *Mycosarcoma* or *Ustilago* for *Pseudozyma*, *Thecaphora* for *Rhombiella* and *Thecaphorella*, and *Urocystis* for *Paepalopsis*.

Table 20 Examples of economically important *Ustilaginomycetes*

Species	Host	References
Mycosarcoma maydis (formerly known as *Ustilago maydis*)	*Zea mays*	McTaggart et al. (2016), Kruse et al. (2017)
Sporisorium scitamineum	*Sugarcane*	Bhuiyan et al. (2021)
Ustilago avenae	*Avena sativa*	Hu et al. (2018)
Ustilago hordei	*Hordeum vulgare* and *Avena sativa*	Ökmen et al. (2021)
Ustilago nuda	*Hordeum vulgare*	Kruse et al. (2017)
Ustilago tritici	*Triticum aestivum*	Nielsen and Thomas (1996), Thambugala et al. (2020)

According to Kijpornyongpan et al. (2018), the class comprises three orders: *Ustilaginales*, *Urocystidales*, and *Uleiellales* (Bauer et al. 1997; Riess et al. 2016). The order *Ustilaginales* contains eight families, 49 genera, and 851 species (Kirk et al. 2008). *Urocystidales* has six families and 400 taxa (Begerow et al. 2006, 2014), and the order *Uleiellales* is comprised of one family (*Uleiellaceae*), a single genus (*Uleiella*), and two species (Riess et al. 2016). There are no recognized subclasses under *Ustilaginomycetes*.

Many pleomorphic taxa among the members of *Ustilaginomycetes* have been reported (Kirk et al. 2008). Wang et al. (2015a) proposed taxonomic revisions to adopt one name (between two generic names) when the links between the morphs are confirmed in *Ustilaginomycetes*. Since the discontinuation of dual names for fungi (Hawksworth et al. 2011), Wang et al. (2015a) and Kruse et al. (2017) have made important publications dealing with the recent nomenclatural changes.

Phylogenetic analyses of the rRNA gene (SSU, ITS, LSU, *atp6*, and *tub* sequence data) of Hibbett et al. (2007) and Begerow et al. (2006) accommodated this class in subphylum *Ustilaginomycotina*. He et al. (2019) provided the divergence time estimates for the various orders and families in the class *Ustilaginomycetes*. According to Wijayawardene et al. (2022a), the class comprises four orders (*Uleiellales*, *Urocystidales*, *Ustilaginales*, and *Violaceomycetales*), 15 families, and 68 genera. However, two genera,

Table 21 Medicinally/clinically significant *Ustilaginomycetes* in humans

Species	References
Mycosarcoma maydis	Wołczańska and Szysz (2018)
Moesziomyces antarcticus (formerly known as *Pseudozyma antarctica*)	Gugnani (2022)
Moesziomyces aphidis (formerly known as *Pseudozyma aphidis*)	Gugnani (2022)
Moesziomyces bullatus	Okolo et al. (2015)
Moesziomyces parantarcticus (formerly known as *Pseudozyma parantarctica*)	Gugnani (2022)
Pseudozyma alboarmeniaca	Mekha et al. (2014)
Pseudozyma crassa	Mekha et al. (2014)
Pseudozyma siamensis	Mekha et al. (2014)
Pseudozyma thailandica	Gugnani (2022)
Dirkmeia churashimaensis	Chowdhary et al. (2020), Hu et al. (2021)

Capitulocladosporium and *Eriocortex* are classified in *Ustilaginomycetes* genera *incertae sedis.*

Type order: ***Ustilaginales*** Bek., Kurs Botaniki 1: 221 (1864).
Type family: ***Ustilaginaceae*** Tul. & C. Tul. [as 'Ustilagineae'], Annls Sci. Nat., Bot., sér. 3 7: 14 (1847).
Type genus: ***Ustilago*** (Pers.) Roussel, Fl. Calvados, Edn 2: 47 (1806).
Type species: not indicated (see editorial comments in Index Fungorum 2023).

Subphylum *Wallemiomycotina* Doweld, Index Fungorum 73: 1 (2014).
Notes: Doweld (2014j) introduced *Wallemiomycotina* to accommodate a single phylum, i.e. *Wallemiomycetes*. He et al. (2024) accepted this placement.

Wallemiomycetes Zalar, de Hoog & Schroers, Antonie van Leeuwenhoek 87(4): 322 (2005).

Index Fungorum Registration Identifier 501496.

Sexual morph: *Basidiomata* absent; *Basidia* singly or in clusters, irregular in shape, arising from primary cells with a probasidium; single sterigmata or sterigmata-like cells present; *basidiospores* produced by some genera; single basidiospore in one basidium; globose, rarely subglobose; hirsute; hyaline; double-walled; browning on maturity (Nguyen et al. 2013). **Asexual morph: hyphomycetous.** *Conidiophores* solitary or aggregated, unbranched, erect or sometimes sympodial, smooth-walled, and little constricted below the apex. *Conidiogenous cells* continuing from conidiophores, verruculose, cylindrical, biaxially extending, disarticulating basipetally, four arthrospore-like conidia, forming chains. *Conidia* single-cell, verruculose or spherical, short cylindrical, thick-walled, and pale brown (Zalar et al. 2005; Jančič et al. 2015; Díaz-Valderrama et al. 2017).

Life modes and distribution: The members of *Wallemiomycetes* are cosmopolitan in distribution and are xerophilic and halophilic in nature. The members are airborne and found to be associated with solar salts, salt crystals, dried plant parts such as hay and seeds, dried food, and are also responsible for food spoilage and agricultural aerosols (Zalar et al. 2005; Díaz-Valderrama et al. 2017; Zajc and Gunde-Cimerman 2018). Some strains are known to cause subcutaneous skin infections in humans (de Hoog et al. 2000) and hypersensitivity pneumonitis (farmer's lung disease), caused by *Wallemia sebi* (Lappalainen et al. 1998; Roussel et al. 2005).

Notes: The class *Wallemiomycetes* was introduced by Zalar et al. (2005) and is one of the smallest classes of *Basidiomycota*. Matheny et al. (2006) attempted to resolve the phylogenetic position of *Wallemiomycetes* using nuclear protein-coding genes. Zhao et al. (2017) tried to resolve the phylogenetic obscurity of the class based on the concepts of molecular data.

The class *Wallemiomycetes* is placed in phylogenetic trees in slightly different ways depending on which gene regions are analysed and which phylogenetic inference method is used (Zalar et al. 2005; Matheny et al. 2006). Analyses of the parsimony of the nrDNA data revealed that *Wallemiomycetes* is an early diverging branch of the *Basidiomycota* and that it occupies a basal position close to *Entorrhizomycetidae* (Matheny et al. 2006). He et al. (2024) confirmed that *Wallemiomycetes* belongs to the subphylum *Wallemiomycotina.* The class comprises two orders, *Geminibasidiales* and *Wallemiales* (Wijayawardene et al. 2022a; He et al. 2024).

Some members of *Wallemiomycetes* are medicinally important taxa. *Wallemia sebi* causes allergies, bronchial asthma, farmer's lung disease (in humans), chronic ulcerative skin lesions, and fatal livestock toxicosis (*fide* Cole and Samson 1979; Hanhela et al. 1995; Lappalainen et al. 1998, 2012; Reboux et al. 2001; Roussel et al. 2005; Zajc and

Gunde-Cimerman 2018). *Wallemia muriae* causes farmer's lung disease and bronchial asthma in humans (*fide* Zajc and Gunde-Cimerman 2018). *Wallemiomycetes mellicola* causes phaeohyphomycosis on the foot in immunocompetent human (Zajc and Gunde-Cimerman 2018).

Type order: ***Wallemiales*** Zalar, de Hoog & Schroers, Antonie van Leeuwenhoek 87(4): 322 (2005).
Type family: ***Wallemiaceae*** R.T. Moore, Rhizoctonia Species, Taxonomy, Molecular Biology, Ecology, Pathology and Disease Control (Dordrecht): 20 (1996).
Type genus: ***Wallemia*** Johan-Olsen, Skr. VidenskSelsk. Christiania, Kl. I, Math.-Natur. (no. 12): 6 (1887).
Type species: ***Wallemia ichthyophaga*** Johan-Olsen [as 'ichthiophaga'], Skr. VidenskSelsk. Christiania, Kl. I, Math.-Natur.(no. 12): 6 (1887).

BLASTOCLADIOMYCOTA T.Y. James, Mycologia 98(6): 867 (2007) [2006].

Index Fungorum Registration Identifier 501464.

Thallus monocentric or polycentric, may form hyphae, varies greatly in size and extent or degrees of complexity; zoospore with a single posteriorly directed whiplash-type flagellum possessing a lipid-filled organelle often called a side-body complex (SBC) composed of several lipid droplets, characterized by the presence of distinctive anteriorly located membrane-bounded ribosomal nuclear cap adjacent to the cone-shaped nucleus which abuts the kinetosome, cytoplasmic microtubules extending anteriorly from the proximal (upper) part of the kinetosome (the basal body of the flagellum) to surround the nuclear envelopes, absence of electron opaque plug in the transitional zone at the base of zoospore flagellum. Asexual reproduction through uniflagellated zoospores produced in zoosporangium, sexual reproduction by planogamete (sexual gamete) fusion and life cycle with sporic meiosis displaying alternation of gametophytic and sporophytic generations (James et al. 2006b).

Life mode and distribution: Saprobic on a wide variety of animal and plant substrates in both aquatic and terrestrial habitats. Some representatives are parasites of algae, fungi, plants and invertebrates of freshwater and soil environments, and occasionally found to be facultatively anaerobic that grow under foul conditions (Sparrow 1960; Karling 1977; James et al. 2006a, b, 2014; Hibbett et al. 2007; Powell 2017).

Notes: James et al. (2006b) introduced the phylum *Blastocladiomycota* since it formed a monophyletic clade, distinct from other early divergent lineages in the Kingdom *Fungi*. *Blastocladia* Reinsch (Reinsch 1877) the type genus of the phylum *Blastocladiomycota* was accommodated in its own family, *Blastocladiaceae* by Petersen (1910). Later, the Order *Blastocladiales* was introduced by Kanouse (1927). Fitzpatrick (1930) regarded *Blastocladiales* in the class *Phycomycetes* (i.e. 'A class formerly used for *Fungi* and now treated in Chromista (q.v.) and some fungi (*Chytridiomycota* and *Zygomycota*) *fide* Kirk et al. 2008). However, Alexopoulos (1966) accommodated *Blastocladiales* in *Chytridiomycetes*.

Tehler (1988) used the term '*Blastocladiomycota*', as a division of 'Subkingdom *Eumycota*' but did not provide type details or descriptions thus invalid. Doweld (2001) introduced *Blastocladiomycota* Doweld 2001 but invalid (Art. 38.1(a) (Shenzhen); 'Published as 'nom. nov.', based on *Allomycotina* Caval.-Sm., 1998 (David, Constancea 83.16: 5) *fide* Index Fungorum 2023). Hence, James et al. (2006b) provided proper diagnosis and description of the phylum thus, *Blastocladiomycota* T.Y. James 2006 [2007] is the correct name. Subsequent studies agreed with the conclusions in James et al. (2006b) and confirmed its phylogenetic placement in the fungal tree (e.g. Hibbett et al. 2007). Porter et al. (2011) showed the family placements of *Blastocladiomycota* but did not assign/ mention any subphyla or classes but their tree clearly showed the separation of *Physodermataceae*. Agreeing with Porter et al. (2011), Tedersoo et al. (2018) introduced Subphylum *Blastocladiomycotina* Tedersoo et al. and the Class *Physodermatomycetes* Tedersoo et al. Following studies by Wijayawardene et al. (2018b, 2020a) and Voigt et al. (2021) also agreed with the higher-level classification proposed by Tedersoo et al. (2018).

Currently comprises one subphylum (*Blastocladiomycotina*) and two classes.

Blastocladiomycetes Doweld, Prosyllabus Tracheophytorum, Tentamen Systematis Plantarum Vascularium (Tracheophyta) (Moscow): LXXVII (2001).

Isonym: *Blastocladiomycetes* T.Y. James, Mycologia 98 (6): 868 (2007).

Index Fungorum Registration Identifier 90742; Fig. 33

Thallus monocentric, polycentric or filamentous (sometimes presenting pseudosepta); zoospore with a single posteriorly oriented whiplash flagellum that lacks electron-opaque shield present in the kinetosome transition region, characterized by the presence of lateral membrane cisterna known as side-body complex (SBC), membrane-bound ribosomal aggregation known as a ribosomal cap (nuclear cap) containing a single cone-shaped nucleus that terminates adjacent to the kinetosome, cytoplasmic microtubules with anteriorly radiating roots leading from the proximal portion of the kinetosome continuing on to wrap around a nucleus; resting sporangium darkly pigmented and usually ornamented with spines or other projections. Asexual reproduction through posteriorly uniflagellate chemotactic zoospores (flagellated asexual spores), sexual reproduction through planogamete fusion with a sporic meiosis type of life cycle involving

Fig. 33 Microscopic characteristics of *Allomyces* spp. (*Blastocladiaceae*, *Blastocladiales*, *Blastocladiomycetes*). **a** Mature thallus of *Allomyces neomoniliformis* with some empty zoosporangia and resistant sporangia. **b** Young developing thallus of *Allomyces moniliformis.* **c** Dark brown and thick-walled resistant sporangia of *Allomyces neomoniliformis.* **d**–**f** Hypha with thin-walled zoosporangia in *Allomyces moniliformis.* **g**–**i** Thin-walled zoosporangia with papillae of *Allomyces moniliformis.* Scale bars: **a** = 60 µm, **b** = 100 µm, **c** = 40 µm, **d**–**f** = 100 µm, **g**–**i** = 50 µm

alternation of a haploid gametophytic (which produces gametes) with a diploid sporophytic (produces asexual spores) generation (James et al. 2006b).

Life mode and distribution: The members of *Blastocladiomycetes* are widely distributed in a broad range of aquatic and terrestrial ecosystems throughout the world and are reported commonly as saprotrophs, feeding on decomposing organic matter, with different types of life cycle. This very large and morphologically diverse class also contains many parasites of various soil inhabiting small invertebrates, their eggs and fungi in water-logged soil or water (Sparrow 1960; Karling 1977; James et al. 2014; Powell 2017).

Notes: Doweld (2001) introduced this class to accommodate *Blastocladia* Reinsch 1877 (*Blastocladiaceae*, *Blastocladiales*). James et al. (2006b) also introduced *Blastocladiomycetes* but it is an isonym of *Blastocladiomycetes* Doweld. Currently, the class comprises three orders i.e. **1.** *Blastocladiales* (families *Blastocladiaceae* H.E. Petersen, *Catenariaceae* Couch, *Paraphysodermataceae* Doweld, and *Sorochytriaceae* Dewel); **2.** *Callimastigales* Doweld (families: *Callimastigaceae* Fonseca); **3.** *Catenomycetales* Doweld (*Catenomycetaceae* Doweld, *Coelomomycetaceae* Couch).

Type order: ***Blastocladiales*** H.E. Petersen [as 'Blastocladiineae'], Bot. Tidsskr. 29: 357 (1909).

Type family: ***Blastocladiaceae*** H.E. Petersen, Bot. Tidsskr. 29: 357 (1909).
Type genus: ***Blastocladia*** Reinsch, Jb. wiss. Bot. 11(2): 291 (1877).
Type species: ***Blastocladia pringsheimii*** Reinsch [as 'pringsheimi'], Jb. wiss. Bot. 11(2): 367 (1877).

Physodermatomycetes Tedersoo, Sánchez-Ramírez, Kõljalg, Bahram, Döring, Schigel, T. May, M. Ryberg & Abarenkov, Fungal Divers. 90: 148 (2018).

Index Fungorum ID: 553995; Fig. 34

Thallus monocentric to polycentric, eucarpic, epibiotic with slightly branched and limited rhizoids generally arising from a single axis near the base of the thin-walled sporangium, with endogenous (intracellular) development; Golgi apparatus or dictyosome with stacked cisternae and vesicles in sporangium; zoospores produces bipolar growth; the posteriorly uniflagellate zoospores present a characteristic nuclear cap of ribosomes (membrane-bound aggregated ribosomes) with adjacent nucleus attached to centriole; resting sporangium thick-walled and typically darkly pigmented; germination and development of sporangium through protruding endosporangium (Tedersoo et al. 2018).

Life mode and distribution: Representatives within this class are common obligate parasites of microalgae, pteridophytes and angiosperms in aquatic and marshy habitats throughout the world (Sparrow 1960).

Notes: Tedersoo et al. (2018) introduced this class to accommodate *Physoderma* Wallr. (*Physodermataceae*, *Physodermatales*). Characterized by bearing both monocentric thallus with an endobiotic polycentric thallus. Spores germinate producing zoospores that infect the specific host. The initial infestation generates the monocentric, epibiotic zoosporangium that is attached to endobiotic rhizoids that are limited to a single host cell where the zoosporangium is characterized as *Rhizidium* or *Phlyctochytrium*. The zoospores liberate and infect healthy new host cells, where the infestation transmits through number of generations. The internally proliferous sporangia produce a second flush of zoospores after the liberation of the first round. The zoospores develop into an endobiotic polycentric thallus which is often extensive. The highly branched thallus with rhizoids infects a large number of host cells. These rhizoids possess intercalary cells, which contain septa are evident for sexual reproduction. The endobiotic thallus produces large, dark-coloured resting spores with thick-wall and with the shape of host cells. Resting spores appear as formed by intercalary cells (Sparrow 1962; Karling 1977; James et al. 2014; Powell 2017).

Type order: ***Physodermatales*** Caval.-Sm., Eur. J. Protist. 49:157.
Type family: ***Physodermataceae*** Sparrow, Mycologia 44(6): 768 (1952).
Type genus: ***Physoderma*** Wallr., Fl.crypt. Germ. (Norimbergae) 2: 192 (1833).
Type species: ***Physoderma maculare*** Wallr., Fl. crypt. Germ. (Norimbergae) 2: 192 (1833).

CALCARISPORIELLOMYCOTA Tedersoo, Sánchez-Ramírez, Kõljalg, Bahram, Döring, Schigel, T. May, M. Ryberg & Abarenkov, Fungal Divers. 90: 152 (2018).

Index Fungorum Registration Identifier 554019.

Members are characterized with a branched thallus with septate hyphae. The vegetative hyphae smooth and thin, thin-walled and hyaline. In the case of presence of sporangiophores are hyaline, smooth, simple and originated from undifferentiated hyphae. The sporangia are unispored, ellipsoid with or without a tiny columella. Spores hyaline, thin-walled, smooth, uninucleate, ovoid, with a rounded base. At the presence of chlamydospores, characterized with single cell, thick spiny walls, elongated to globose, born laterally on short hyphae. The sexual morph is unknown (Hirose et al. 2012; Zhao et al. 2022).

Life modes and distribution: Saprobic in soil and non-nematophagous in soils.

Notes: Tedersoo et al. (2018) showed that *Calcarisporiella thermophila*, the type species of *Calcarisporiella* and *Echinochlamydosporium variabile*, the type species of *Echinochlamydosporium* formed a distinct phylogenetic lineage in the Kingdom *Fungi*. Hence, Tedersoo et al. (2018) introduced *Calcarisporiellomycota*.

Calcarisporiellomycetes Tedersoo, Sánchez-Ramírez, Kõljalg, Bahram, Döring, Schigel, T. May, M. Ryberg & Abarenkov, Fungal Diversity 90: 152 (2018).

Index Fungorum Registration Identifier: 554020; Fig. 35

Similar to the phylum description.

Notes: *Calcarisporiellomycetes* comprises only one order and one family i.e. *Calcarisporiellales*, *Calcarisporiellaceae*, resepectively. *Calcarisporiella* and *Echinochlamydosporium* are the genera contained by *Calcarisporiellomycetes*. *Calcarisporiella* is a monotypic anamorphic genus and was previously considered to be an ascomycetous anamorphic genus belong to *Pezizomycotina* based on morphology of the anamorph. Besides, the spore formation process, and the presence of septate hyphae were other concerns for the revisions of the classification (Zhao et al. 2005; Kirk et al. 2008).

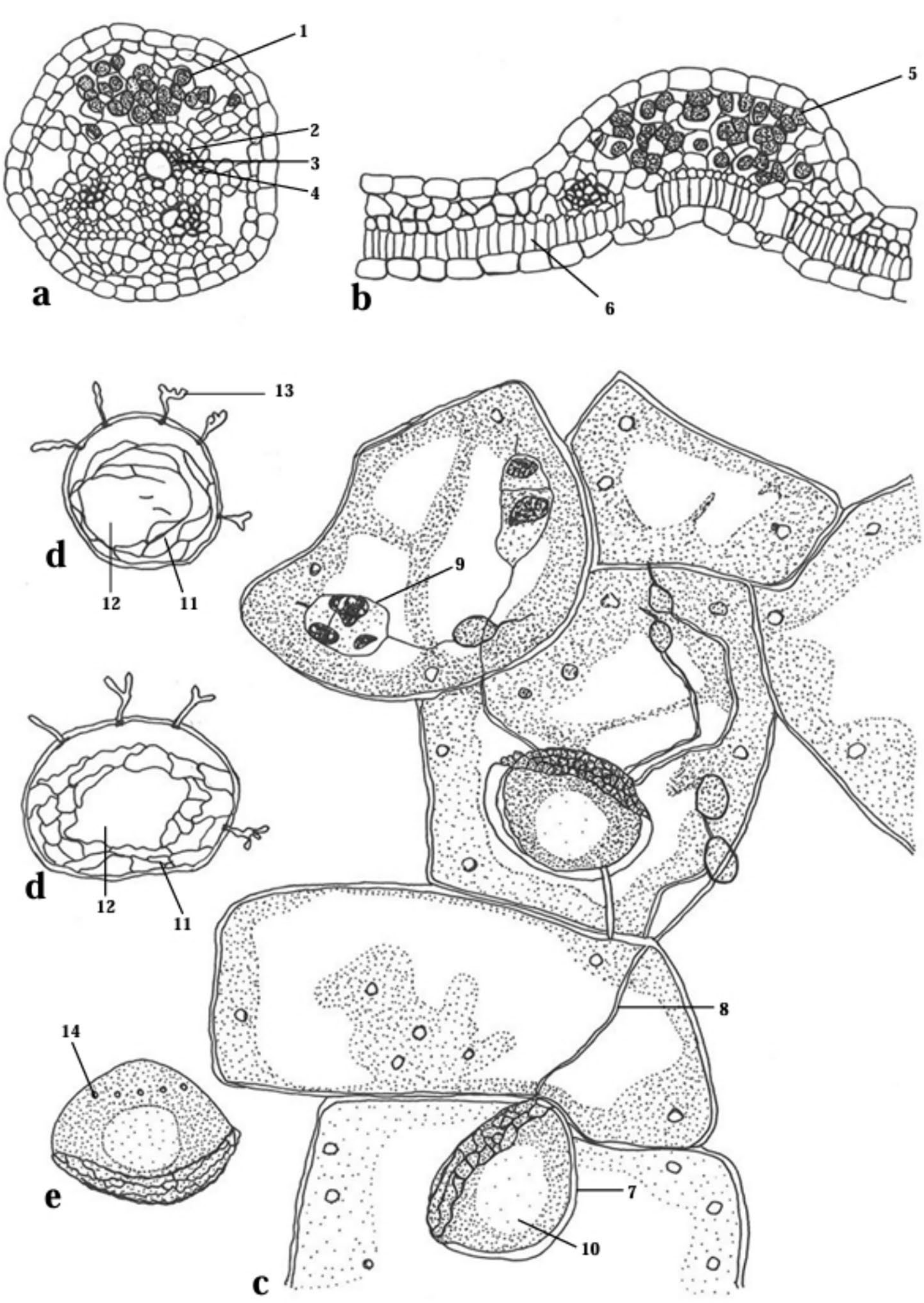


Fig. 34 *Physoderma marsileae* **a** Petiole showing very gall histology and normal tissue. Resting spores (1), endodermis (2), protoxylem (3), pericycle (4), ×100. **b** Leaflet showing gall histology and normal tissue and expanded portion of leaflet and row of resting spores (5), and one-half of palisade cells (6), ×100. **c** Mature resting spores (7) within host cells, showing rhizoidal system (8) and turbinate organs (9). Also large central body in resting spore (10), ×1790. **d** Resting spore showing wrinkled area (11) and concave area (12) with antler-like haustorial processes (13), ×1790. **e** Mature resting spore showing wrinkled area and supraequatorial ring of pits (14), ×1790 (redrawn from Brewster 1952)

Type order: ***Calcarisporiellales*** Tedersoo, Sánchez-Ramírez, Kõljalg, Bahram, Döring, Schigel, T. May, M. Ryberg & Abarenkov, Fungal Diversity 90: 152 (2018).
Type family: ***Calcarisporiellaceae*** Tedersoo, Sánchez-Ramírez, Kõljalg, Bahram, Döring, Schigel, T. May, M. Ryberg & Abarenkov, Fungal Diversity 90: 152 (2018).
Type genus: ***Calcarisporiella*** de Hoog, Stud. Mycol. 7: 68 (1974).
Type species: ***Calcarisporiella thermophila*** (H.C. Evans) de Hoog, Stud. Mycol. 7: 68 (1974).

CHYTRIDIOMYCOTA Doweld, Prosyllabus Tracheophytorum, Tentamen Systematis Plantarum Vascularium (Tracheophyta) (Moscow): LXXVII (2001);

= *Caulochytriomycota* Doweld, Index Fungorum 49: 1 (2014).

Index Fungorum Registration Identifier 550346; Fig. 36

Fungi with eucarpic, monocentric or polycentric thallus, endogenous or exogenous development; some with plasmodial thallus; asexual reproduction usually by zoospores posteriorly uniflagellate, nine ciliary props, microbody–lipid globule complex (MLC) consisting of a cisterna which may

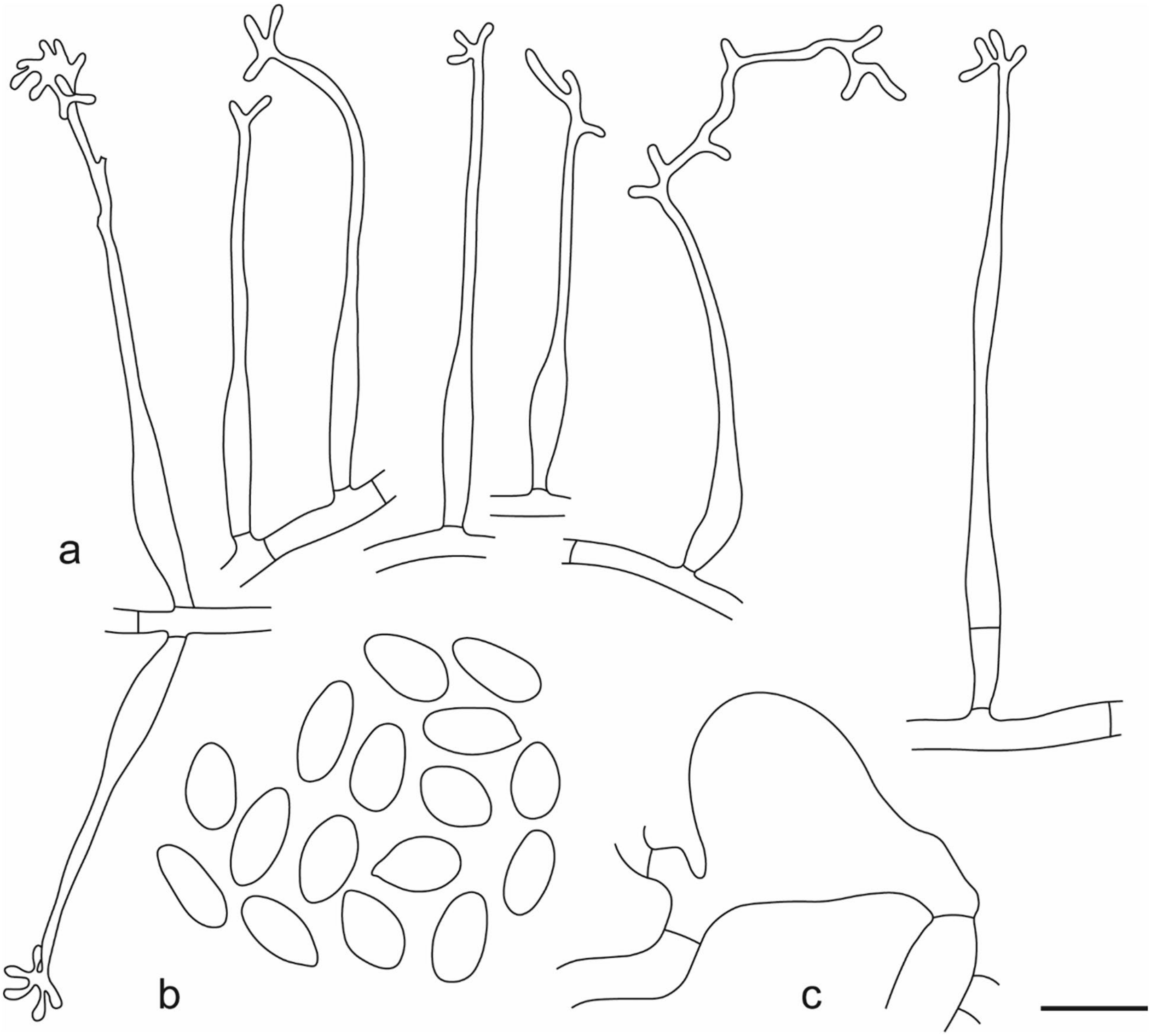


Fig. 35 *Calcarisporiella thermophila* (Basionym = *Calcarisporium thermophile*) (holotype, CBS 279.70). **a** Conidiogenous cells. **b** Conidia. **c** Inflated hyphal cell in culture at 45 °C. Scale bar **a**, **b**, **c** = 10 mm (redrawn from de Hoog 1974)

be simple or fenestrated, microbodies and mitochondria associated with lipid globules; Golgi apparatus with stacked cisternae; nuclear envelope fenestrated at poles during mitosis; resting spores, when present, formed asexually or sexually by conjugation of thalli (Hibbett et al. 2007; Powell and Letcher 2014; Adl et al. 2019).

Life modes and distribution: Saprotrophic in aquatic or terrestrial ecosystems, or facultative and obligate parasites of algae, amphibians, fungi, protists and plant tissues.

Notes: Doweld (2001) introduced the phylum *Chytridiomycota*. Several major studies, before 2010 concluded that *Chytridiomycota* taxa are polyphyletic (e.g. James et al. 2006a, b). Thus, Hibbett et al. (2007) restricted the phylum to include only two classes, i.e. *Chytridiomycetes* and *Monoblepharidomycetes*. Tedersoo et al. (2018) however elevated *Monoblepharidomycetes* to phylum as *Monoblepharomycota* thus not belonging to *Chytridiomycota*. Furthermore, Tedersoo et al. (2018) introduced eight new classes in *Chytridiomycota*; viz., *Cladochytriomycetes* Tedersoo et al., *Lobulomycetes* Tedersoo et al., *Mesochytriomycetes* Tedersoo et al., *Polychytriomycetes* Tedersoo et al., *Rhizophlyctidomycetes* Tedersoo et al., *Rhizophydiomycetes* Tedersoo et al., *Spizellomycetes* Tedersoo et al. and *Synchytriomycetes* Tedersoo et al. Interestingly, James et al. (2006b) showed that the classes introduced by Tedersoo et al. (2018) are well-separated orders in their analyses, except for *Mesochytriomycetes* and *Lobulomycetes*. Seto et al. (2017) confirmed the results

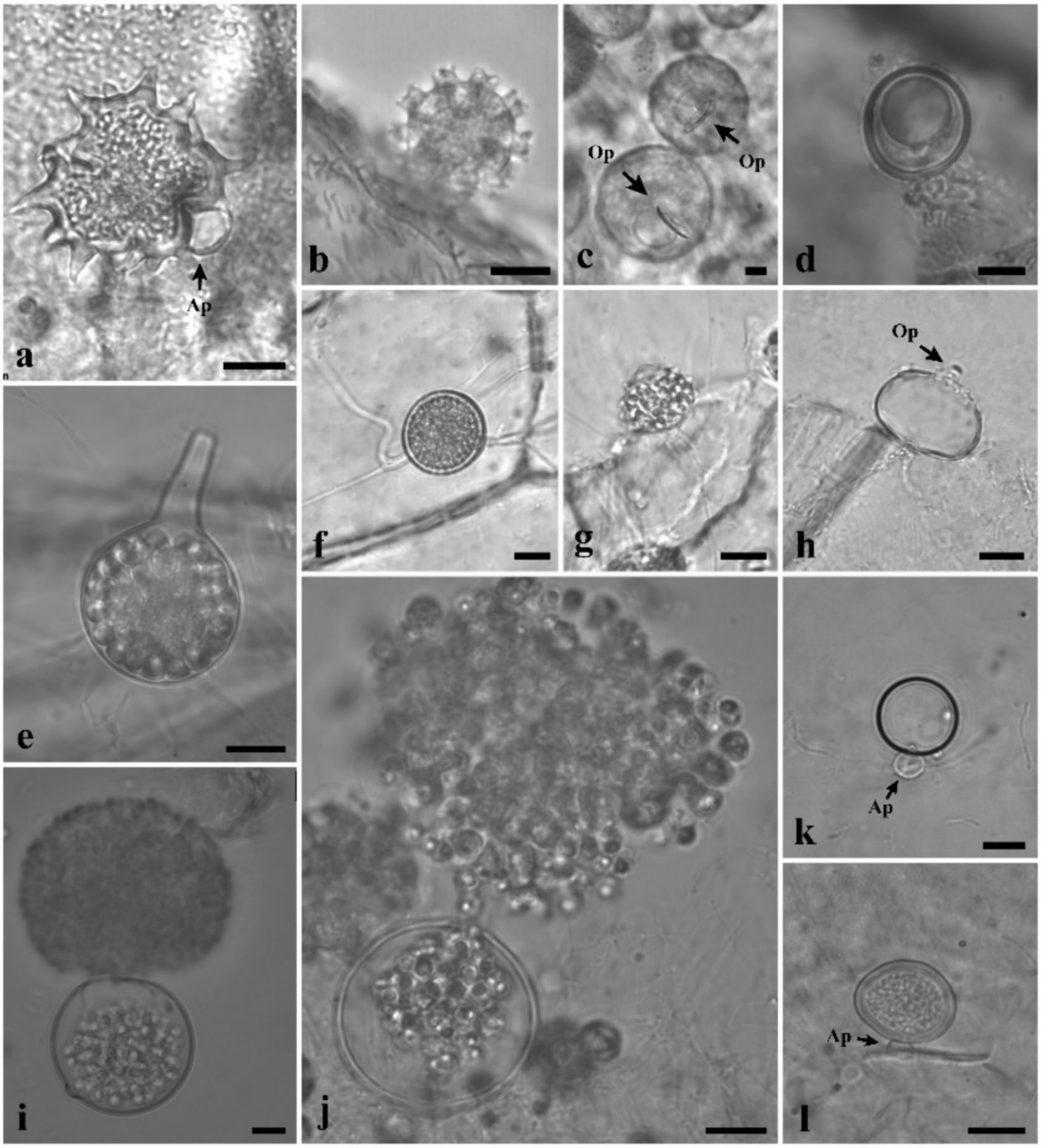


Fig. 36 *Chytridiomycota* (*Chytridiales*). **a** Resting spore of *Asterophlyctis sarcoptoides* on shrimp exoskeleton. **b** Zoosporangium of *Phlyctochytrium aureliae* on snake skin. **c**, **d** *Chytriomyces hyalinus* on onion skin. **c** Zoosporangium. **d** Resting spore. **e**, **f** *Entophlyctis luteolus* on onion skin. **e** Zoosporangium. **f** Resting spore. **g**, **h** *Fayochytriomyces spinosus* on onion skin. **g** Zoosporangium. **h** Empty zoosporangium. **i** Zoosporangium discharge of *Rhizidium crepaturum* on shrimp exoskeleton. **j** Zoosporangium discharge of *Rodmanochytrium sphaericum* on shrimp exoskeleton. **k**, **l** *Rhizoclosmatium globosum* on shrimp exoskeleton. **k** Empty zoosporangium. **l** Resting spore. *Ap* apophysis; *Op* operculum. Scale bars: **a**–**l** = 10 µm

of James et al. (2006b) and confirmed the separation of *Mesochytriales* and *Lobulomycetales*.

Tedersoo et al. (2018) introduced the Subkingdom *Chytridiomyceta* Tedersoo et al. to accommodate *Chytridiomycota* along with *Monoblepharomycota* and *Neocallimastigomycota*. Furthermore, Tedersoo et al. (2018) introduced *Chytridiomycotina* Tedersoo et al., the only subphylum in *Chytridiomycota*.

Recent higher-level classification studies showed that *Caulochytrium protostelioides* (only representative taxon of *Caulochytriomycota*) nested in *Chytridiomycota* (Ahrendt et al. 2018; Strassert and Monaghan 2022a, b; supplementary tree). The type species lacks genomic data but here we agree with previous studies and our phylogenomic analysis and regard *Caulochytriomycota* as a synonym of *Chytridiomycota* and regard *Caulochytriomycetes* as a class in *Chytridiomycota.* Hence, currently, *Chytridiomycota* comprises ten classes.

Caulochytriomycetes Doweld, Index Fungorum 49: 1 (2014).

Index Fungorum Registration Identifier 550345 (Fig. 37).

Sporangia thin-walled, of two types, sessile and hollow-stalked aerial. Zoospores posteriorly uniflagellate, flagellum laterally inserted, flagellar insertion subapical to parabasal. Rhizoplast striated, attaches the proximal end of the kinetosome to a specialized region of the nuclear envelope; no nuclear cap; microbody-lipid globule complex comprises several lipid globules, branching microbody, membrane cisternae and circular mitochondria. Pulsating vacuolar system associated with the flagellar apparatus and endoplasmic reticulum with dictyosomes and coated vesicles (Doweld 2014a).

Life modes and distribution: Saprobic (Voos and Olive 1968) and parasitic on the mycelium of *Cladosporium* on *Acalypha hispida* (Olive 1980).

Notes: Doweld (2014a) introduced this class to accommodate *Caulochytrium* (*Caulochytriaceae, Caulochytriales*). Traditionally, *Caulochytrium* was accommodated in *Chytridiomycota* by several studies (e.g. Subramanian 1974; Olive 1980, 1983). However, Hibbett et al. (2007) mentioned the placement of the genus is uncertain. Doweld (2014a) introduced the subphylum *Caulochytriomycotina* and *Caulochytriomycota*. However, Galindo et al. (2021) and Strassert and Monaghan (2022a, b) and our analyses (Fig. 1) showed that *Caulochytrium protosteliodes* (non-type species) resided in *Chytridiomycota*.

Type order: ***Caulochytriales*** Doweld, Index Fungorum 49: 1 (2014).
Type family: ***Caulochytriaceae*** Subram., Curr. Sci. 43: 723 (1974).
Type genus: ***Caulochytrium*** Voos & L.S. Olive, Mycologia 60(3): 731 (1968).
Type species: ***Caulochytrium gloeosporii*** Voos & L.S. Olive, Mycologia 60(3): 731 (1968).

Chytridiomycetes Caval.-Sm., Biol. Rev. 73:246. 1998, emend. Tedersoo et al., Fungal Divers. 90: 148 (2018).

Index Fungorum Registration Identifier 816490.

Thallus eucarpic, monocentric or polycentric, endobiotic, interbiotic or epibiotic; plasmodial thallus sometimes present. Zoosporangium endogenous or exogenous to the zoospore cyst, inoperculate or operculate, apophysate or non-apophysate. Zoospores, when present, posteriorly uniflagellate with a non-flagellum centriole and a flagellum kinetosome, typically with kinetosome-associated structures; the microbody-lipid globule complex (MLC) cisterna is adjacent to the lipid globule. Resting spores, when present, formed asexually or sexually by conjugation of thalli (Sparrow 1960; Doweld 2014g; Powell and Letcher 2014; Letcher et al. 2018; Adl et al. 2019; Voigt et al. 2021).

Life modes: Saprobic in aquatic or terrestrial ecosystems, or usually facultative and obligate parasites of plants, animals, protists and algae.

Notes: Cavalier-Smith (1998) provided a brief Latin description of *Chytridiomycetes* which was emended by Tedersoo et al. (2018). The class comprises four orders; viz*., Chytridiales* Cohn, *Nephridiophagales* Doweld, *Polyphagales* Doweld and *Saccopodiales* Doweld (Wijayawardene et al. 2020a, 2022a; Voigt et al. 2021). *Chytridiales* is composed of four families based on ultrastructural and molecular studies, *Asterophlyctaceae*, *Chytridiaceae*, *Chytriomycetaceae* and *Pseudorhizidiaceae*, with 26 genera and more than 330 species. Members of *Phlyctochytriaceae* and *Phlyctorhizaceae* were transferred to other families within the order (James et al. 2006b; Vélez et al. 2011; Letcher et al. 2012; Vélez et al. 2013; Letcher and Powell 2014; Leshem et al. 2016; Letcher and Powell 2018; Letcher et al. 2018; Powell et al. 2018; Seto and Degawa 2018; Jesus et al. 2021). The members of *Scherfelliomycetaceae* are lacking sequences thus, classification is uncertain.

Nephridiophagales, erected by Doweld (2014g), is composed of *Nephridiophagaceae*, with four genera and 19 species (Wijayawardene et al. 2018b; Voigt et al. 2021). *Polyphagales* was created by Doweld (2014h) to include *Polyphagaceae*, currently with two genera and 16 species (Index Fungorum 2023). *Saccopodiales* was also erected by Doweld (2014i) to accommodate *Saccopodiaceae*, with one monotypic genus.

Type order: ***Chytridiales*** Cohn, Jber. schles. Ges. vaterl. Kultur 57: 279 (1879).
Type family: ***Chytridiaceae*** Bek., Kurs Botaniki 1: 271 (1864).
Type genus: ***Chytridium*** A. Braun, Betracht. Erschein. verjüng. Natur, Edn 2 (Leipzig): 198 (1851).
Type species: ***Chytridium olla*** A. Braun, Betracht. Erschein. verjüng. Natur, Edn 2 (Leipzig): 198 (1851).

Cladochytriomycetes Tedersoo, Sánchez-Ramírez, Kõljalg, Bahram, Döring, Schigel, T. May, M. Ryberg & Abarenkov, Fungal Diversity 90: 148 (2018).

Index Fungorum Registration Identifier 553997; Fig. 38

Thallus eucarpic, monocentric or polycentric; rhizoids catenulate, isodiametric or tapering. Zoospore chytridioid but with a cord-like microtubular root between the kinetosome and fenestrated cisterna, composed of up to 25 microtubules interconnected by linkers; a cisterna, microbody, and mitochondrion closely associated with the lipid globule;

mostly saprotrophic or pathogenic on algae (extracted from Tedersoo et al. 2018).

Life modes: Mostly saprotrophic or pathogenic on algae.

Notes: James et al. (2006b) and Seto et al. (2017) recognized *Cladochytriales* as a distinct clade in *Chytridiomycota.* Hence, Tedersoo et al. (2018) upgraded *Cladochytriales* (including five families i.e. *Catenochytridiaceae* Doweld, *Cladochytriaceae* J. Schröt., *Endochytriaceae* Sparrow ex D.J.S. Barr, *Nowakowskiellaceae* Sparrow ex Mozl.-Standr. and *Septochytriaceae* Mozl.-Standr.) to class level. Voigt et al. (2021) also agreed with the new class, *Cladochytriomycetes* and confirmed its placement in *Chytridiomycota*.

Currently, the class comprises only one order, i.e. *Cladochytriales* Mozl.-Standr.

Type order: *Cladochytriales* Mozl.-Standr., Mycol. Res. 113(4): 502 (2009).
Type family: *Cladochytriaceae* J. Schröt., in Engler & Prantl, Nat. Pflanzenfam., Teil. I (Leipzig) 1(1): 80 (1897).
Type genus: *Cladochytrium* Nowak., in Cohn, Beitr. Biol. Pfl. 2: 92 (1877) [1876].
Type species: *Cladochytrium tenue* Nowak., Beitr. Kenntn. Chytr.: 92 (1877) [1876].

Lobulomycetes Tedersoo, Sánchez-Ramírez, Kõljalg, Bahram, Döring, Schigel, T. May, M. Ryberg & Abarenkov, Fungal Diversity 90: 148 (2018).

Index Fungorum Registration Identifier 553999; Fig. 39

Thallus monocentric, eucarpic, with endogenous development; zoospore with opaque flagellar plug, anterior or posterior plug extensions; one or two lipid globules; lacking microtubule root, Golgi apparatus, striated inclusion, and electron opaque bodies near kinetosome (extracted from Simmons et al. 2009).

Life modes and habitats: Saprobes, present in soil, dung, marine and freshwater habitats (Simmons et al. 2009, 2012).

Notes: Simmons et al. (2009) showed that the new genus, *Lobulomyces* D. R. Simmons (type species: *Lobulomyces angularis* (Longcore) D. R. Simmons) has a distinct phylogenetic lineage in the Phylum *Chytridiomycota*, thus, introduced the family *Lobulomycetaceae* D. R. Simmons and the order *Lobulomycetales* D. R. Simmons, to accommodate the genus. Subsequent studies by Simmons et al. (2012) (who introduced *Alogomyces* D.R. Simmons & Letcher) and Seto and Degawa (2015) (who introduced *Cyclopsomyces* K. Seto & Degawa) confirmed the phylogenetics placement of *Lobulomycetales* in *Chytridiomycota*.

Tedersoo et al. (2018), however, introduced *Lobulomycetes* Tedersoo et al., a separate class to accommodate the subclade of *Lobulomycetales* in the Phylum *Chytridiomycota*. Wijayawardene et al. (2020a) and Voigt et al. (2021) agreed with this conclusion.

Type order: *Lobulomycetales* D.R. Simmons, Mycol. Res. 113(4): 453 (2009).
Type family: *Lobulomycetaceae* D.R. Simmons, Mycol. Res. 113(4): 453 (2009).
Type genus: *Lobulomyces* D.R. Simmons, Mycol. Res. 113(4): 454(2009).
Type species: *Lobulomyces angularis* (Longcore) D.R. Simmons, Mycol. Res. 113(4): 454 (2009).

Mesochytriomycetes Tedersoo, Sánchez-Ramírez, Kõljalg, Bahram, Döring, Schigel, T. May, M. Ryberg & Abarenkov, Fungal Diversity 90: 148 (2018).

Index Fungorum Registration Identifier 553998.

Thallus simple, with inoperculate, monocentric, epibiotic sporangium having endogenous development and slightly branched rhizoids near the sporangial base; zoospore centriole at an angle of ca. 30 degrees to kinetosome (extracted from Tedersoo et al. 2018).

Life modes and distribution: Parasites of freshwater algae, cosmopolitan.

Notes: The order *Mesochytriales* Doweld was introduced by Doweld (2013b) with the family *Mesochytriaceae* Doweld. Karpov et al. (2014c) also introduced *Mesochytriales* Karpov & Aleoshin but it is an isonym. Moreover, Karpov et al. (2014c) confirmed the phylogenetic placement of the order *Mesochytriales* and *Gromochytriales* Karpov & Aleoshin, in *Chytridiomycota*. However, Tedersoo et al. (2018) established a new class, *Mesochytriomycetes* to accommodate *Mesochytriales* and *Gromochytriales.* This arrangement was accepted by Voigt et al. (2021).

Currently, the class comprises two orders, viz., *Mesochytriales* and *Gromochytriales.*

Type order: *Mesochytriales* Doweld, Index Fungorum 45: 1 (2013).
Type family: *Mesochytriaceae* Doweld, Index Fungorum 45: 1 (2013).
Type genus: *Mesochytrium* B.V. Gromov, Mamkaeva & Pljusch, Nova Hedwigia 71(1–2): 159 (2000).
Type species: *Mesochytrium penetrans* B.V. Gromov, Mamkaeva & Pljusch, Nova Hedwigia 71(1–2): 159 (2000).

Polychytriomycetes Tedersoo, Sánchez-Ramírez, Kõljalg, Bahram, Döring, Schigel, T. May, M. Ryberg & Abarenkov, Fungal Diversity 90: 148 (2018).

Index Fungorum Registration Identifier 554000; Fig. 40c-e

Thallus polycentric or monocentric; monocentric species with multiple rhizoidal axes. Motile zoospores spherical, usually > 4 um diam., with or without flagellar plug and kinetosome spur; 0–3 microtubule roots present; nonflagellated centriole equal to or longer than diameter and attached to kinetosome throughout its length; cultures grow on chitin (extracted from Tedersoo et al. (2018), which was prepared using Longcore and Simmons (2012) and Powell and Letcher (2014)).

Life modes and distribution: Mostly in soil and freshwater, cosmopolitan.

Notes: Longcore and Simmons (2012) introduced the order *Polychytriales* in *Chytridiomycota* since *Polychytrium* Ajello, the type of the order, is segregated from the other members of the phylum. Tedersoo et al. (2018) upgraded the order to a class.

Type order: ***Polychytriales*** Longcore & D.R. Simmons, Mycologia 104(1): 279 (2012).
Type family: ***Polychytriaceae*** Doweld, Index Fungorum 89: 1 (2014).
Type genus: ***Polychytrium*** Ajello, Mycologia 34(4): 442 (1942).
Type species: ***Polychytrium aggregatum*** Ajello, Mycologia 34(4): 442 (1942).

Rhizophlyctidomycetes Tedersoo, Sánchez-Ramírez, Kõljalg, Bahram, Döring, Schigel, T. May, M. Ryberg & Abarenkov, Fungal Diversity 90: 148 (2018).

Index Fungorum Registration Identifier 554001.

Monocentric and eucarpic thallus; sporangium inoperculate or endo-operculate, interbiotic, with one or several discharge apparatus and multiple rhizoids; zoospores with a non-flagellated centriole positioned at an acute angle to the kinetosome, without microtubule roots and microtubules; organelles of the 'microbody-lipid globule complex (MLC) loosely arranged (Powell and Letcher 2014).

Life modes and distribution: Commonly saprotrophic on cellulosic substrates in the terrestrial ecosystems.

Notes: *Rhizophlyctidomycetes* was erected by Tedersoo et al. (2018). This class is composed of the order *Rhizophlyctidales*, which was proposed based on molecular monophyly and zoospore ultrastructure of *Rhizophlyctis rosea*-like isolates by Letcher et al. (2008a, b). Four monophyletic families, with different types of ultrastructural organization of the zoospores, are into this order, *Arizonaphlyctidaceae*, *Borealophlyctidaceae*, *Rhizophlyctidaceae* and *Sonorophlyctidaceae*, which have four genera, *Arizonaphlyctis*, *Borealophlyctis*, *Rhizophlyctis* and *Sonoraphlyctis*, respectively, and around 30 species (Powell and Letcher 2014).

Type order: ***Rhizophlyctidales*** Letcher, in Letcher, Powell, Barr, Churchill, Wakefield & Picard, Mycol. Res. 112(9): 1034 (2008).
Type family: ***Rhizophlyctidaceae*** H.E. Petersen [as 'Rhizophlyctaceae'], Bot. Tidsskr. 29: 357 (1909).
Type genus: ***Rhizophlyctis*** A. Fisch., in Winter, Rabenh. Krypt.-Fl., Edn 2 (Leipzig) 1(4): 114 (1892).
Type species: ***Rhizophlyctis rosea*** (de Bary & Woronin) A. Fisch., in Winter, Rabenh. Krypt.-Fl., Edn 2 (Leipzig) 1(4): 122 (1892).

Rhizophydiomycetes Tedersoo, Sánchez-Ramírez, Kõljalg, Bahram, Döring, Schigel, T.May, M. Ryberg & Abarenkov, Fungal Diversity 90: 149 (2018).

Index Fungorum Registration Identifier 554002; Fig. 40a

Thallus monocentric; ribosomes enclosed by a system of double membranes; mitochondria, microbodies, lipid globules, and membrane cisterna are typically associated as a microbody-lipid globule complex. The nonflagellated centriole and kinetosome lie parallel or slightly angled toward each other and are connected by fibrillar material. The base of the flagellum proper lacks an electron-opaque plug (extracted from Tedersoo et al. 2018 who modified the descriptions from Letcher et al. 2006; Powell and Letcher 2014).

Life modes and habitats: parasites and saprobes mostly in soil and freshwater.

Notes: The order *Rhizophydiales* was introduced by Letcher et al. (2006) and was accepted by James et al. (2006b) and Seto et al. (2017). Tedersoo et al. (2018) introduced *Rhizophydiomycetes* to accommodate *Rhizophydiales*. Compare to other classes in *Chytridiomycota*, *Rhizophydiomycetes* is rich in genera and families (James et al. 2006b; Wijayawardene et al. 2020a).

Type order: ***Rhizophydiales*** Letcher, in Letcher, Powell, Churchill & Chambers, Mycol. Res. 110(8): 908 (2006).
Type family: ***Rhizophydiaceae*** Letcher, in Letcher, Powell, Churchil & Chambers, Mycol. Res. 110(8): 909 (2006).
Type genus: ***Rhizophydium*** Schenk ex Rabenh., Flora Europaea algarum aquae dulcis et submarinae 3: 280 (1868) [1867].
Type species: ***Rhizophydium globosum*** (A. Braun) Rabenh., Flora Europaea algarum aquae dulcis et submarinae 3: 280 (1868) [1867].

Spizellomycetes Tedersoo, Sánchez-Ramírez, Kõljalg, Bahram, Döring, Schigel, T. May, M. Ryberg & Abarenkov, Fungal Diversity 90: 149 (2018).

Index Fungorum Registration Identifier 554003; Fig. 40b

Thallus monocentric, eucarpic; sprorangium inoperculate; nucleus of zoospores associated directly or indirectly with kinetosome; rumposomes absent; replacement of the translation elongation factor 1-alpha gene by elongation factor-like gene in genome (extracted from Tedersoo et al. (2018) who provided the modified descriptions from Barr (1980) and Powell and Letcher (2014)).

Life modes and habitats: mostly saprobes in soil and parasites of animals, fungi and stramenopiles.

Notes: Barr (1980) introduced *Spizellomycetaceae* D.J.S. Barr and *Spizellomycetales* D.J.S. Barr to accommodate *Spizellomyces* D.J.S. Barr. The phylogenetic placement of *Spizellomycetales* in *Chytridiomycota* was broadly accepted (e.g. James et al. 2006b; Seto et al. 2017). Tedersoo et al. (2018) upgraded the order to class rank. Currently, the class consists of one order and two families.

Type order: *Spizellomycetales* D.J.S. Barr, Can. J. Bot. 58: 2384 (1980).
Type family: *Spizellomycetaceae* D.J.S. Barr, Can. J. Bot. 58(22): 2384 (1980).
Type genus: *Spizellomyces* D.J.S. Barr, Can. J. Bot. 58(22): 2384 (1980).
Type species: *Spizellomyces punctatus* (W.J. Koch) D.J.S. Barr [as 'punctatum'], Can. J. Bot. 58(22): 2384 (1980).

Synchytriomycetes Tedersoo, Sánchez-Ramírez, Kõljalg, Bahram, Döring, Schigel, T. May, M. Ryberg & Abarenkov, Fungal Diversity 90: 149 (2018).

Index Fungorum Registration Identifier 554004.

Thallus endobiotic, holocarpic, in a form of a resting spore or sorus surrounded by a membrane, colonial in some stages of development; zoospores posterior, uniflagellate; with a single lipid globule surrounded by cisternae of endoplasmic reticulum and microbodies; gamma-like vesicles present; nuclear cap lacking; two kinetosomes almost in parallel, transversely striated; dictyosome solitary, associated with posterior rumposome; flagellar apparatus comprises kinetosome and secondary centriole; flagellar terminal plate biconcave if present (extracted from Tedersoo et al. 2018 who provided the description based on Doweld (2014b) and Powell and Letcher (2014)).

Life modes and habitats: mostly pathogens of terrestrial plants.

Notes: James et al. (2006a, b) and Sekimoto et al. (2011) confirmed the placement of *Synchytrium* in *Chytridiomycota*. Doweld (2014b) introduced the order *Synchytriales* Doweld in *Chytridiomycota*. Powell and Letcher (2014), Smith et al. (2014) and Longcore et al. (2016) accepted *Synchytriales* as a distinct order in *Chytridiomycetes*. Tedersoo et al. (2018) upgraded *Synchytriales* to a class as *Synchytriomycetes*. Wijayawardene et al. (2020a, 2022a) and Voigt et al. (2021) agreed with the conclusion of Tedersoo et al. (2018).

Currently, *Synchytriomycetes* comprises only one order, i.e. *Synchytriales*.

Type order: *Synchytriales* Doweld, Index Fungorum 92: 1 (2014).
Type family: *Synchytriaceae* J. Schröt., in Engler & Prantl, Nat. Pflanzenfam., Teil. I (Leipzig) 1(1): 71 (1897).
Type genus: *Synchytrium* de Bary & Woronin, Verh. Naturf. Ges. Freiburg 3(2): 46 (1863).
Type species: *Synchytrium taraxaci* de Bary & Woronin, Verh. Naturf. Ges. Freiburg 3(2): 46 (1863).

ENTOMOPHTHOROMYCOTA Humber, Mycotaxon 120: 481 (2012).

Index Fungorum Registration Identifier 564375.

Conidiophores rising from mycelia or host body, usually phototropic, simple or apically branched, with an apical conidiogenous cell giving rise to a single conidium, or with septa and each cell forming a single conidium. Primary conidia mostly forcibly discharged, with outer wall continuous from that of conidiogenous cells, and inner wall invaginating to form two-layer septa separating conidia and conidiogenous cells. Secondary conidia usually formed, forcibly discharged from short secondary conidiophores and usually similar in shape to primary conidia, or passively dispersed from long, thin secondary conidiophores and usually distinct from primary conidia. Resting spores with thick and 2-layer walls, colored or hyaline, smooth or decorated. Zygospores or azygospores laterally or in the axis of the parental cells. Nuclear numbers more than two in mature spores. Mature spores forming germ conidiophores and germ conidia (secondary-conidia-like) or forming germ mycelia and germ conidia (primary-conidia-like).

Life modes and distribution: Saprobes in soil or litter, primary pathogens of arthropods (insect, mites, spiders) or other soil invertebrates (nematodes, tardigrades), or highly specific pathogens of desmid algae, fern gametophytes. Arthropod pathogens may form specialized organs: rhizoids with or without differentiated holdfasts may anchor hosts to substrates, and cystidia may perforate host cuticle and facilitate the emergence of conidiophores.

Notes: Hibbett et al. (2007) recognized *Entomophthoromycotina* Humber as a distinct subphylum along with three other subphyla *Mucoromycotina*, *Kickxellomycotina*, and

Zoopagomycotina. Humber (2012) elevated this subphylum to a phylum rank as *Entomophthoromycota*, including three classes, viz., *Basidiobolomycetes* Humber, *Neozygitomycetes* and *Entomophthoromycetes.* The placement of *Basidiobolomycetes* in *Entomophthoromycota* is not accepted in subsequent studies (e.g. Sekimoto et al. 2011; Gryganskyi et al. 2013), but placed in the phylum *Basidiobolomycota* instead (Tedersoo et al. 2018). And thus, *Entomophthoromycota* currently comprises two classes *Neozygitomycetes* and *Entomophthoromycetes* (Gryganskyi et al. 2013; Tedersoo et al. 2018; Wijayawardene et al. 2018b, 2020a; Voigt et al. 2021). Moreover, Tedersoo et al. (2018) considered that *Entomophthoromycota* is closely related to *Kickxellomycota* and *Zoopagomycota*, and introduced the subkingdom *Zoopagomyceta* to accommodate these three phyla.

Controversial opinions: It is worth to note that Spatafora et al. (2016) reassigned the subphylum *Entomophthoromycotina* into the phylum *Zoopagomycota.* Galindo et al. (2021) and Strassert and Monaghan (2022a, b) agreed on this placement. Therefore, the high-level taxonomic status of this fungal group needs more evidence to be clarified.

Entomophthoromycetes Humber, Mycotaxon 120: 486 (2012).

Index Fungorum Registration Identifier 564381; Fig. 41

Vegetative growth as coenocytic mycelia or rod-like to variably shaped hyphal bodies, walled; if wall-less, amoeboid. Conidiophores simple or digitately branched and with a single apical conidiogenous cell, or unbranched, septate and forming one conidium per cell. Primary conidia unitunicate or bitunicate, variously shaped, uni- to multinucleate, with flat, conical or rounded basal papilla, forcibly discharged by papillar eversion in most genera. Secondary conidia more or less similar in shape to primary conidia and forcibly discharged if formed on short secondary conidiophore, or elongate and passively dispersed if formed on elongated capillary secondary conidiophore. Nuclei with a small nucleolus, with interphasic heterochromatin present in *Entomophthoraceae* only, intranuclear mitosis, with a small lateral metaphase plate, with interphasic chromosomes partly condensed and stained readily in *Entomophthoraceae* but euchromatic in other families. Resting spores globose to subglobose, formed as zygospores or azygospores.

Life mode and distribution: Obligately pathogenic for invertebrates (Entomophthoraceae, Meristacraceae, some Ancylistaceae), saprobic (some Ancylistaceae), or phytopathogenic (Completoriaceae and Ancylistaceae).

Notes: The class *Entomophthoromycetes* was introduced by Humber (2012) to accommodate the order *Entomophthorales* (*Ancylistaceae*, *Completoriaceae*, *Entomophthoraceae* and *Meristacraceae*), which was supported by Gryganskyi et al. (2013). Recently, Nie et al. (2022) introduced two new genera in *Entomophthorales*, i.e. *Capillidium*, typified by *Capillidium heterosporum* (Drechsler) B. Huang & Y. Nie and composed of other six new combinations, and *Neoconidiobolus*, typified by *Neoconidiobolus thromboides* (Drechsler) B. Huang & Y. Nie. Subsequently, *Capillidiaceae*, *Conidiobolaceae* and *Neoconidiobolaceae,* three other families of *Entomophthorales*, was established by Gryganskyi et al. (2022).

Type order: *Entomophthorales* G. Winter [as 'Entomophthoreae'], Rabenh. Krypt.-Fl., Edn 2 (Leipzig) 1.1: 74 (1880) [1884].
Type family: *Entomophthoraceae* A.B. Frank, Synopsis der Drei Naturreiche. Ein Handbuch …, Edn 2: 1258 (1874).
Type genus: *Entomophthora* Fresen., Bot. Ztg. 14: 883 (1856).
Type species: *Entomophthora muscae* (Cohn) Fresen., Bot. Ztg. 14: 883 (1856).

Neozygitomycetes Humber, Mycotaxon 120: 485 (2012).
Index Fungorum Registration Identifier 564377.

Vegetative hyphal bodies rod-like, walled or protoplastic, elongating until ± synchronous mitosis, with daughter cells separated by septa. Nuclear number in all cell types strongly regulated, usually 3–5 in vegetative cells and conidia and 2 in resting spores. Mitoses intranuclear, ± synchronous in any cell. Nuclei fusoid at metaphase with central, fusoid spindle, without nucleus-associated mitotic organelles. Chromosomes euchromatic during interphase. Conidiophores simple, forming apical conidiogenous cell and one conidium. Primary conidia subglobose to broadly ovoid, with a short basal papilla, comparatively flat; forcibly discharged to short distance by papillar eversion. Secondary conidia usually forming quickly after primary conidial discharge, most commonly forming as capilliconidia. Resting spores buding from a short conjugation bridge between rounded-up gametangia.

Life modes and distribution: Pathogens of either aphids or mites.

Notes: Humber (2012) recognized the family *Neozygitaceae* as a distinct lineage in ‘*Zygomycota*’ and thus introduced the order *Neozygitales* and the Class *Neozygitomycetes* in the newly introduced Phylum *Entomophthoromycota*.
Type order: *Neozygitales* Humber, Mycotaxon: 486 (2012).
Type family: *Neozygitaceae* Ben Ze'ev, R.G. Kenneth & Uziel, Mycotaxon 28(2): 321 (1987).
Type genus: *Neozygites* Witlaczil, Arch. Mikr. Anat. 24: 599 (1885).
Type species: *Neozygites fresenii* (Nowak.) Remaud. & S. Keller, Mycotaxon 11(1): 332 (1980).

= *Neozygites aphidis* Witlaczil, Arch. Mikr. Anat. 24: 599 (1885).

ENTORRHIZOMYCOTA R. Bauer, Garnica, Oberw., Riess, Weiß & Begerow, PLoS ONE 10(7): e0128183, 10 (2015).

Index Fungorum Registration Identifier 808783; Fig. 42

Hyphae first grew intercellularly between cortical cells, and develop to intracellular hyphae inside host tissue, forming intracellular septate coils bearing terminal teliospores. Teliospores germinate internally, becoming four-celled; hyphae with regular septa, with or rarely without dolipores, without Woronin bodies or membrane caps. Clamp connections absent. Haustoria present (modified from Bauer et al. 2015; Tedersoo et al. 2018).

Life modes and distribution: Phytoparasitic by forming root galls in Cyperaceae or Juncaceae or rarely in Eudicodyledons.

Notes: Over the last two decades molecular phylogenies have gradually elevated the *Entorrhiza* to a new phylum. Bauer et al. (1997, 2001) initially regarded *Entorrhiza* as a basal lineage inside *Ustilaginomycotina* on the basis of ultrastructure and morphology, and the first molecular studies to include rDNA of *Entorrhiza* have focused exclusively on the members of *Ustilaginomycotina*, recovering the basal position of *Entorrhiza* to the rest of the group (Begerow et al. 2006). Further analyses with rDNAs using more inclusive samplings of fungal species inferred an even deeper placement of *Entorrhiza*, concluding that *Entorrhiza* should be viewed either as a sister group of the *Basidiomycota* or an *incertae sedis* among *Basidiomycota* (Matheny et al. 2006; Hibbett et al. 2007).

A five-gene analysis by Bauer et al. (2015), which employed a concatenated dataset of rDNAs and partial RNA polymerase II subunit sequences, has affirmed that *Entorrhiza* represents a distinct early lineage of higher fungi, warranting an introduction of a new fungal phylum *Entorrhizomycota*. The five-gene analysis reconstructed *Entorrhiza* as a sister group to the rest of *Dikarya*, although the alternative topology, with *Entorrhiza* sister to *Basidiomycota*, could not be rejected by a statistical significance test (Bauer et al. 2015). To this day, the exact placement of *Entorrhizomycota* within *Dikarya* remains uncertain. Transcriptomic or genomic data for this phylum are lacking, and the available data are limited to the rDNA sequences and the partial RPB genes from Bauer et al. (2015).

Entorrhizomycetes Begerow, M. Stoll & R. Bauer, Mycologia 98(6): 908 (2007) [2006].

Index Fungorum Registration Identifier 501482.

Description is similar to the phylum description.

Notes: Bauer et al. (2015) introduced *Entorrhizomycetes* as the type class of *Entorrhizomycota*. Currently, *Entorrhizomycetes* comprises two orders *Entorrhizales* R. Bauer & Oberw. and *Talbotiomycetales* K. Riess et al.

Type order: *Entorrhizales* R. Bauer & Oberw., in Bauer, Oberwinkler & Vánky, Can. J. Bot. 75: 1311 (1997).
Type family: *Entorrhizaceae* R. Bauer & Oberw., in Bauer, Oberwinkler & Vánky, Can. J. Bot. 75(8): 1311 (1997).
Type genus: *Entorrhiza* C.A. Weber, Bot. Ztg. 42: 378 (1884).
Type species: *Entorrhiza cypericola* (Magnus) C.A. Weber, Bot. Ztg. 42: 378 (1884).

GLOMEROMYCOTA C. Walker & A. Schüßler, in Schüßler, Schwarzott & Walker, Mycol. Res. 105(12): 1416 (2001).

Index Fungorum Registration Identifier 90511; Fig. 43

The core of the symbiotic trade-off is represented by arbuscules, specific structures produced by AMF in plant root cells, where the fungi supply minerals and water in exchange for 20% of the carbon fixed by the plants. **Sexual morph:** Unknown. **Asexual morph:** acaulosporoid, ambisporoid, entrophosporoid, entrosacculoid, gigasporoid, glomoid, otosporoid or scutellosporoid glomerospores. Glomerospores are multinucleate, globose, subglobose, ellipsoid, ovoid or irregular, hyaline or pigmented, ranging from 30 to 1.050 µm, consisting of one to four walls with one to multiple layers that may or may not stain in Melzer's reagent (Fig. 44). *Glomeromycota* produce extraradical mycelium, intraradical hyphae and arbuscules. Intraradical vesicles—a storage and propagative structure—are also formed by members of all orders except *Gigasporales*. Instead, *Gigasporales* form extraradical auxiliary cells, which also function as storage (de La Providencia et al. 2005; de Souza et al. 2005), but not as propagative structures. Species of *Pacispora* (*Diversisporales*) form both intraradical vesicles and extraradical auxiliary cells. The intraradical mycelium stains strongly or weakly with trypan blue. The mycelium is coenocytic and hyphal anastomosis, which play a key role in genetic exchange among compatible individuals and in the formation of interconnected mycorrhizal networks, have been observed in a limited number of isolates. Extraradical glomerospores are single, in epigeous or sub-hypogeous loose or compact clusters or glomerocarps.

Life modes and distribution: Arbuscular Mycorrhizal Fungi (AMF) are obligate biotrophic symbionts, forming arbuscular mycorrhiza with ca. 80% of terrestrial and an unknown number of aquatic plants, and one species forming symbiosis with cyanobacteria of the genus *Nostoc* (Fig. 43). The phylum is worldwide distributed, with occurrences in all continents.

Notes: The class *Glomeromycetes* (= *Glomomycetes*) was described by Cavalier-Smith (1998) in the phylum '*Zygomycota*' with two orders (*Glomerales* and *Endogonales*) as sister clades. Schüßler et al. (2001) erected the phylum *Glomeromycota*, raising *Glomeromycetes* to the rank of phylum. Oehl et al. (2011a), using spore morphology and molecular analyses of the ribosomal gene sequences, concluded that *Glomeromycota* constitutes a phylum formed by three classes (*Archaeosporomycetes*, *Glomeromycetes*, *Paraglomeromycetes*).

Currently, six orders, 17 families, 49 genera, and approximately 360 species are recognized in *Glomeromycota* (Błaszkowski et al. 2022; Silva et al. 2022b; Wijayawardene et al. 2022a; Chen et al. 2023a, b; Corazon-Guivin et al. 2023; da Silva et al. 2023). Previous phylogenomic analyses (Galindo et al. 2021; Mikhailov et al. 2022; Strassert and Monaghan 2022a, b) did not solve the ambiguities about the phylogenetic position of the phylum. Despite the conflicting results of the Bayesian inference and the disagreement between the ML and Bayesian trees, eventually the reconstructions obtained in the present work with the CAT-PMSF method placed the *Glomeromycota* phylum sister to *Dikarya* with nearly full support.

Archaeosporomycetes Sieverd., G.A. Silva, B.T. Goto & Oehl, Mycotaxon 116: 374 (2011).

Index Fungorum Registration Identifier 519686.

Asexual morph: acaulosporoid, entrophosporoid and/or glomoid glomerospores. *Archaeosporomycetes* include dimorphic and, to a lesser extension, monomorphic species, producing acaulosporoid (produced laterally on the neck of a sporiferous saccule), entrophosporoid (produced intercalary the neck of a sporiferous saccule) and glomoid spores (formed at the tip of sporogenous hyphae, occasionally intercalary). Only one species, *Geosiphon pyriforme* (Kütz) Wettst, produces a distinct symbiotic association with cyanobacteria, or blue-green algae, of the genus *Nostoc* (Fig. 43), with no evidence, so far, of symbiosis with plants (https://geosiphon.jimdosite.com/). Spores are globose, subglobose, ellipsoid, ovoid or sometimes irregular, hyaline to white, yellow to brown. Spores present one (glomoid spores) or two spore walls (acaulosporoid and entrophosporoid spores), which contain several layers of different types, including evanescent, laminated, flexible, semi-flexible, permanent, semi-permanent, smooth or coriaceous layers. Acaulosporoid spores germinate through a germ tube emerging from a germinal shield (orb) formed on the upper surface of the inner wall. Some species present Melzer's reaction in the spore wall, absent in the inner wall. Representatives of this class form extraradical mycelium, intraradical hyphae, arbuscules and vesicles that stain pale or not at all in trypan blue. **Sexual morph:** Unknown.

Life modes and distribution: Obligate biotrophic symbionts, forming arbuscular mycorrhiza with terrestrial plant species and one species forming symbiosis with cyanobacteria of the genus *Nostoc* but not with plants. The members of *Archaeosporomycetes* show a worldwide distribution, occurring in countries with temperate, tropical, subtropical and arid climates. Its representatives have been found associated with plant roots in diverse habitats, including sand dunes, forests, grasslands, polluted places, gardens, and humid ecosystems (Schüßler and Wolf 2005; Błaszkowski et al. 2021). Fossil records for *Archaeosporomycetes* are limited to *Archaeosporites rhyniensis* (Harper et al. 2020) and *Mycokidstonia sphaerialoides* (Walker et al. 2021), both from Devonian (400 mya). The development and establishment of the mycorrhizal symbiosis follow the general pathway of *Glomeromycota*. The exception is represented by *Geosiphon* which forms specialized structures called bladders where cyanobacteria are living and transferring photoassimilates in exchange of nutrients from the fungus (Kluge 2002).

Notes: The class *Archaeosporomycetes* was introduced by Oehl et al. (2011b), including the order *Archaeosporales* previously erected by Schüßler et al. (2001). Currently, *Archaeosporomycetes* contains one order (*Archaeosporales*), four families (*Ambisporaceae*, *Archaeosporaceae*, *Geosiphonaceae*, *Polonosporaceae*), four genera (*Ambispora*, *Archaeospora*, *Geosiphon*, *Polonospora*) and 20 species. Representatives of *Archaeosporomycetes* are known to form arbuscular mycorrhizal (AM) symbiosis with plant roots (*Ambisporaceae*, *Archaeosporaceae*, *Polonosporaceae*) or non-AM symbiosis with photosynthetic and nitrogen-fixing cyanobacteria (*Geosiphonaceae*). The phylogenetic relationships between *Geosiphonaceae* and the other families in *Archaeosporomycetes* need more investigations to be clarified (Oehl et al. 2011a; Błaszkowski et al. 2021). Some species like *Ambispora fecundispora*, *A. nicolsonii*, *A. reticulata*, *Archaeospora myriocarpa* and *A. undulata* need a phylogenetic placement since molecular data are not available yet. Phylogenetic analysis based on environmental DNA (eDNA) metabarcoding indicated clades potentially representing new taxa in *Archaeosporomycetes* (Błaszkowski et al. 2021). Genome and transcriptome assemblies are available for two *Ambispora* species, and for *Geosiphon* whose genome possesses all the characteristics of known genomes of AM fungi (Malar et al. 2021; Montoliu-Nerin et al. 2021).

Economic and ecological significances, examples: Even if most studies have been carried out with species of *Glomeromycetes*, it has been shown that some representatives of *Archaeosporomycetes* also have economic and ecological importance. *Archaeospora myriocarpa* had high effectiveness in cassava and coffee plants in greenhouse and field trials (Sieverding 1990). *Archaeospora trappei* promoted herbivory tolerance in *Plantago lanceolata* (Bennett et al. 2009) and *Geosiphon* can increase heavy metal tolerance (Schüßler and Wolf 2005). Cabrales et al. (2019) showed that AMF inocula, including those with *Ambispora leptoticha*, improved maize yield in acidic soils. Furthermore, in an experiment conducted in soybean cultivars, *A. leptoticha* improved drought stress tolerance and productivity when co-inoculated with the nitrogen-fixing bacterium *Bradyrhizobium liaoningense* (Ashwin et al. 2023). *Ambispora appendicula*, when used as inoculum, increased tolerance against coffee leaf rust (Vallejos-Torres et al. 2023) and conferred bioprotective effects to cassava plants against the nematodes *Meloidogyne* spp. (Séry et al. 2016).

Type order: *Archaeosporales* C. Walker & A. Schüßler, in Schüßler, Schwarzott & Walker, Mycol. Res. 105(12): 1418 (2001).
Type family: *Archaeosporaceae* J.B. Morton & D. Redecker, Mycologia 93(1): 182 (2001).
Type genus: *Archaeospora* J.B. Morton & D. Redecker, Mycologia 93(1): 183 (2001).
Type species: *Archaeospora trappei* (R.N. Ames & Linderman) J.B. Morton & D. Redecker 2001.

Glomeromycetes Caval.-Sm., Biol. Rev. 73: 246 (1998), emend. Oehl, G.A. Silva, B.T. Goto & Sieverd, Mycotaxon 116: 365–379 (2011).

Index Fungorum Registration Identifier 90168.
Type cited as '*Glomomycetes*'.

Asexual morph: acaulosporoid, entrophosporoid, entrosacculoid, gigasporoid, glomoid, otosporoid or scutellosporoid glomerospores. Acaulosporoid spores develop laterally on the neck of a sporiferous saccule, singly in soil or rarely in aggregates. Spores are globose, subglobose, more rarely ovoid or irregular, consisting of three walls: an outer wall with one to five layers (swl1–5), sometimes ornamented with projections, depressions, or double ornamentations; a middle bi-layered wall (mwl1–2); and an inner tri-layered wall (iwl1–3), generally with the outer surface ornamented with granular outgrowths (beaded layer). Entrophosporoid spores formed within the necks of sporiferous saccules, singly in soil or rarely in roots. Spores are globose to subglobose, consisting of an outer wall with two layers (swl1–2), reactive in Melzer's, continuous with the wall of the stalk and the saccule, and an inner three-layered wall (iwl1–3) with no Melzer's reaction. Entrosacculoid spores produced inside sporiferous saccule, singly in soil. Spores are globose to subglobose, consisting of three walls: an outer wall with one to three layers (swl1–3), a middle bi-layered wall (mwl1–2); and an inner bi-layered wall (iwl1–2), generally with the upper surface ornamented with granular outgrowths (beaded layer). Gigasporoid spores produced terminally on sporogenous (bulbous) cells that arise from sporogenous hyphae, featuring germ warts on the inner surface of the mono-walled spore wall. Spores are single in soils, large (usually > 200 µm), globose to subglobose, sometimes ovoid, with two to three layers (swl1–3). Sporogenous cell composed of two layers continuous with the first two layers of the spore wall. Glomoid spores produced terminally, subterminally or intercalary from subtending hyphae, either in soils or occasionally within roots, singly, in loose clusters or in compact epigeous and sub-hypogeous glomerocarps, with or without peridium, sometimes arising radially from a central plexus of hyphae. Spores are globose, subglobose, irregular or ellipsoid, consisting of one wall, with one to six layers (swl1–6). Subtending hyphae straight, cylindrical to funnel-shaped, inflated or constricted at the spore base. Pore open or most frequently occluded by a conspicuous septum. Otosporoid spores, possessing two multiple-layered walls, formed in the proximity of a terminal or intercalary sporiferous saccule, laterally on its neck. Scutellosporoid spores produced on sporogenous (bulbous) cells, with two to four (multi-layered) spore walls. Germinal shields are hyaline, light yellow to (dark-brown) pigmented, mono- to multiply-lobed, with germinal tube initiations positioned on compartments (lobes) of the germinal shields. Dimorphic species in the order *Entrophosporales* produce both entrophosporoid and glomoid types. Acaulosporoid, entrophosporoid, entrosacculoid, glomoid and otosporoid species form mycorrhizae with arbuscles, vesicles, and hyphae that stain blue to dark blue in trypan blue. Gigasporoid and scutellosporoid species produce extraradical auxiliary cells instead of intraradical vesicles. **Sexual morph:** Unknown.

Life modes and distribution: The members of the class are worldwide distributed, with occurrences in over 175 countries, encompassing all continents. However, analyzes of distribution patterns revealed that some families in *Glomeromycetes* tend to be concentrated in geographic regions influenced by climate and soil (Davison et al. 2021). *Acaulosporaceae* and *Gigasporaceae*, for instance, occur frequently in tropical zones such as Africa and South America, while *Glomeraceae* is well represented in temperate zones such as Europe, Asia and Oceania (Stürmer et al. 2018). Furthermore, *Glomeromycetes* spp. are able to form mycorrhizal symbiosis with a wide range of terrestrial and aquatic hosts, and are largely tolerant to stress conditions, including deserts, saline environments, polluted areas, flooded regimes or even in hypoxic environments, such as eutrophic lakes (Ragupathy et al. 1990; Mehrotra 1998; Paul et al. 2007; Baar et al. 2011; Jobim and Goto 2016; El-Gazzar et al. 2020; Queiroz et al. 2020, 2022; Chen et al. 2022; Gomes et al. 2022; Malicka et al. 2022).

Notes: Cavalier-Smith (1998) introduced the class *Glomomycetes* (later corrected to *Glomeromycetes* by Schüßler et al. 2001) in the *Zygomycota* phylum with *Glomerales* and *Endogonales* as sister clades. Schüßler et al. (2001) described the phylum *Glomeromycota* and transferred *Glomeromycetes* to the new phylum reorganized in four orders: *Glomerales*, and the newly described *Archaeosporales*, *Diversisporales*, and *Paraglomerales*. Oehl et al. (2008) introduced the new order *Gigasporales* in *Glomeromycetes*, and more recently Błaszkowski et al. (2022) erected the order *Entrophosporales* to accommodate a single family, *Entrophosporaceae*, previously classified in *Glomerales* as *Claroideoglomeraceae* (Schüßler and Walker 2010). Currently, four orders, eleven families, 41 genera, and approximately 300 species are recognized in *Glomeromycetes* (Silva et al. 2022b; Wijayawardene et al. 2022a), making it the most species-rich and the most diverse class in morphological, molecular, and ecological aspects within *Glomeromycota*. Genome assemblies are available for the genera *Acaulospora*, *Cetraspora*, *Dentiscutata*, *Diversispora*, *Entrophospora*, *Funneliformis*, *Fuscutata*, *Gigaspora*, *Glomus*, *Oehlia*, *Racocetra*, *Rhizoglomus* and *Scutellospora* (Kobayashi et al. 2018; Sun et al. 2019a, b; Montoliu-Nerin et al. 2021; Sahraei et al. 2022). Transcriptomes are available for *Acaulospora*, *Diversispora*, *Funneliformis*, *Gigaspora*, *Racocetra*, *Rhizoglomus* and *Scutellospora* (Beaudet et al. 2018).

The oldest fossil records for *Glomeromycetes* are hyphae and spores (glomoid) from Wisconsin, dated to the Ordovician period (460 mya) (Redecker et al. 2000). However, the most impressive records were obtained from the Lower Devonian (400 mya). The fossils shared morphological features similar to existent taxa, for instance, *Scutellosporites devonicus* (Dotzler et al. 2006) presenting scutellosporoid spores, or *Glomites rhyniensis* (Taylor et al. 1995) and *G. sporocarpoides* (Karatygin et al. 2006), both with glomoid spores.

Economic and ecological significances, examples: *Glomeromycetes* enhance plant performance by increasing water and nutrient absorption, photosynthetic rate, growth, and tolerance to biotic and abiotic stress, e.g., drought, salinity, pathogens and heavy metals. In addition, this symbiosis promotes soil biogeochemical cycling and enhances aggregate stability (Latef et al. 2016; Singh et al. 2020; Falcão and Silva 2023).

The majority of model species used in biochemical, genetic and ecological studies of AM symbiosis are classified within the class *Glomeromycetes*, belonging mostly to the genera *Rhizoglomus* (with *R. irregulare* as the most studied species), *Gigaspora* and *Funneliformis*. Notably, *Funneliformis mosseae*, *Rhizoglomus clarum*, *R. irregulare* and *R. intraradices* are the most used components of commercial inoculants (Basiru and Hijri 2022), and have shown positive responses in inoculations of several agricultural crops, e.g., banana, bean, cassava, lettuce, maize, olive, potato, rice, soybean, tomato and walnut (Sahodaran et al. 2019; Santana et al. 2019; Singh et al. 2019; Campo et al. 2020; Chenchouni et al. 2020; Deja-Sikora et al. 2020; Huang et al. 2020; Moreira et al. 2020; Musyoka et al. 2020; Cavallari et al. 2021; Santander et al. 2021; Jumrani et al. 2022). Furthermore, *Glomeromycetes* spp. are also beneficial to non-agricultural plants, including medicinal and ornamental plants, and those representing forest plant communities (Ma et al. 2019; Zhang et al. 2019; Mirzaie et al. 2020; Klinsukon et al. 2021; Medeiros et al. 2021). *Glomeromycetes* have been detected in decomposing leaf litter (Bunn et al. 2019; Lima et al. 2023), which is a potential substrate for the recovery of impacted environments (Medeiros et al. 2021). Therefore, they can be successfully used by inoculum producers for crop production, sustainable agriculture and ecological restoration (Basiru and Hijri 2022; Duell et al. 2022).

Type order: ***Glomerales*** J.B. Morton & Benny [as 'Glomales'], Mycotaxon 37: 473 (1990).
Type family: ***Glomeraceae*** Piroz. & Dalpé [as 'Glomaceae'], Symbiosis 7: 19 (1989).
Type genus: ***Glomus*** Tul. & C. Tul., G. bot. ital. 2(1): 63 (1844).
Type species: ***Glomus macrocarpum*** Tul. & C. Tul., Giornale Botanico Italiano 1 (2): 63 (1845).

Paraglomeromycetes Oehl, G.A. Silva, B.T. Goto & Sieverd., Mycotaxon 116: 374 (2011).

Index Fungorum Registration Identifier 519687.

Obligate biotrophic symbionts, forming arbuscular mycorrhiza with the majority of terrestrial and aquatic plant species. **Sexual morph**: Unknown. **Asexual morph**: glomoid glomerospores. Spores globose to subglobose, sometimes ovoid or irregular, hyaline or pigmented, small (50–130 µm), formed singly or in loose clusters, in soil or inside roots. Spore structure consists of one wall with two to three layers, or two walls with many layers (e.g., *Paraglomus* spp.). Spore wall layer 1 is usually evanescent, short-lived and completely sloughed off in mature spores. Layer 2 is generally laminate, while layer 3, when present, is flexible, hyaline. Some *Paraglomus* spp. might have ornamentations on the spore wall. Inner spore wall consisting of two to three hyaline and flexible layers. Layers of the outer or inner walls may not exhibit any reaction in Melzer's reagent, or turn orange, yellow to pinkish-yellow. Subtending hyphae are straight or curved, cylindrical to slightly funnel-shaped, or rarely flared or inflated, with a pore open or occluded by a straight or curved septum. The wall of the subtending hypha is continuous with the spore wall layers. Germinal shield or orb unknown. Spores germinate directly through the spore wall. Mycorrhizal structures stain faintly or not at all in trypan blue. Sporocarps unknown.

Life modes and distribution: Members of *Paraglomeromycetes* are generally ubiquitous in the world as they were found in alpine, temperate, mediterranean to tropical, subtropical, arid and humid areas (Mello et al. 2013; Błaszkowski et al. 2017). Some studies highlighted the occurrence of *Paraglomeromycetes* in highly polluted areas (Dranguet et al. 2017; Malicka et al. 2022). Notably, *Paraglomus occultum* is widely distributed (Mello et al. 2013), as well as *P. turpe* which has been detected in several agricultural soils of Europe (Oehl et al. 2016). On the other hand, *Pervetustus simplex* seems to have a restricted distribution, as it has only been found in eight countries. Analogously, *P. bolivianum* has been detected in a prairie, Santa Cruz, Bolivia; in *Caatinga* region, Pernambuco, Brazil (Oehl and Sieverding 2004; Mello et al. 2013; Lima et al. 2022) and most recently in southeast Mexico, Oaxaca in the rhizosphere of *Agave angustifolia* and *A. karwinskii* (Sanchez et al. 2018; Polo-Marcial et al. 2021).

Notes: Morton and Redecker (2001) erected the family *Paraglomeraceae* in the order *Glomales* (=*Glomerales*), *Zygomycota* (Morton and Benny 1990) with a single genus, *Paraglomus,* and two species, *P. brasilianum* and *P. occultum*. Originally, the two species were described as *Glomus* spp., relying mainly on nrDNA phylogenies, fatty acid profiles, immunological reactions, and faint coloration of the intraradical hyphae in trypan blue. Schüßler et al. (2001), based on the high divergence of sequences, transferred *Paraglomeraceae* into the new order *Paraglomerales*, *Glomeromycota.* Oehl et al. (2011a), using spore morphology and phylogenies reconstructed from ribosomal sequences, introduced the class *Paraglomeromycetes* to accommodate this order.

The species *Paraglomus albidum*, *P. laccatum* and *P. lacteum* were originally described with a single spore wall, differing from other *Paraglomus* spp. with two walls. Mello et al. (2013) suggested that only *P. majewskii* formed a single spore wall, and this species was later transferred to the new genus *Innospora* in *Paraglomeraceae* according to molecular evidence (Błaszkowski et al. 2017). However, since glomoid spores with one wall is a common feature for many taxa in *Glomeromycota*, Błaszkowski et al. (2017) concluded that *Innospora* does not present any exclusive morphological trait that distinguishes this genus from other glomoid genera. In the same paper, Błaszkowski et al. (2017) presented a new species with nrDNA sequences highly divergent from those of other members in *Paraglomeraceae*. Consequently, Błaszkowski et al. (2017) erected a new family, *Pervetustaceae*, with the new genus and species *Pervetustus* and *P. simplex*, respectively.

Currently, *Paraglomeromycetes* contains one order (*Paraglomerales*), two families (*Paraglomeraceae*, *Pervetustaceae*), three genera (*Paraglomus*, *Innospora*, *Pervetustus*), and twelve species (Mello et al. 2013; Błaszkowski et al. 2017; Corazon-Guivin et al. 2020). Up to now, the molecular phylogeny is known only for nine species. Environmental sequences deposited in public databases (Mello et al. 2013; Błaszkowski et al. 2017) suggest the existence of many potentially undescribed species, despite the low number of species currently described in *Paraglomeromycetes*, compared to the other classes.

Genome and transcriptome assemblies are available only for two *Paraglomus* species (Beaudet et al. 2018; Malar et al. 2021; Montoliu-Nerin et al. 2021).

Economic and ecological significances, examples: Few studies involving *P. occultum*, showed benefits for agricultural crops under stress conditions. For instance, in orange tree plants under water stress conditions, *P. occultum* promoted growth and tolerance by acting on sucrose metabolism and leaf osmotic regulation (Wu et al. 2017). In tomato plants under salt stress, it increased the expression of stress-responsive genes and the nitrogen balance index (Liang et al. 2022). In orange groves, through the glomalin-related soil protein fractions, it contributed to the soil's total nitrogen content (Meng et al. 2020). Zhang et al. (2018a, b) showed that *P. occultum* established common mycelium networks among orange seedlings and, thereby, increased plant growth and profitably modified the root architecture of the recipient plants. Furthermore, *P. occultum* increased the expression of defense genes against pathogens in plants with citrus canker (Xie et al. 2019).

Type order: ***Paraglomerales*** C. Walker & A. Schüßler, in Schüßler, Schwarzott & Walker, Mycol. Res. 105(12): 1418 (2001).

Type family: ***Paraglomeraceae*** J.B. Morton & D. Redecker [as 'Paraglomaceae'], Mycologia 93(1): 188 (2001).

Type genus: ***Paraglomus*** J.B. Morton & D. Redecker, Mycologia 93(1): 188 (2001).

Type species: ***Paraglomus occultum*** (C. Walker) J.B. Morton & D. Redecker (2001).

KICKXELLOMYCOTA Tedersoo, Sánchez-Ramírez, Kõljalg, Bahram, Döring, Schigel, T. May, M. Ryberg & Abarenkov, Fungal Diversity 90: 150 (2018).

Index Fungorum Registration Identifier 554009.

Thallus arising from a holdfast on other fungi as a haustorial parasite, or branched, septate, subaerial hyphae; *mycelium* branched or unbranched, regularly septate; septa with median, disciform cavities containing plugs; asexual production by 1- or 2-spored merosporangia, trichospores, or arthrospores; sexual reproduction by zygospores that are globose, biconical, or allantoid and coiled (adopted from Hibbett et al. 2007 which was placed to subphylum *Kickxellomycotina*).

Life modes and distribution: Saprobes or weak non-haustorial mycoparasites in soil and dung; widespread.

Notes: Hibbett et al. (2007) introduced *Kickxellomycotina* to accommodate *Kickxellales* Kreisel ex R. K. Benj.. In the last two decades, several studies have added a considerable number of taxa based on both morphology and phylogeny (e.g. Kurihara et al. 2008; Chuang et al. 2017; Ri et al. 2022). The placement of *Kickxellales* in '*Zygomycota*' was confirmed in different studies (e.g. Tanabe et al. 2000; White et al. 2006). Tretter et al. (2014) provided a comprehensive background on molecular phylogenetic placements of the taxa of *Kickxellomycotina* (based on SSU, LSU, ITS, MCM7, TSR1, *rpb1*, *rpb2*, *β-tubulin*) and recognized four orders (i.e. *Asellariales*, *Dimargaritales*, *Harpellales* and *Kickxellales*) and four orphan genera (*Barbatospora*, *Orphella*, *Ramicandelaber*, *Spiromyces*). However, the above mentioned studies did not recognize any class in *Kickxellomycotina* but only orders. Tedersoo et al. (2018) elevated the sub-phylum *Kickxellomycotina* to phylum rank and introduced *Kickxellomycota*. At the same time, Tedersoo et al. (2018) introduced six new classes, viz., *Asellariomycetes*, *Barbatosporomycetes*, *Dimargaritomycetes*, *Harpellomycetes*, *Kickxellomycetes* (type class) and *Ramicandelaberomycetes*. We believe this approach in Tedersoo et al. (2018) provided more stable condition for the Kingdom of *Fungi*.

Controversial opinions: Strassert and Monaghan (2022a, b) regarded *Kickxellomycota* as a subphylum of *Zoopagomycota*, i.e. *Kickxellomycotina*.

Asellariomycetes Tedersoo, Sánchez-Ramírez, Kõljalg, Bahram, Döring, Schigel, T. May, M. Ryberg & Abarenkov, Fungal Diversity 90: 151 (2018); Fig. 45

Thalli Branched, filamentous, with harpelloid septa; basal cells for attachment to gut cuticle of a host; sholdfasts elaborate, plugged septum, generative cells disarticulate and function as propagules, do not produce external and deciduous trichospores; no dictyosomes; no zygospore; sexual reproduction absent or extremely uncommon (Benjamin 1979; Lichtwardt and Lichtwardt 1986).

Life modes and distribution: saprobes, have adapted to semi-terrestrial insects (*Collembola*) and isopods dwelling in freshwater, marine, and terrestrial environments.

Notes: Manier and Lichtwardt (1969) introduced *Asellariaceae* to accommodate *Asellaria*. Subsequently, Lichtwardt and Manier (1978) upgraded *Asellariaceae* to an ordinal level and introduced *Asellariales*. Tedersoo et al. (2018) showed that *Asellariales* has a distinct phylogenetic lineage in the Phylum *Kickxellomycota*. *Asellariaceae* is the only family in the order *Asellariales*.

Type order: *Asellariales* Manier ex Manier & Lichtw., in Lichtwardt & Manier, Mycotaxon 7(3): 442 (1978).
Type family: *Asellariaceae* Manier ex Manier & Lichtw., Annls Sci. Nat., Bot. Biol. Vég., sér. 12 9: 526 (1968).
Type genus: *Asellaria* R.A. Poiss., Bull. biol. Fr. Belg. 66: 232 (1932).
Type species: *Asellaria caulleryi* R.A. Poiss., Bull. biol. Fr. Belg. 66: 233 (1932).

Barbatosporomycetes Tedersoo, Sánchez-Ramírez, Kõljalg, Bahram, Döring, Schigel, T. May, M. Ryberg & Abarenkov, Fungal Diversity 90: 151 (2018).

Index Fungorum Registration Identifier 554012; Fig. 46

Thallus branched with a basal cell, bearing trichospores; trichospores cylindrical, without a collar, with multiple fine basal appendages, may bear a cylindrical sleeve or wall at the terminal end, which on dehiscence may reveal appendage-like filaments; zygospores unknown (adopted from Doweld 2014c).

Notes: Tretter et al. (2013) confirmed the phylogenetic placement of *Barbatospora* in *Kickxellomycota*. Doweld (2014c) introduced *Barbatosporaceae* and *Barbatosporales* which currently comprise only one genus, i.e. *Barbatospora*. The genus is also monotypic thus the family is represented by the type species of *Barbatospora*. Tedersoo et al. (2018) introduced *Barbatosporomycetes* in the phylum *Kickxellomycota*.

Type order: *Barbatosporales* Doweld, Index Fungorum 87: 1 (2014).
Type family: *Barbatosporaceae* Doweld, Index Fungorum 87: 1 (2014).
Type genus: *Barbatospora* M.M. White, Siri & Lichtw., Mycologia 98(2): 335 (2006).
Type species: *Barbatospora ambicaudata* M.M. White, Siri & Lichtw., Mycologia 98(2): 335 (2006).

Dimargaritomycetes Tedersoo, Sánchez-Ramírez, Kõljalg, Bahram, Döring, Schigel, T. May, M. Ryberg & Abarenkov, Fungal Diversity 90: 151 (2018).

Index Fungorum Registration Identifier 554013; Fig. 47

Vegetative hyphae delicate, hyaline, branched, regularly septate, giving rise to numerous small, slightly swollen appressoria producing restricted, more or less ramified, aseptate haustoria; sporangiophores white or light colored, erect, septate, simple or branched, forming two-spored merosporangia directly on the surfaces of terminal enlargements or on cellular branchlets produced laterally or terminally; sporangiospores hyaline, subglobose, ellipsoid, or bacilliform; spores at maturity remaining dry or immersed in liquid; septa of both the vegetative and fruiting hyphae characteristically with median disciform cavities containing solid, colorless, more or less biconvex plugs bearing small, usually globose enlargements at their poles; zygospores globoid, thick-walled, hyaline, formed from the fusion of similar (adopted from Benjamin 1959).

Life modes and distribution: Parasites or facultative parasites of other *Mucorales.*

Notes: Benjamin (1959) introduced the family *Dimargaritaceae* to accommodate four genera viz., *Dimargaris*, *Dispira*, *Spinalia* and *Tieghemiomyces*. Later, Benjamin (1979) upgraded *Dimargaritaceae* to ordinal level and introduced *Dimargaritales.* Tanabe et al. (2000) confirmed the placement of *Dimargaritales* in '*Zygomycota*' using SSU rDNA sequences. Later, James et al. (2006a) included *Dimargaris bacillispora* in their phylogenetic study of the kingdom *Fungi* and confirmed its placement in '*Zygomycota*'. White et al. (2006) showed that *Dimargaritales* clustered with *Neozygites* and accommodated in '*Zygomycota*'. However, Tretter et al. (2013) provided the most comprehensive approach for *Dimargaritales* and confirmed the placement in subphylum *Kickxellomycotina*. Tedersoo et al. (2018) elevated *Kickxellomycotina* to a phylum while upgrading *Dimargaritales* to a new class, *Dimargaritomycetes.*

Type order: ***Dimargaritales*** R.K. Benj., in Kendrick, The Whole Fungus 2: 607 (1979).
Type family: ***Dimargaritaceae*** R.K. Benj., Aliso 4(2): 364 (1959).
Type genus: ***Dimargaris*** Tiegh., Annls Sci. Nat., Bot., sér. 6 1: 154 (1875).
Type species: ***Dimargaris cristalligena*** Tiegh., Annls Sci. Nat., Bot., sér. 6 1: 154 (1875).

Harpellomycetes Tedersoo, Sánchez-Ramírez, Kõljalg, Bahram, Döring, Schigel, T. May, M. Ryberg & Abarenkov, Fungal Diversity 90: 151 (2018).

Index Fungorum Registration Identifier 554014; Fig. 48

Thallus simple or branched, with basal cell attached to the host; hyphae septate; septa contain a lenticular cavity; sexual reproduction via conical or biconical zygospores; asexual reproduction via exogeneous, lateral, elongate monosporous trichospores; endosymbionts of mostly freshwater arthropods (Benjamin 1979).

Life modes and distribution: Reported as parasites of freshwater arthropods larval stages, widespread (Kirk et al. 2008).

Notes: The order *Harpellales* was introduced by Lichtwardt and Manier (1978) based on the family *Harpellaceae* L. Léger & Duboscq 1929 which was invalid (see Index Fungorum 2024). Hence, Cannon and Kirk (2007) validated *Harpellaceae* 1929 as *Harpellaceae* L. Léger & Duboscq ex P.M. Kirk & P.F. Cannon 2007.

According to Tretter et al. (2013), *Harpellales* is a well-established order in *Kickxellomycotina* and confirmed its placement close to *Asellariales*. Tedersoo et al. (2018) upgraded the order *Harpellales* to the class *Harpellomycetes*. Currently, the class comprises one order and two families.

Type order: ***Harpellales*** Lichtw. & Manier, Mycotaxon 7(3): 442 (1978).
Type family: ***Harpellaceae*** L. Léger & Duboscq ex P.M. Kirk & P.F. Cannon, Fungal Families of the World: 152 (2007).
Type genus: ***Harpella*** L. Léger & Duboscq, C. r. hebd. Séanc. Acad. Sci., Paris 188: 951 (1929).
Type species: ***Harpella melusinae*** L. Léger & Duboscq, C. r. hebd. Séanc. Acad. Sci., Paris 188: 951 (1929).

Kickxellomycetes Tedersoo, Sánchez-Ramírez, Kõljalg, Bahram, Döring, Schigel, T. May, M. Ryberg & Abarenkov, Fungal Diversity 90: 150 (2018).
Index Fungorum Registration Identifier 554010; Fig. 49

Thallus branched, with septate hyphae giving rise to septate sporangiophores; septa with median disciform cavities containing colorless biconvex or biumbonate plugs that are persistent in 2–3% KOH; asexual reproduction by 1-spored sporangioles formed on pseudophialides that arise from globoid to elongate fertile branchlets termed sporocladia; sexual reproduction by nearly globose zygospores (adopted from Benjamin 1979).

Life modes and distribution: Saprobes, weak non-haustorial mycoparasites in soil and dung, excrement of cave crickets (Benjamin 1979; Ri et al. 2022).

Notes: Tedersoo et al. (2018) introduced *Kickxellomycetes* to accommodate the order *Kickxellales* which was widely accepted in previous studies (e.g. White et al. 2006; Hibbett et al. 2007). Currently, the class comprises one order and one family (Wijayawardene et al. 2022a).

Type order: ***Kickxellales*** Kreisel ex R.K. Benj., in Kendrick, The Whole Fungus 2: 610 (1979).
Type family: ***Kickxellaceae*** Linder, Farlowia 1(1): 56 (1943) [1943–1944].
Type genus: ***Kickxella*** Coem., Bull. Soc. R. Bot. Belg. 1: 156 (1862).

Type species: ***Kickxella alabastrina*** Coem., Bull. Soc. R. Bot. Belg. 1: 156 (1862).

Ramicandelaberomycetes Tedersoo, Sánchez-Ramírez, Kõljalg, Bahram, Döring, Schigel, T. May, M. Ryberg & Abarenkov, Fungal Diversity 90: 151 (2018).

Index Fungorum Registration Identifier 554015; Fig. 50

Mycelium composed of colorless, branched, septate hyphae. *Stolons* hyaline, septate, producing rhizoids at the apex. Sporangiophores derived from the distal parts of stolons, septate, at first prostrated, verticillately branched once or twice by the development of branches, erect in age, often disarticulated at third or fourth septa from rhizoids, often producing fertile terminal heads. Branches verticillately producing branchlets, becoming broad in age, cylindrical or ellipsoidal, irregularly producing shorter branchlets. *Sporocladia* at first composed of branchlets on branches of sporangiophores, elongate, attenuate distally, often composed of broadened branches of sporangiophores in age. *Sporogenous cells* (pseudophialides) arising from sporocladia and fertile heads, at first subspherical, in age subspherical or hemispherical, producing sporangiola. *Sporangiola* narrow fusiform, slightly curved, aseptate, hyaline. *Sporangial wall* adnate to the sporangiospore. Zygospores and chlamydospores not observed (extracted from Ogawa et al. 2001).

Life modes and distribution: Isolated from soil from Japan and Taiwan (Ogawa et al. 2001; Kurihara et al. 2004; Chuang et al. 2013).

Notes: Doweld (2014d) introduced *Ramicandelaberaceae* and *Ramicandelaberales* to accommodate the genus *Ramicandelaber*. The phylogenetic placement of *Ramicandelaber* in *Kickxellomycotina* was confirmed by Chuang et al. (2013) and Tretter et al. (2014). Tedersoo et al. (2018) recognized the phylogenetic lineage of *Ramicandelaber* in *Kickxellomycota* and upgraded *Ramicandelaberales* to a class, *Ramicandelaberomycetes*.

Currently, the class comprises one order and one family.

Type order: ***Ramicandelaberales*** Doweld, Index Fungorum 69: 1 (2014).
Type family: ***Ramicandelaberaceae*** Doweld, Index Fungorum 69: 1 (2014).
Type genus: ***Ramicandelaber*** Y. Ogawa, S. Hayashi, Degawa & Yaguchi, Mycoscience 42(2): 193 (2001).
Type species: ***Ramicandelaber longisporus*** Y. Ogawa, S. Hayashi, Degawa & Y. Yaguchi, Mycoscience 42(2): 193 (2001).

MONOBLEPHAROMYCOTA Doweld, Prosyllabus Tracheophytorum, Tentamen Systematis Plantarum Vascularium (Tracheophyta) (Moscow): LXXVII (2001).

Index Fungorum Registration Identifier 90752.

Fungi with mycelial, rhizomycelial or monocentric thallus; when mycelial, hyphal thallus with a foam appearance due the vacuolated cytoplasm. **Asexual reproduction** by zoospores or autospores; sexual reproduction, when present, oogamous by means of posteriorly uniflagellate antherozoids borne in antheridia and nonflagellate female gametes borne in oogonia. The main ultrastructure features of the monoblephs' zoospores are the ribosomes aggregation around the nucleus, numerous lipid droplets predominantly posterior, and many spherical mitochondria. The ribosomes are loosely enclosed by several strands of endoplasmic reticulum, the microtubule root radiates anteriorly from a striated disk that partially encircles the kinetosome, and the rumposome is adjacent to the microbody in microbody-lipid globule complex (MLC) (Powell and Letcher 2014; Karpov et al. 2017a; Adl et al. 2019; Tedersoo et al. 2018).

Life modes and distribution: Saprotrophic especially in plant material, such as submerged fruits and twigs, and algae, in aquatic ecosystems; sometimes in terrestrial ecosystems.

Notes: The type genus of *Monoblepharomycota*, *Monoblepharis* Cornu was a well-studied genus, even before molecular techniques were available (e.g. Sparrow 1933; Marek 1984). Doweld (2001) introduced the phylum *Monoblepharomycota* to accommodate *Monoblepharidomycetes* J. H. Schaffn. and *Hyaloraphidiomycetes* Doweld, which are composed of eucarpic and holocarpic species in the orders *Monoblepharidales* and *Hyaloraphidiales*, respectively. James et al. (2006a, b) recognized the *Monoblepharidales* taxa are phylogenetically related to *Chytridiales*. Dee et al. (2015) consider *Monoblepharidomycetes s.l.* phylogeny have already been showed *Hyaloraphidium* as basal genus, and the mycelial genera as a monophlyletic sister group to the monocentric species, like as *Harpochytrium* and *Oedogoniomyces*.

Currently, *Monoblepharomycota* comprises one subphylum (i.e. *Monoblepharomycotina*) and two classes i.e. *Hyaloraphidiomycetes* and *Monoblepharidomycetes*.

Hyaloraphidiomycetes Doweld, Prosyllabus Tracheophytorum, Tentamen Systematis Plantarum Vascularium (Tracheophyta) (Moscow): LXXVII (2001).

Index Fungorum Registration Identifier 585035.

Fungi with holocarpic thallus which consists of a cell usually elongate without rhizoidal system. *Autosporos* form within the mother cell and released by rupture of wall cell, the number of spores per cell is 4–8, irregular sometimes. The spores usually contain one nucleus, but up to four nuclei were observed in mature cells; mitochondria are elongated and sometimes even thread-like; large organelles present,

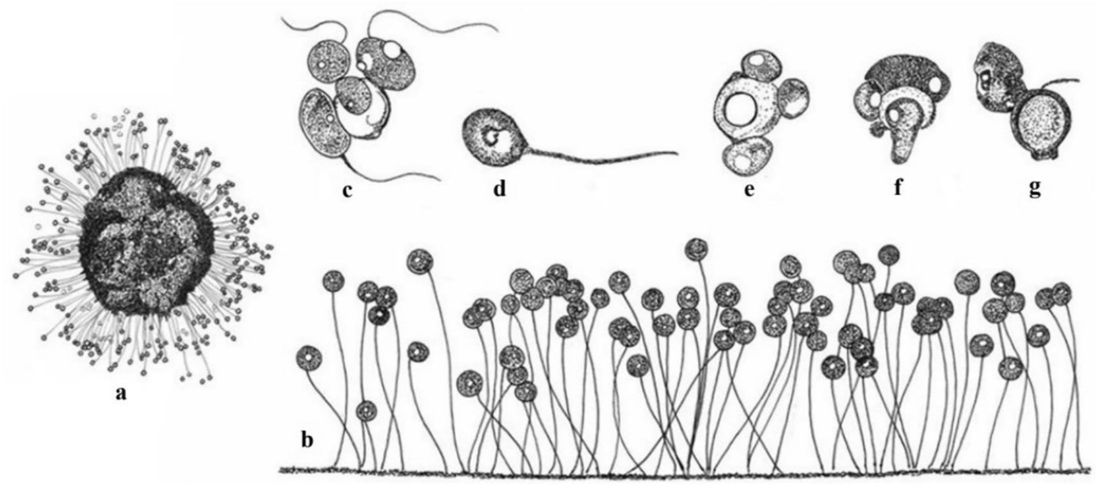


Fig. 37 *Caulochytrium protostelioides*. **a** Sporangiocarps arising from clump of zoosporangia (×350). **b** Sporangiocarps on agar surface (×600). **c** Twelve zoospores that emerged from the three empty aerial sporangia (×1800). **d** Four zoospores from a single aerial sporangium (×2000). **e** Encystment of four zoospores from an aerial sporangium (×2000). **f** Small aerial sporangium with two zoospores emerging (×2000). **g** Empty aerial sporangium with single exit papilla (×2000)

sometimes associated with lipid globules, mitochondria and cisternae of the endoplasmic reticulum resembles the microbody-lipid globule complex (MLC) of *Chytridiomycetes*; centrioles, basal bodies and flagella were not observed. **Sexual reproduction** Unknown.

Life modes and distribution: Saprotrophic in freshwater ecosystems.

Notes: The class *Hyaloraphidiomycetes* (including the order *Hyaloraphidiales* and family *Hyaloraphidiaceae*) was established by Doweld (2001) to accommodate the genus *Hyaloraphidium*. The class comprises a single, monotypic genus (i.e. *H. curvatum*), was previously considered a colorless green alga. Molecular studies with *H. curvatum* showed that it is a sister group of the monoblephs.

Type order: ***Hyaloraphidiales*** Doweld, Prosyllabus HyaloraphidialesTracheophytorum, Tentamen Systematics Plantarum Vascularium (Tracheophyta) (Moscou): LXXVII (2001).
Type family: ***Hyaloraphidiaceae*** Doweld, HyaloraphidiaceaeProsyllabus Tracheophytorum, Tentamen Systematics Plantarum Vascularium (Tracheophyta) (Moscou): LXXVII (2001).
Type genus: ***Hyaloraphidium*** Korshikov, Hyaloraphidium in Pascher & Korshikov, Arch. Protistenk. 74: 251 (1931).
Type species: ***Hyaloraphidium curvatum*** Korshikov, in Pascher & Korshikov, Arch. Protistenk. 74: 351 (1931).

Monoblepharidomycetes J.H. Schaffn, Ohio Naturalist 9(4): 449 (1909) emend. Karpov et al., Fungal Biology 121: 734 (2017).

Index Fungorum Registration Identifier 90244 (Figs. 51 and 52).

Thallus mycelial, rhizomycelial, or monocentric, when mycelial with or without constrictions, pseudosepta and catenulations. Monocentric forms may be planktonic, epibiotic, with an extracellular basal foot or holdfast. **Asexual reproduction** by zoospores; sexual reproduction, when present, oogamous by means of posteriorly uniflagellate antherozoids borne in antheridia and nonflagellate female gametes borne in oogonia (Karpov et al. 2017a modified). The main ultrastructure features of the monoblephs' zoospores are the ribosomes aggregation around the nucleus, numerous lipid droplets predominantly posterior, and many spherical mitochondria. The ribosomes are lossely enclosed by several strands of endoplasmic reticulum, the microtubule root radiates anteriorly from a striated disk that partially encircles the kinetosome, and the rumposome is adjacent to the microbody in microbody-lipid globule complex (MLC) (Powell and Letcher 2014; Adl et al. 2019).

Life modes and distribution: Saprobic on vegetable and animal debris, Oomycetes and in association with algae in freshwater ecosystems and organic material in tropical and subtropical soils.

Notes: *Monoblepharidomycetes* was established by Schaffner (1909) and emended by Karpov et al. (2017a), however they described the class with *Hyaloraphidium,* genus considered here into *Hyaloraphidiomycetes*. Currently,

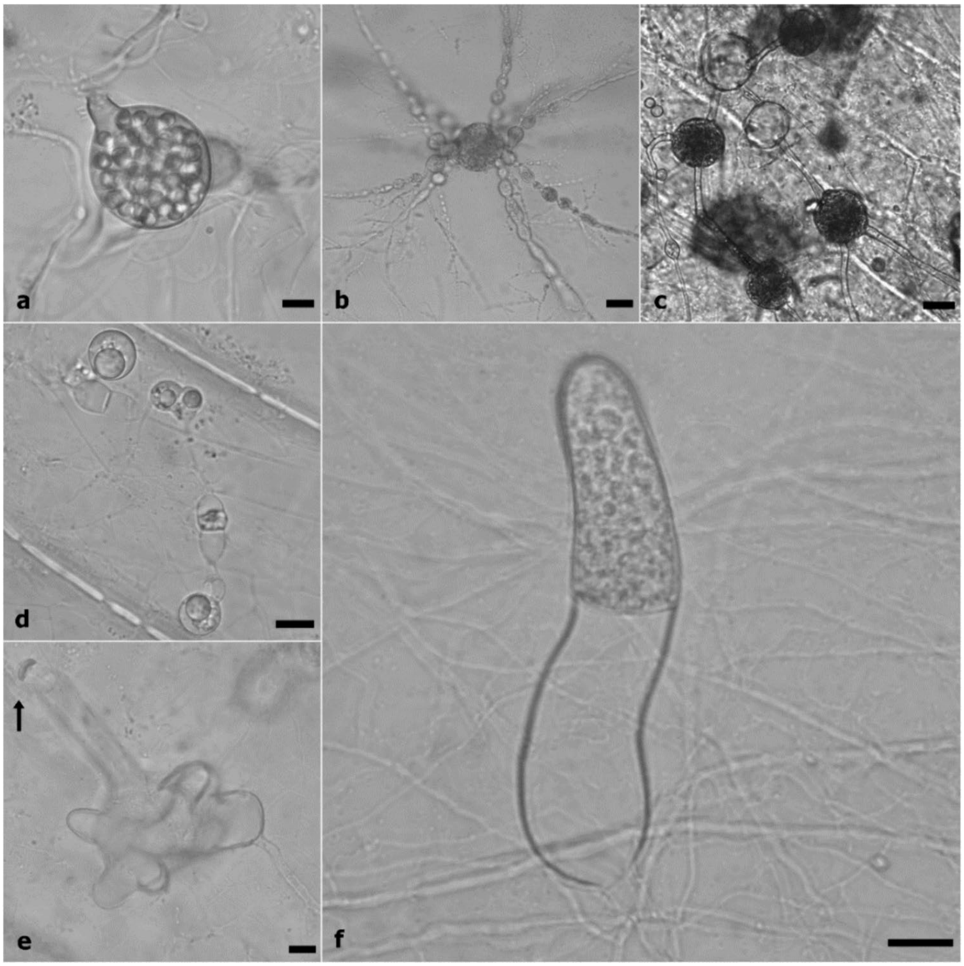


Fig. 38 Morphologies of *Cladochytriales*. **a** *Nowakowskiella* sp. **b** *Catenochytridium* sp. **c** *Septochytrium* sp. **d** *Can we* sp. **e** *Endochytrium* sp. **f** *Cylindrochytridium* sp. Scale bars: **a**–**f** = 10 µm

Monoblepharidomycetes comprises the order *Monoblepharidales*, with the families *Gonapodyaceae*, *Harpochytriaceae*, *Monoblepharidaceae*, *Oedogoniomycetaceae* and *Telasphaerulaceae*, six saprotrophic genera (*Gonapodya*, *Harpochytrium*, *Monoblepharella*, *Monoblepharis*, *Oedogoniomyces* and *Telasphaerula*) and around 28 species (Powell and Letcher 2014; Karpov et al. 2017a).

Type order: ***Monoblepharidales*** Sparrow, Mycologia 34(1): 115 (1942).
Type family: ***Monoblepharidaceae*** Warm., Haandb. syst. Bot.,Edn 2 (Kjøbenhavn): 57 (1884).
Type genus: ***Monoblepharis*** Cornu, Bull. Soc. bot. Fr. 18: 59 (1871).
Type species: ***Monoblepharis sphaerica*** Cornu, Bull. Soc. bot. Fr. 18: 59 (1872) [1871].

MORTIERELLOMYCOTA Tedersoo, Sánchez-Ramírez, Kõljalg, Bahram, Döring, Schigel, T. May, M. Ryberg & Abarenkov, Fungal Diversity 90: 152 (2018).

Index Fungorum Registration Identifier 554018.

Thallus with dichotomously branching, anastomosing hyphae, bearing stylospores; *Sporangiophores* initially coenocytic, irregularily septated when mature; asexual reproduction via sporangia and sporangioles; sporangia spherical, multi-spored; no columella; sporangioles terminal, borne on erecting hyphae; *Spores* ellipsoid or globose or irregular, smooth or ornamented; zygospores naked; mostly saprotrophs in soil (from Tedersoo et al. (2018) which was based on Hoffmann et al. (2011) and Doweld (2014f)).

Life modes and distribution: Saprobic, plant-mutualistic or entomopathogenic, widespread.

Notes: The genus *Mortierella* Coem. and other morphologically resemble genera were well studied and higher ranks have been introduced based on their unique morphological characteristics (see Cavalier-Smith 1998; Doweld 2014f). Hoffmann et al. (2011) introduced the subphylum *Mortierellomycotina* based on phylogenetic analyses and morphological characteristics. However, Hoffman et al. (2011) accommodated *Mortierellomycotina* in '*Zygomycota*'. Tedersoo et al. (2018) introduced the phylum *Mortierellomycota* to

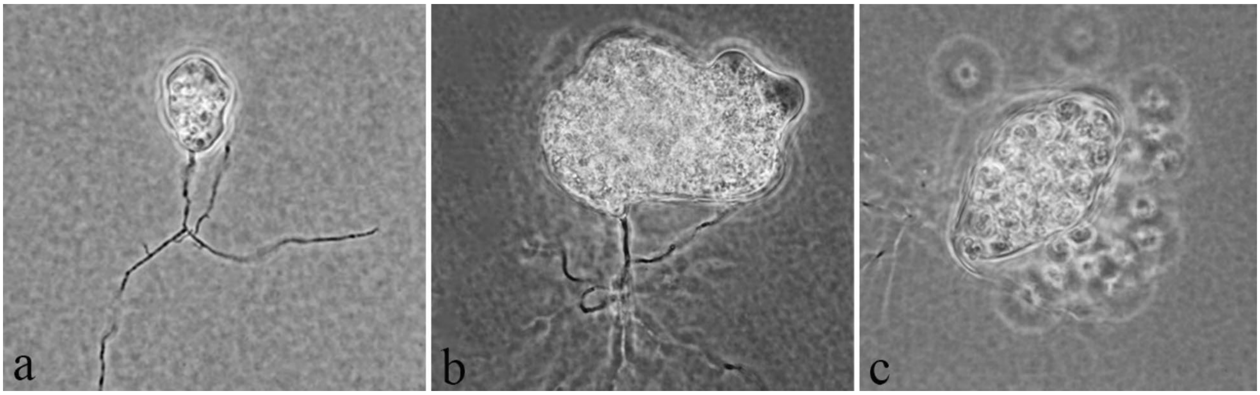


Fig. 39 Morphology of *Lobulomyces angularis* JEL045. **a** Young thallus with branching of rhizoidal axis. **b**, **c** Mature thallus discharging zoospores (photo credit to Dr. Joyce E. Longcore)

accommodate *Mortierella* and other genera included in *Mortierellomycotina.* Currently, the phylum comprises one subphylum, one class, one order and one family.

Mortierellomycetes Doweld, Index Fungorum 46: 1 (2013).

Index Fungorum Registration Identifier 550332; Figs. 53, 54

Sexual morph: Homo- and heterothallic formation of zygospores on suspensors lacking appendages, thick-walled, naked or dimpled (Takashima et al. 2016). **Asexual morph**: Rapid mycelial growth, often forming conspicuous rosette-like/zonate pattern on the plates. *Thallus* consisting of coenocytic, anastomosing, dichotomously branching hyphae, sometimes with rhizoids, chlamydospores or stylospores (aerial, stalked, spiny chlamydospores). *Sporangiophores* with inflated base and attenuate apex, erect, branched or unbranched, initially not septated, potentially irregularly septated when fully stalked. *Sporangia* spherical, multi-spored; columella lacking or rudimentary. *Sporangiospores* globose to ellipsoid or irregular, either laevigate or ornamented (Hoffmann et al. 2011; Dowel 2014f). *Sporangiola* terminal, borne on erecting hyphae, ramifications primarily horizontally expanding. *Sporocarps* containing sporangia are observed exclusively in the genus *Modicella* (Smith et al. 2013).

Life modes and distribution: Saprobic, plant-mutualistic or entomopathogenic in soil or organic substrates.

Notes: *Mortierellomycetes* belong to the phylum *Mortierellomycota*, the latter corresponding to the subphylum *Mortierellomycotina* (Tedersoo et al. 2018). The family *Mortierellaceae* was reorganized based on a phylogenomic approach (Vandepol et al. 2020), resulting in 15 monophyletic genera: *Actinomortierella*, *Benniella*, *Dissophora*, *Entomortierella*, *Gamsiella*, *Gryganskiella*, *Haplosporangium*, *Linnemannia*, *Lobosporangium*, *Lunasporangiospora*, *Modicella*, *Mortierella*, *Necromortierella*, *Podila* and *Tyroliella.*

Members of *Mortierellomycetes* exhibit a global distribution across various climates (tropical, subtropical temperate, arctic-alpine) (Gams 1977; Domsch et al. 1980), and thrive in snow-covered soil (Linnemann 1941; Wagner et al. 2013; Telagathoti et al. 2021). While most taxa are soil saprobes, some have been reported as plant mutualistic or entomopathogenic fungi. Additionally, many species are associated with endohyphal or epihyphal bacteria (Takashima et al. 2020; Telagathoti et al. 2021).

Type order: ***Mortierellales*** Caval.-Sm., Biological Reviews of the Cambridge Philosophical Society 73: 246 (1998).
Type family: ***Mortierellaceae*** Luerss., Handbuch der systematischen Botanik mit besonderer Berücksichtigung der Arzneipflanzen 1: 63 (1877).
Type genus: ***Mortierella*** Coem., Bull. Acad. R. Sci. Belg., Cl. Sci., sér. 2 15: 536 (1863).
Type species: ***Mortierella polycephala*** Coem., Bull. Acad. R. Sci. Belg., Cl. Sci., sér. 2 16: 536 (1863).

MUCOROMYCOTA Doweld, *Prosyllabus Tracheophytorum*, Tentamen Systematis Plantarum Vascularium (Tracheophyta) (Moscow): LXXVII (2001).

Index Fungorum Registration Identifier 90756.

Several members of the *Mucoromycota* produce visible colonies and conspicuous spores. *Hyphae* commonly differentiates into rhizoids, chlamydospores, and stolons, with fixation, resistance, and dissemination functions, respectively. The *Mucoromycota* produce their sporangia by cleaving multinucleate cytoplasm. *Sporangiophores* terminate in a varied-shaped columella that persists and extends into sporangium, sporangiola, or in a varied-shaped vesicle where merosporangia or sporangiola arise from. Each sporangium has a wide range of sporangiospores, with some smaller ones

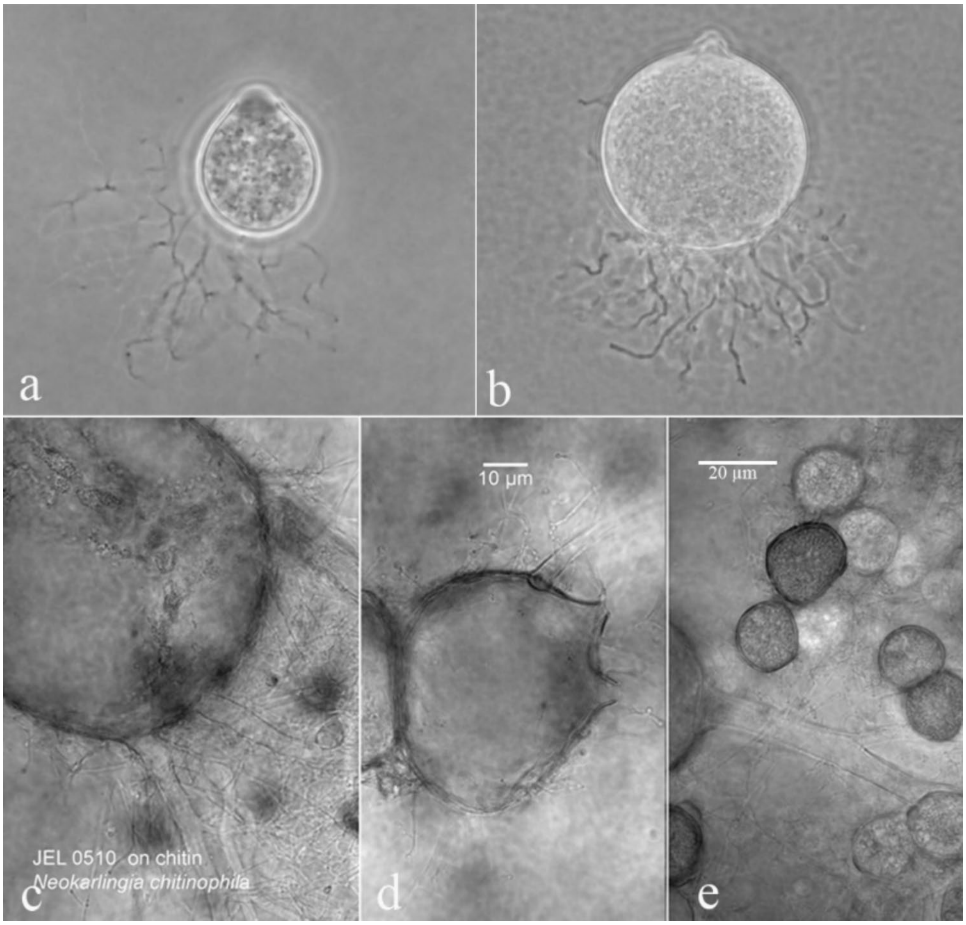


Fig. 40 Taxa belonging to different classes of *Chytridiomycota*. **a** *Batrachochytrium dendrobatidis* (JEL197, type) in *Rhizophydiomycetes*. **b** *Thoreauomyces humboldti* (JEL095, type) in *Spizellomycetes*. **c–e** *Neokarlingia chitinophila* (JEL510) in *Polychytriomycetes*. **c** Zoosporangium. **d** Zoosporangium with multiple papillae. **e** Resting spores. (photo credit to Dr. Joyce E. Longcore)

(called sporangiola) having only one or a few spores, and others (called merosporangia) having 5–20 merosporangiospores (Benny et al. 2014; Spatafora et al. 2016; Kendrick 2017). Sexual stages are represented by zygospores with apposed or opposed suspensors in this phylum. Hyphae of compatible mating types give arise zygophores, which fuse haploid nuclei. Sporocarps with zygospores are formed in few species.

Life modes and distribution: Saprobes, ectomycorrhizal, endophytes, and facultative (non-haustorial) parasites of fungi, plants and animals, causing mucormycosis mostly in immunocompromised patients.

Note: *Mucoromycota* was first described by Doweld (2001), but it was previously introduced as “nom. nov,” based on *Melanomycotina* (Cavalier-Smith 1998). Fungi of this phylum have been formerly included in phylum ‘*Zygomycota*’ (identity is invalid now). The information was derived from molecular and phylogenetic evidence on monophyly and divergence times. Zhao et al. (2023) updated the *Mucoromycota* classification framework. In particular, *Mucoromycota* fungi are characterized by their reproductive structures. Species that produce stolons anchor their hyphae to the substrate with rhizoids, which penetrate the surface of the host and grow in saprotrophic way. During maturity, most species have a fragile sporangium wall that is easily disrupted, allowing sporangiospores to escape. Some species have an apophysis below the columella, which is an expansion of the sporangiophore. For sexual reproduction, trisporic acid initiates the conversion of vegetative hyphae to zygophores (Benny et al. 2014) that enlarge after making contact by expanding the cell wall forming gametangia, which are adherent cells that contain the haploid nuclei. The zygospore is formed after plasmogamy and karyogamy in a zygosporangium, which is a thick-walled, smooth or with warty projections structure. It is most common for a zygosporangium to germinate into a germ sporangium, germ sporangiolum or germ merosporangium in which spores are produced (Alexopoulos et al. 1996; Benny 2012). Some specimens of *Mucoromycota* can form azygosporangia, which are zygosporangia-like structures formed by parthenogenesis and not by sexual reproduction (Wagner et al. 2020).

Endogonomycetes Doweld, Index Fungorum 57: 1 (2014).

Index Fungorum Registration Identifier 550357; Fig. 55

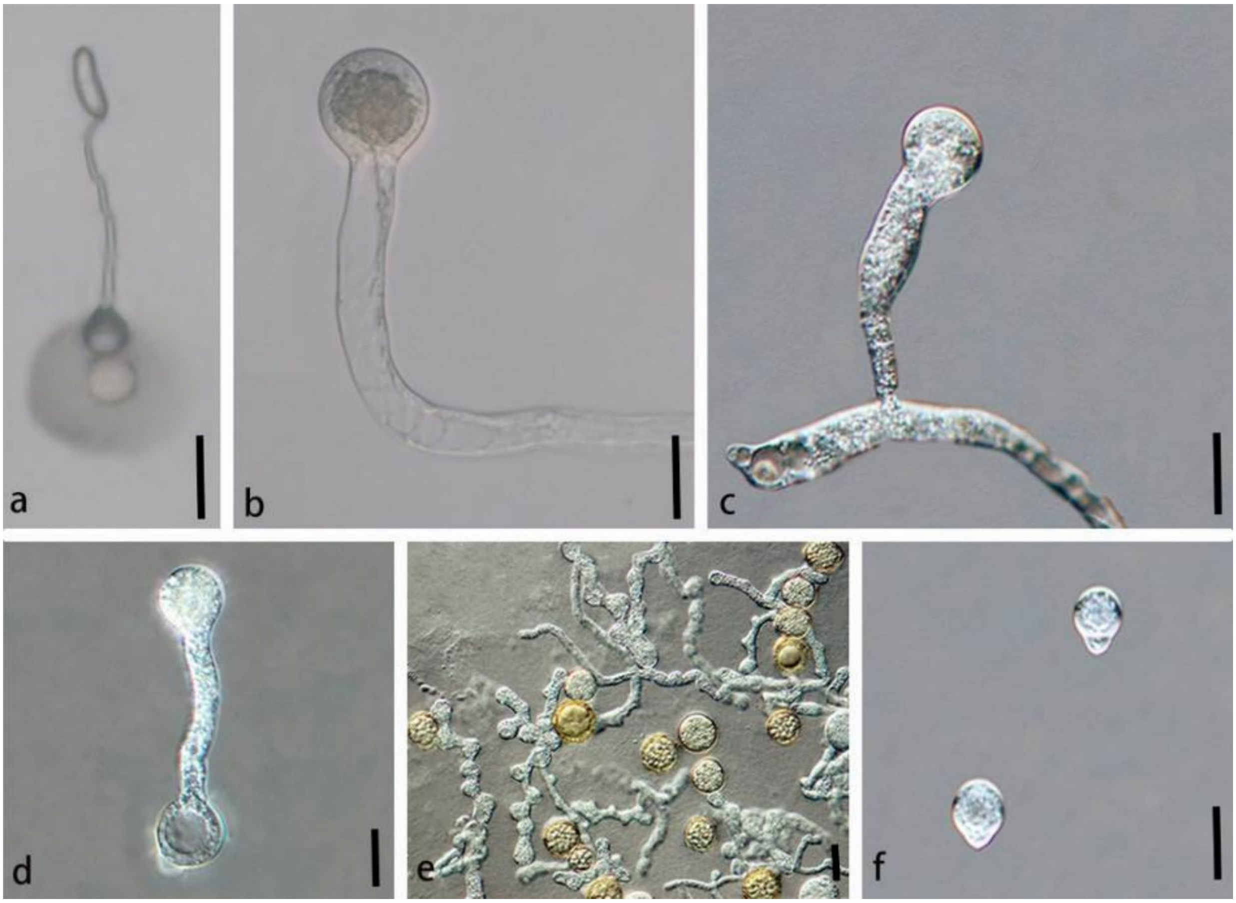


Fig. 41 Representative characters of *Capillidiaceae*. **a** *Capillidium adiaeretum* (capilliconidia). **b** *Capillidium adiaeretum* (primary conidiophore). **c** *Capillidium rhysosporum* (primary conidiophore). **d** *Capillidium heterosporum* (secondary conidia). **e** *Capillidium rugosum* (zygosporus). **f** *Capillidium rhysosporum* (primary conidia). Bars: **a**–**f** = 20 µm

Coenocytic, filamentous, underground sporocarps. Usually hypogeous or rarely epigeous, saprobic, and free-living, some forming ectomycorrhizal associations. In addition to coenocytic somatic hyphae, there may be septa that include micropores. Reproduction by globose or ovoid zygospores with unequal or nearly equal suspensors that are formed in sporocarps. Sexual and somatic hyphae are similar (Benny 2005; Desirò et al. 2017).

Life modes and distribution: Saprobes and ectomycorrhizal, widespread.

Note: *Endogonomycetes* (*Endogonales*) may have been one of the earliest mycorrhizal partners associated with land plants (Chang et al. 2019). There is a lack of collection of these fungi, and molecular data are needed to determine phylogenetic affiliations for many taxa. Mostly, *Endogonales* lineages cannot be maintained *in vitro*, similarly to *Glomeromycotina*, obligately biotrophs mycorrhizal fungi (Spatafora et al. 2016; Desirò et al. 2017). The isolation and maintenance of a few species have, however, been successful in the laboratory with considerable effort (Field et al. 2015; Yamamoto et al. 2017). Desirò et al. (2017) developed a multigene tree of *Endogonales* based on sporophores collected from four continents over the past three decades and found two deeply divergent phylogenetic clades within *Endogonales* with significant unexplained diversity. Typical mycorrhizal lifestyle signatures are found in the genomes of *Endogonaceae* and suggest that *Endogonales* might have colonized land through mycorrhizal associations with plants during their early evolution (Chang et al. 2019). Aside from ectomycorrhizal species, *Endogonomycetes* (*Endogonales*) also include saprobic species (Bidartondo et al. 2011). According to Tedersoo and Smith (2013), ectomycorrhizae evolved twice within *Endogonales*. In the *Endogonomycetes*, zygospores are produced in sporocarps, and (asexually) chlamydospores can also be formed (Bidartondo et al. 2011; Desirò et al. 2014; Dickie et al. 2015; Chang et al. 2019).

Type order: ***Endogonales*** Jacz. & P.A. Jacz., Opredelitel' Gribov, I Ficomiţeti (Leningrad): 8 (1931).

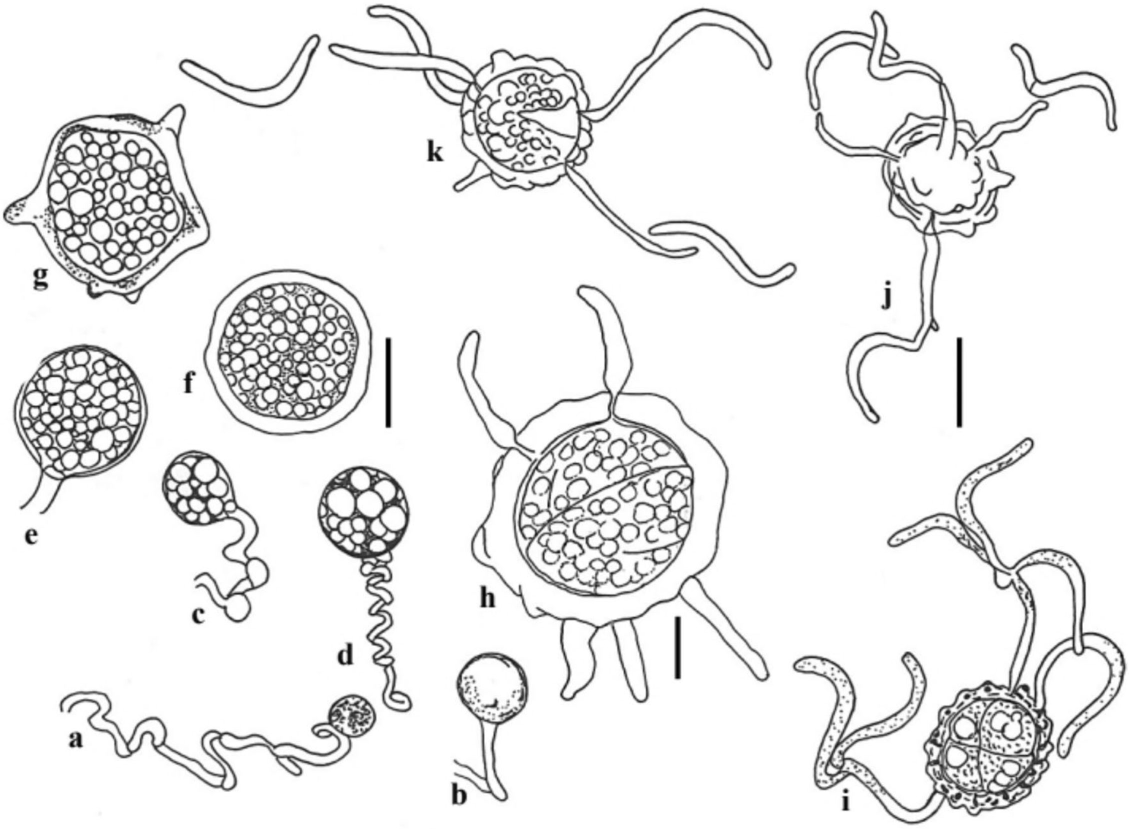


Fig. 42 *Entorrhiza casparyana*. **a–g** Intracellular more or less coiled hyphae and teliospores in different developing stages (host cells not drawn). **h–k** Germinating teliospores in different developing stages. Note the sigmoid shape of the propagules. Scale bar **a–g, j–k** = 20 µm, **h** = 10 µm in (h) (redrawn from Bauer et al. 2015)

Type family: ***Endogonaceae*** Paol., Syll. fung. (Abellini) 8: 905 (1889).
Type genus: ***Endogone*** Link, Mag. Gesell. naturf.Freunde, Berlin 3(1–2): 33 (1809).
Type species: ***Endogone pisiformis*** Link, Mag. Gesell. naturf. Freunde, Berlin 3(1–2): 33 (1809).

Mucoromycetes Doweld, *Prosyllabus Tracheophytorum*, Tentamen Systematis Plantarum Vascularium (Tracheophyta) (Moscow): LXXVII (2001).

Index Fungorum Registration Identifier 90755; Fig. 56

Mycelium is abundant, rapidly growing, and anamorphic structures are normally formed in large quantities in it. Mycelium consists of non-septate or irregularly septated cells (Walther et al. 2019; Wagner et al. 2020). *Sporangiospores* in anamorphic form are produced in multispored sporangia, as well as in one to few-spored sporangiola and merosporangia. The sporangium can be deliquescent, evanescent or persistent-walled, and the release of spores occur actively (less common) or passively. Most species do not produce chlamydospores, arthrospores, or yeast cells, (Von Arx 1982). *Columella* with different shapes characterizes sporangia and some sporangiola, but merosporangia and some sporangiola are also formed on a varied-shaped vesicle. *Mucoromycetes* have well-developed columella or vesicle as synapomorphies. *Zygospore* (meiospore) is formed when homothallic or heterothallic species conjugate with each other (Hoffmann et al. 2013). In addition to the specific ornamentation of the exospores (warty, rough, smooth), zygospores also display protective appendages such as antler-like or finger-like on their support cells (suspensors) (Zycha et al. 1969). Some *Mucoromycetes* species exhibit dimorphism, capable of switching from filamentous, multicellular to yeast-like states (Bartnicki-Garcia and Nickerson 1962). It has been revealed through the application of molecular phylogenetics that some of the above-mentioned morphological characters are not taxonomically significant (Hurdeal et al. 2021).

Life mode and distribution: *Mucoromycetes* (*Mucorales*) are cosmopolitan fungi. In the fungal tree of life, this class belongs to the early-diverging fungal groups (Spatafora et al. 2016). However, there is no information on the ecological role or geographical distribution of most of these species (Voigt

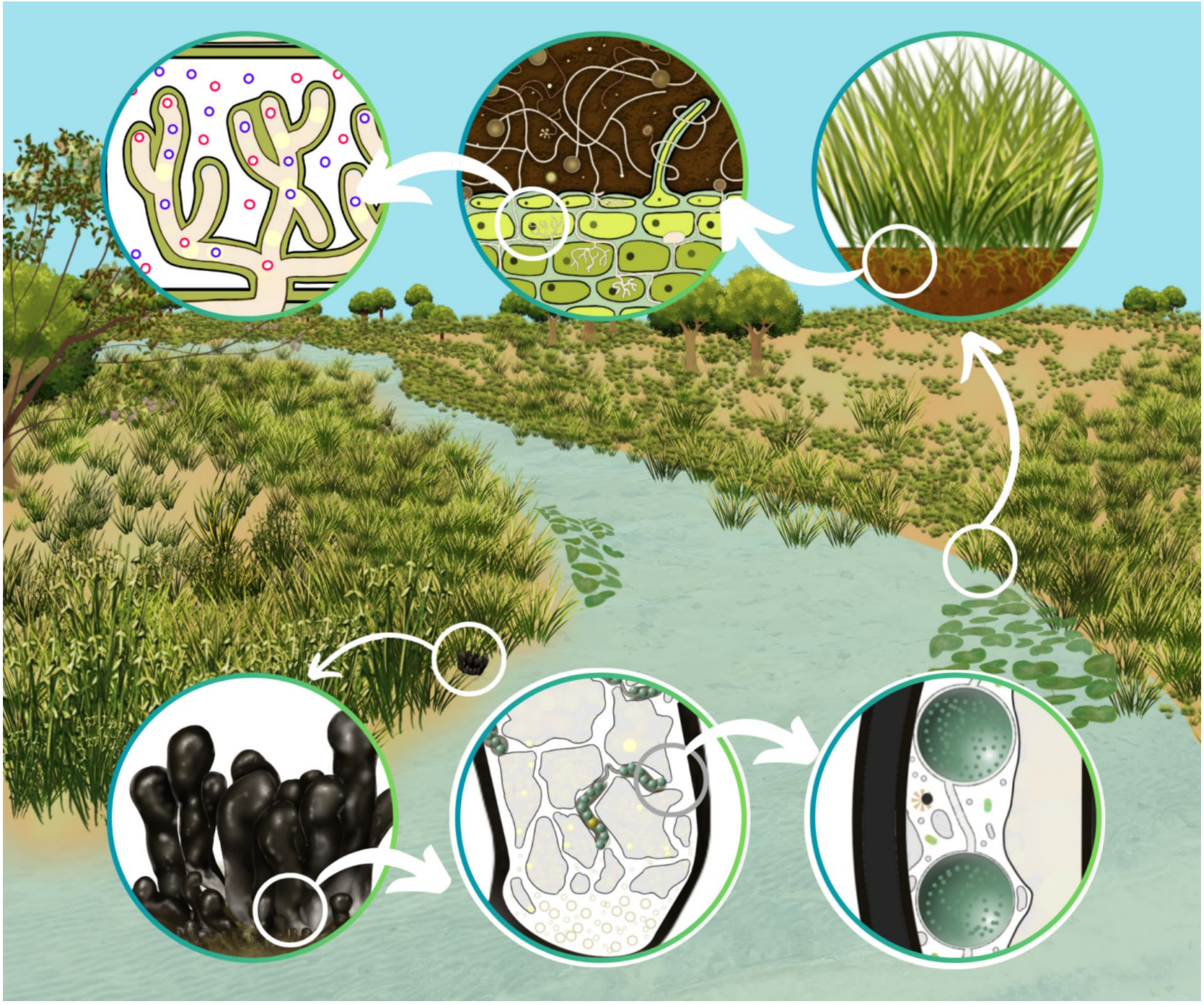


Fig. 43 Types of symbiotic association in *Glomeromycota*. AMF form mycorrhiza with roots of terrestrial and aquatic plants. *Geosiphon pyriforme*, occurring in humid soil environments, is the unique fungus of the *Archaeosporomycetes* that forms an association with photosynthetically and nitrogen-fixing cyanobacteria of the genus *Nostoc*

et al. 2021). Species of this class can be isolated from varied substrates, including soil, fruits, leaves, grains and stored foods, animal excrement and insects (Nguyen et al. 2021; Voigt et al. 2021) (Table 22). In general, specimens of *Mucoromycetes* do not have the ability to degrade complex sugars, such as cellulose and lignin, but they can easily degrade soluble sugars, such as glucose, being referred to by some authors as "sugar fungi" (Benny 2012). However, some specimens are capable of degrading cellulose, pectin, starch, and xylan (Pawłowska et al. 2019). *Mucoromycetes* tend to be, among fungi, pioneers in the colonization of different substrates. Therefore, rapid sporulation and accelerated mycelial growth, even in nutrient-poor culture media, are striking characteristics of most taxa, especially *Mucorales* species (Benny 2008; Benny et al. 2016). Soil and herbivores and small rodents dung are the best substrates for the isolation of these fungi. *Pilobolus* is the the unique obligatory coprophilous genus, and its species present mechanisms of active expulsion of the sporangium with positive phototropism, adhesive sporangia, sporangiospores that survive digestion by herbivores, and the ability to grow in relatively high pH conditions (Dix and Webster 1995). Some species of *Cunninghamella*, *Lichtheimia*, *Mucor* and *Rhizopus*, *Rhizomucor*, *Syncephalastrum* have been reported as pathogens of human (Table 23).

Notes: Among the early diverging fungi, the *Mucoromycetes* (*Mucorales*) are a well-studied group of fungi. A mucoralean fungus reproduces asexually and is classified into different genera and families based on its vegetative and anamorphous structures such as spores or sporangia (Von Arx 1982). In most keys to families and genera, teleomorphs (zygospores) have been neglected or only incidentally used.

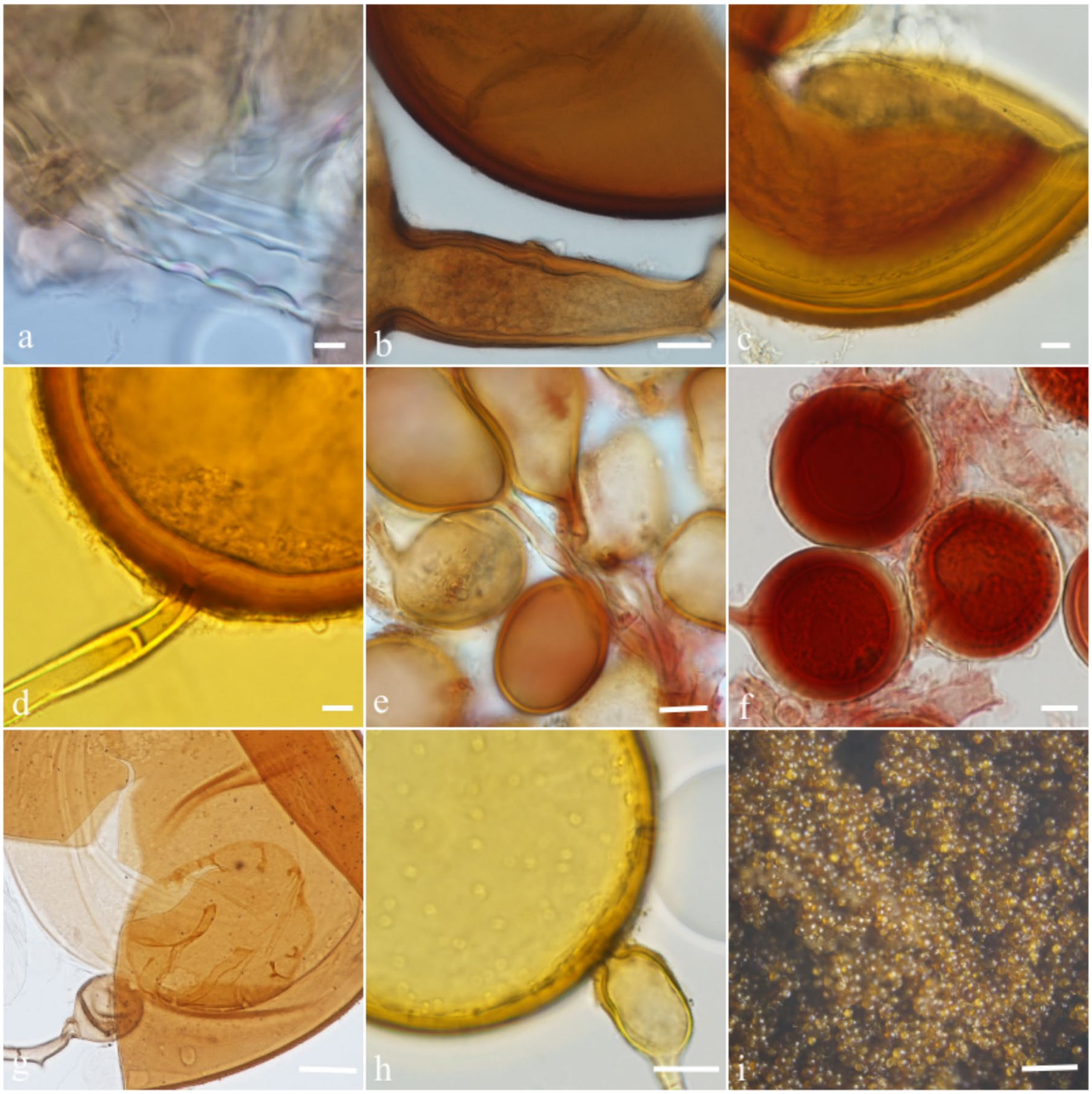


Fig. 44 Microscopic morphology of taxa in *Glomeromycota*. **a** Spore wall of *Ambispora appendicula* (*Ambisporaceae—Archaeosporales*). **b** Detail of sporiferous saccule and spore in *Acaulospora tuberculata* (*Acaulosporaceae—Diversisporales*). **c** Spore with three walls in *Acaulospora* sp. (*Acaulosporaceae—Diversisporales*). **d** Detail of subtending hyphae in *Diversispora varaderana* (*Diversisporaceae—Diversisporales*). **e** Clusters of spores produced by *Dominikia gansuensis* (*Glomeraceae—Glomerales*). **f** Detail of Melzer reaction in spores of *Epigeocarpum crypticum* (*Glomeraceae—Glomerales*). **g** Spore with suspensor-like cell and germinal shield in *Fuscutata aurea* (*Dentiscutataceae—Gigasporales*). **h** Suspensor cell in *Gigaspora* sp. (*Gigasporaceae—Gigasporales*). **i** Large glomerocarps produced by *Rhizoglomus maiae* (*Glomeraceae—Glomerales*). Scale bars **a**, **c**, **d**, **e** = 10 µm; **b**, **g**, **h** = 20 µm; **i** = 250 µm

Over 100 years ago, heterothallic and homothallic modes of sexuality were discovered in *Mucoromycetes* (Blakeslee 1904). The formation of sexual reproductive structures is mediated by volatiles such as trisporoids and beta-carotene (Gooday 1968). We are unsure whether zygospores play a greater role in reproduction and distribution than asexual spores. Germination has only been described and illustrated for a few species under laboratory conditions (Michailides and Spotts 1988; Yu and Ko 1997; Wagner et al. 2020). *Mucoromycetes* are traditionally classified using physiology and morphology but species, genera, and families can be distinguished by only a few distinguishable morphological characters in it. It is difficult to identify the family structure of the *Mucorales*, but molecular data and high-resolution microscopy have enabled the discovery of new, potentially phylogenetic informative characters. The most recent significant changes were done by Zhao et al. (2023).

Industrial applications: *Mucoromycetes* are used in a wide range of biological transformations, including the production

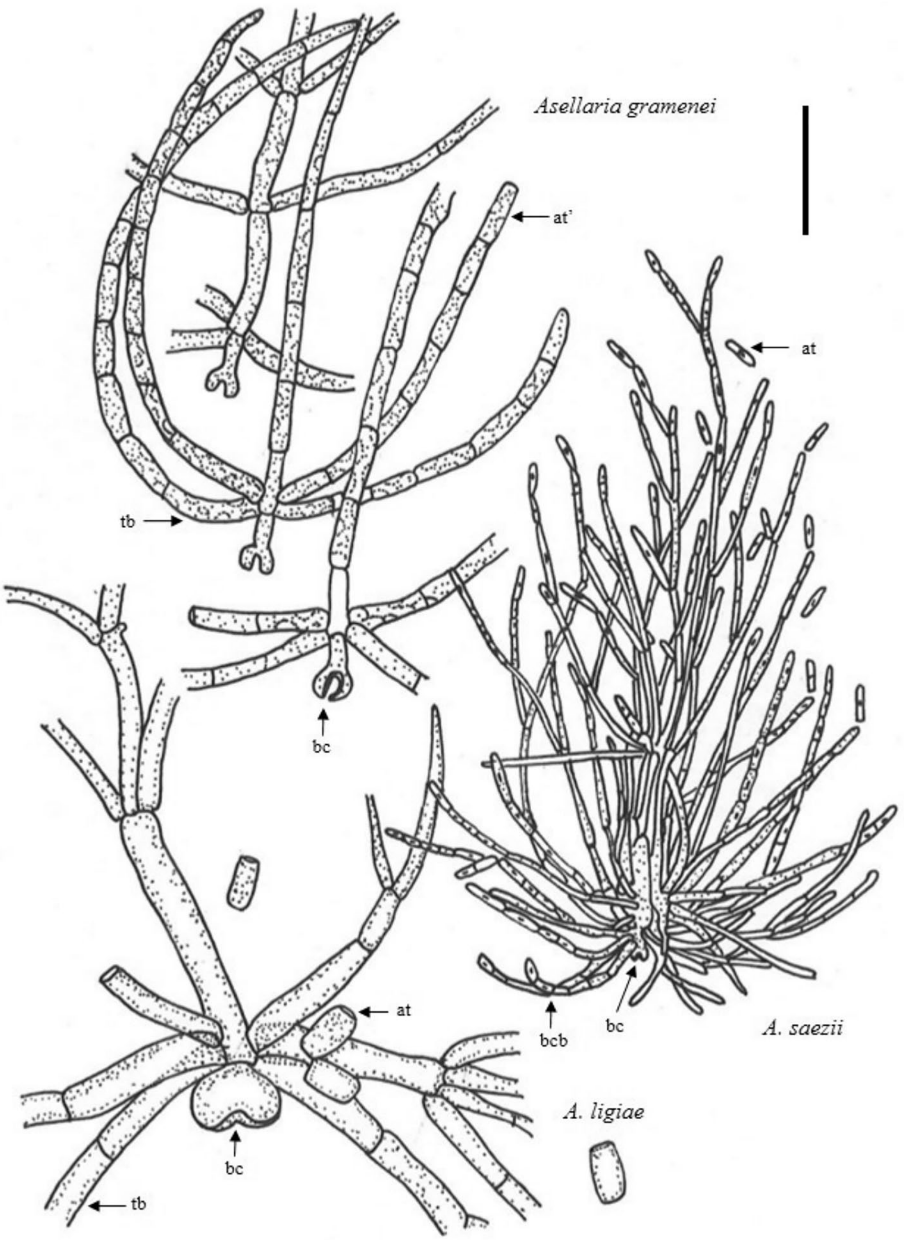


Fig. 45 *Asellaria gramenei, A. saezii* and *A. ligiae*. The species of *Asellaria* are here represented to easily compare shapes and sizes. Indicated here are: bc, basal cell; bcb, basal cell branches; at, arthrospores; at' arthrospores not disarticulated from the thallus; tb, thallial branches. Scale bar = 50 µm for all the figures (redrawn from Valle 2006)

of feed and food additives, pharmaceutical ingredients (including lycopene), and chitosan, an exclusive *Mucoromycetes* (*Mucorales*) product (Shahidi et al. 1999; Gładkowski et al. 2011). Some species have been traditionally used in the production of fermented foods in Asia, such as tofu and tempeh (Hesseltine 1965, 1983; Nout and Kiers 2005). Several *Mucoromycetes* species have been reported as plant pathogens (especially infecting fruits and vegetables) (Martin 1964; Ray and Ravi 2005), facultative parasites of other fungi (Hoffmann et al. 2013), and biotrophic or necrotrophic parasites (not well studied) (Zycha et al. 1969) (Table 24).

Type order: ***Mucorales*** Dumort. [as 'Mucorarieae'], Analyse des familles des plantes: avec l'indication des principaux genres qui s'y rattachent: 73 (1829).
Type family: ***Mucoraceae*** Fr. [as 'Mucoroidei'], Syst. mycol. (Lundae) 1: xlix (1821).
Type genus: ***Mucor*** Fresen., Beitr. Mykol. 1: 7 (1850).
Type species: ***Mucor mucedo*** Fresen., Beitr. Mykol. 1: 7 (1850).

Umbelopsidomycetes Tedersoo, Sánchez-Ramírez, Kõljalg, Bahram, Döring, Schigel, T. May, M. Ryberg & Abarenkov, Fungal Diversity 90: 152 (2018).

Index Fungorum Registration Identifier 554017.

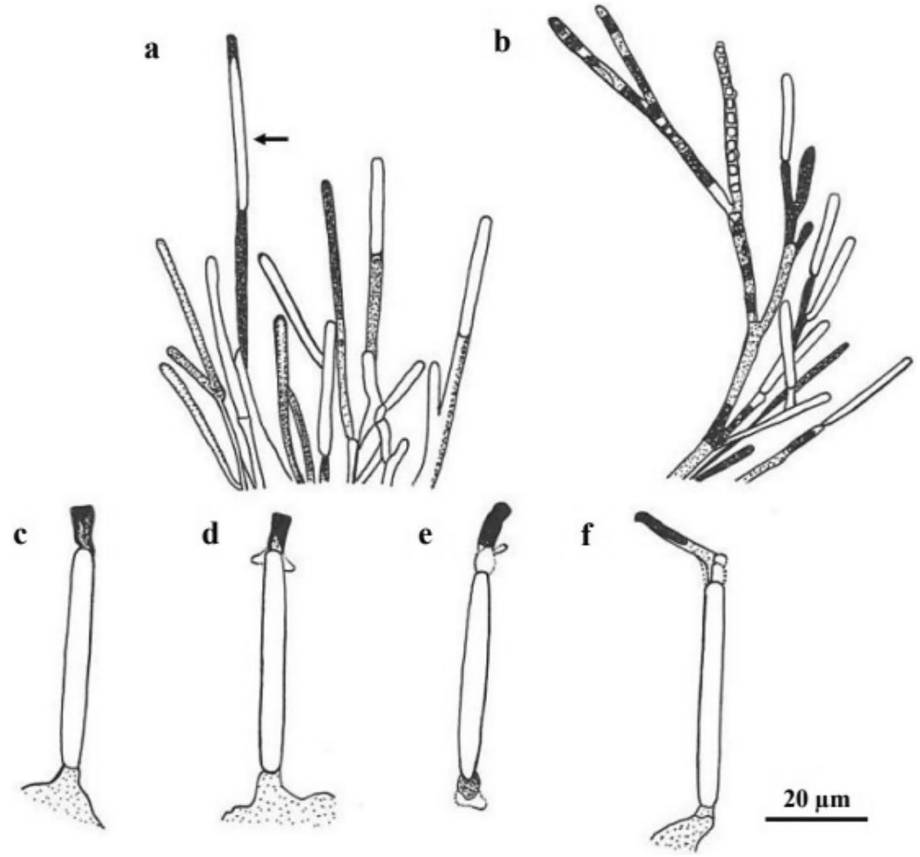


Fig. 46 *Barbatospora ambicaudata* **a** Detaching with a cylindrical wall that resembles a cap at the terminal end. **b** Sporulating branchlets removed from a simuliid larva. **c** Thallus holdfast affixed to a larva's hindgut cuticle. **d–g** A reconstruction of a sequence of development in released trichospores, following dehiscence of the cap-like structure at the terminal end, displaying numerous appendages basally and appendage-like filaments distally (modified drawing from White et al. 2006)

Colonies velutinous, reddish, brownish, grey or ochraceous, slow growing in culture media. *Sporangiophores* arising from vesicles on substrates, cymosely or umbellately branched (Wang et al. 2013). Septa are near the branching and distant from the sporangium. **Asexual reproduction** occurs through elongate or globose, uni- and/or multispored ochraceous, reddish, or hyaline sporangium, and chlamydospores. *Columellae* are small or absent, and sporangiospores are varied-shaped, angular or not, hyaline or pigmented, in some species bearing appendages (Benny 2005; Wang et al. 2013). *Chlamydospores* are abundant and full of lipids in culture. Sexual reproduction are unknown (Spatafora et al. 2016).

Life mode and distribution: The majority of species are saprobes in soil, debris, dung and sugar-rich plant parts (Spatafora et al. 2016). Although *Umbelopsidomycetes* are cosmopolitan fungi, there is no information on the ecological role or geographical distribution of the majority of these fungi.

Notes: *Umbelopsidomycetes* was introduced by Tedersoo et al. (2018) based on divergence time. Previously, species of *Umbelopsidomycetes* (*Umbelopsidales*) were classified as *Mucoromycetes* (*Mucorales*) and *Mortierellomycetes* (*Mortierellales*). Based on molecular data, Meyer and Gams (2003) delineated *Umbelopsis* from *Mortierella* and introduced *Umbelopsidaceae* as a new family. Following data from genome-scale analyses, this group appears to be distinct from *Mucorales* on a phylogenetic level (Spatafora et al. 2016). Some *Umbelopsidomycetes* (*Umbelopsis*) are heat-resistant (Bollen and van der Pol-Luiten 1975), but they are not able to grow at extremely high temperatures.

Type order: ***Umbelopsidales*** Spatafora, Stajich & Bonito, in Spatafora, Chang, Benny, Lazarus, Smith, Berbee, Bonito, Corradi, Grigoriev, Gryganskyi, James, O'Donnell, Roberson, Taylor, Uehling, Vilgalys & White, Mycologia 108(5): 1035 (2016).

Type family: ***Umbelopsidaceae*** W. Gams & W. Mey., in Meyer & Gams, Mycol. Res. 107(3): 348 (2003).

Type genus: ***Umbelopsis*** Amos & H.L. Barnett, Mycologia 58(5): 807 (1966).

Type species: ***Umbelopsis versiformis*** Amos & H.L. Barnett, Mycologia 58(5): 807 (1966).

NEOCALLIMASTIGOMYCOTA M.J. Powell, in Hibbett et al., Mycol. Res. 111(5): 516 (2007).

Index Fungorum Registration Identifier 501279; Fig. 57

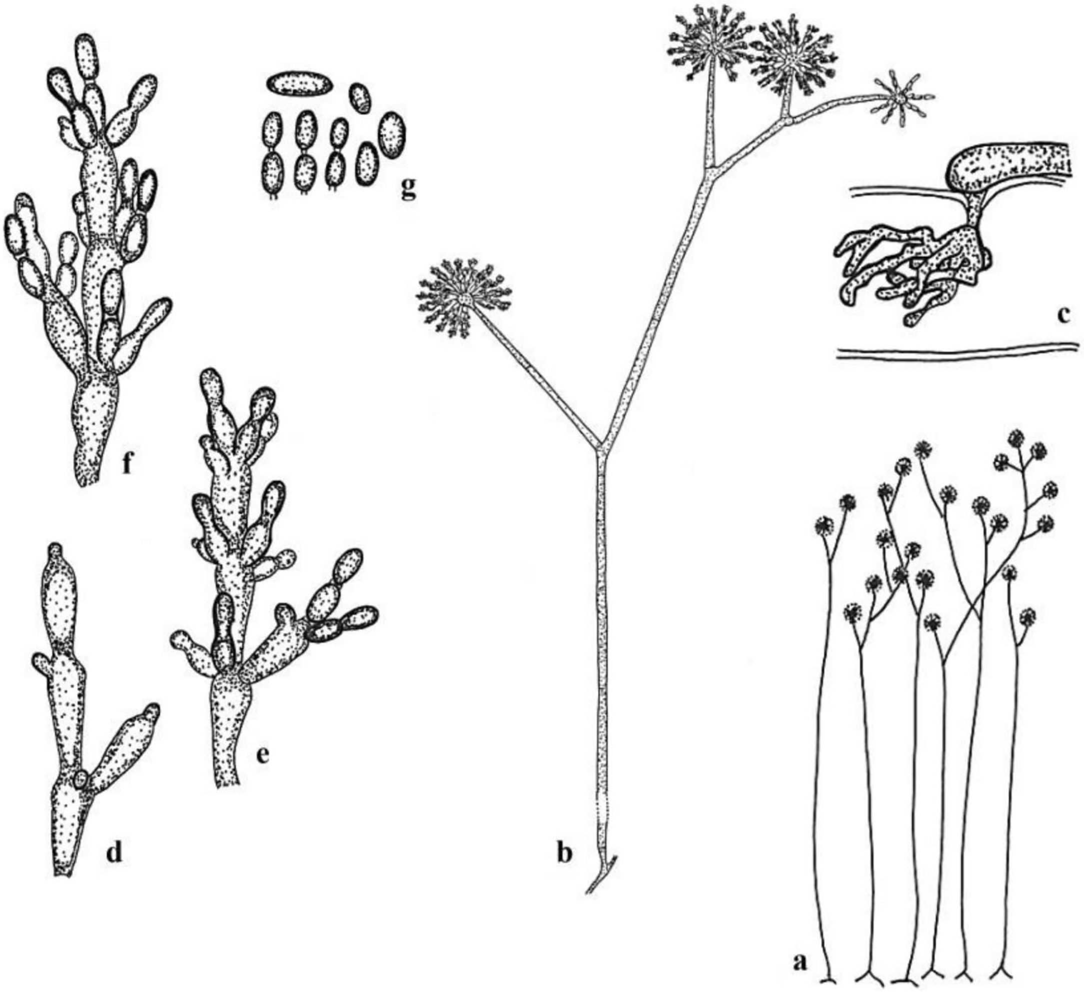


Fig. 47 *Dimargaris xerosporica*. **a** Habit sketches of sporophores. × 30. **b** Typical sporophore showing characteristic cymose branching pattern. The lowermost fertile head is the oldest; the one at the tip of the apparent main axis (upper right) is the yourgest. × 145. **c** Haustorium. × 1080. **d**–**f** Three successive stages in the development af the sporiferous branchlets and merosporangia. × 1360. **g** Three mature merosporangia prior to disappearance of the sporangia wall and four sporangiospores. × 1360 (redrawn from Benjamin 1965)

Obligate anaerobic fungi, present in the alimentary tract of foregut, pseudoforgut, and hindgut fermenting mammalian and few reptilian and avian herbivores. Lifecycle involves the production of and release of motile flagellated spores (zoospores) from sporangia. These zoospores encyst, germinate and develop into a thallus structure that anchors the formation of new sporangia. Produces posteriorly monoflagellated or polyflagellated spores. Thallus development pattern are monocentric or polycentric, rhizoidal growth is either filamentous or bulbous. Lack mitochondria but contains hydrogenosomes of mitochondrial origin. Lack respiratory capacity and produce energy solely by fermentation. Produces cellulosomal structures bearing plant biomass degrading enzymes.

Life modes and distribution: Anaerobic gut fungi of herbivores, widespread.

Notes: The members of *Neocallimastigomycota* have mainly been reported from 'the rumen and alimentary tract of larger mammalian and some reptilian, marsupial and avian herbivores' (Hanafy et al. 2022). The phylogenetic placement of these taxa has been confirmed in early divergent fungi by Li et al. (1993) who introduced the Order *Neocallimastigales* J.L. Li et al. (in *Chytridiomycota*) to accommodate *Neocallimastigaceae* I.B. Heath.

In their phylogenetic analyses, James et al. (2006b) showed that the *Neocallimastix* strain resided in *Chytridiomycota* along with *Chytridiales*, *Monoblepharidales*, and some *Spizellomycetales* and further named this clade as 'euchytrids'. White et al. (2006) also agreed on the placement of *Neocallimastix* in *Chytridiomycota* in their analyses. However, both analyses by James et al. (2006b) and White et al. (2006) used only one strain to represent *Neocallimastigales*. James et al. (2006b) provided a detailed analysis

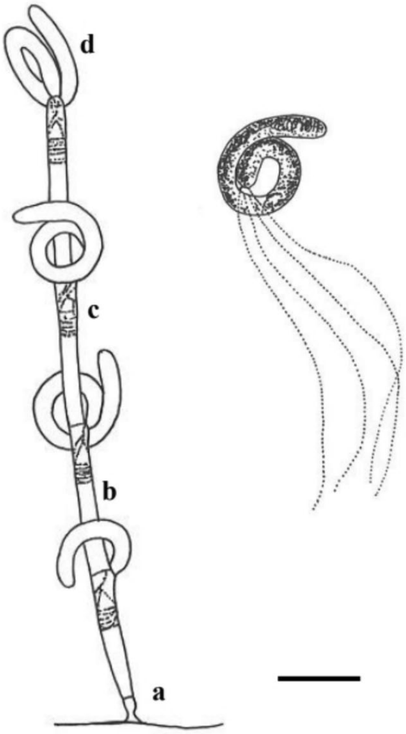


Fig. 48 Sporulating thallus of *Harpella melusinae* and one released spore (from Reichle and Lichtwardt 1972)

of *Chytridiomycota* and recognized *Neocallimastigales* as a well separated, order in the phylum. Hibbett et al. (2007), thus, introduced the class *Neocallimastigomycetes* and the phylum *Neocallimastigomycota* to accommodate these taxa which how a distinct phylogenetic lineage in the kingdom of *Fungi*. Hibbett et al. (2007) was broadly accepted by subsequent studies (e.g. Gruninger et al. 2014; Powell and Letcher 2014; Hanafy et al. 2022). However, Spatafora et al. (2016) recognized *Neocallimastigomycetes* as a distinct class in *Chytridiomycota*.

Tedersoo et al. (2018), Wijayawardene et al. (2020a) and Voigt et al. (2021) have recently recognized *Neocallimastigomycota* as a distinct phylum in their phylogenetic analyses. Currently, *Neocallimastigomycota* comprises one subphylum (*Neocallimastigomycotina*) and one class (*Neocallimastigomycetes*).

Neocallimastigomycetes M. J. Powell, Mycol. Res. 111:516. 2007.

Index Fungorum Registration Identifier 501280; Fig. 55

Description and notes are similar to the phylum description.

Type order: ***Neocallimastigales*** J.L. Li, I.B. Heath & L. Packer [as 'Neocallimasticales'], Can. J. Bot. 71: 403 (1993).

Type family: ***Neocallimastigaceae*** I.B. Heath [as 'Neocallimasticaceae'], in Heath, Bauchop & Skipp, Can. J. Bot. 61(1): 304 (1983).
Type genus: ***Neocallimastix*** Vávra & Joyon ex I.B. Heath, in Heath, Bauchop & Skipp, Can. J. Bot. 61(1): 304 (1983).
Type species: ***Neocallimastix frontalis*** (R.A. Braune) Vávra & Joyon ex I.B. Heath, in Heath, Bauchop & Skipp, Can. J. Bot. 61(1): 306 (1983).

OLPIDIOMYCOTA Doweld, Index Fungorum 42: 1 (2013).

Index Fungorum Registration Identifier 550327.

Asexual morph: Sporangium single, endobiotic, with cell walls; zoospores posteriorly uniflagellate, with a single globule, cone-shaped striated rhizoplast fused to both the functional and vestigial kinetosomes, gamma-like particles and rough endoplasmic reticulum; nucleus associated with the basal body, no nuclear cap. **Sexual morph:** Unknown.

Life modes and distribution: The members of *Olpidiomycetes* distribute in a broad range of ecosystems (worldwide) and are mainly reported as plant pathogens and vectors of plant pathogenic viruses. Phytopathogenic members of the class are root parasites of important crop plants (e.g., *Olpidium*, *Cibdelia*, *Leiolpidium*), while some are reported as pathogenic to algae and rotifers (e.g., *Olpidium*). Some members are saprobes (e.g., *Chytridhaema*) that are important in decomposition and nutrient cycling.

Notes: Doweld (2013a) introduced the phylum *Olpidiomycota* to accommodate *Olpidium* (A. Braun) Rabenh. At the same time, Doweld et al. (2013a) introduced the subphylum *Olpidiomycotina* Doweld. Before the introduction of the phylum, the phylogenetic placement of *Olpidium* taxa in basal fungi has been confirmed by James et al. (2006a,b), White et al. (2006) and Sekimoto et al. (2011) but regarded as uncertain in '*Zygomycota*'/ or '*Chytridiomycota*'. Hibbett et al. (2007), however, did not include *Olpidium* in any higher position but regarded that traditionally the genus has been placed in *Chytridiomycota*. Spatafora et al. (2016) did not include any *Olpidium* taxa in their phylogenetic analyses but mentioned the placement accepted by James et al. (2006a,b) and Sekimoto et al. (2011). Tedersoo et al. (2018), however, clearly showed the placement of *Olpidium s. str.* as a distinct lineage in the kingdom *Fungi*, sister to *Basidiobolomycota*. Furthermore, Tedersoo et al. (2018) introduced the subkingdom *Olpidiomyceta*, which only comprises one phylum.

Olpidiomycetes Doweld, Index Fungorum 42: 1 (2013).

Index Fungorum Registration Identifier 550325; Fig. 58

The description is similar to the description of the phylum.

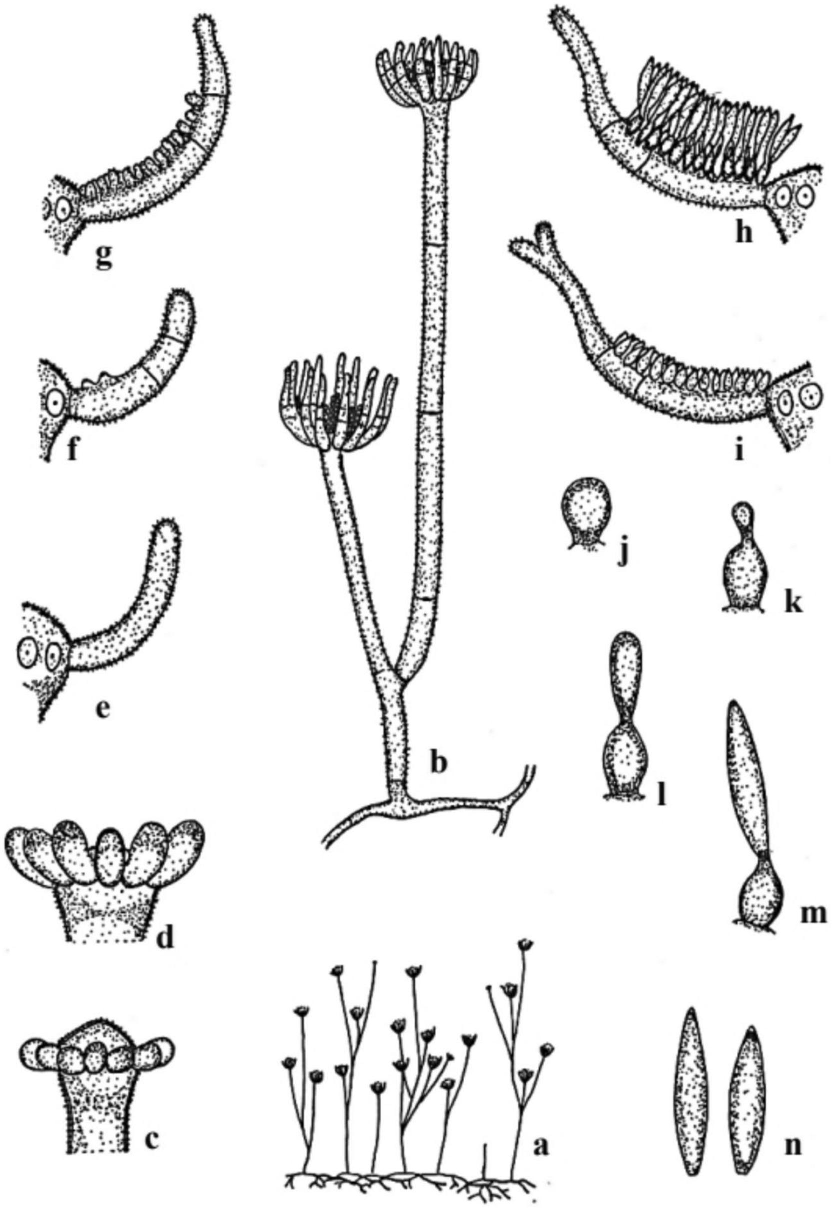


Fig. 49 *Kickxella alabastrina* Coemans. **a** Habit sketch showing general characteristics of the fruiting structures. × 30. **b** Once branched sporangiophore bearing distal whorls of sporocladia. × 180. **c**, **d** Early stages in the development of the sporocladia showing their simultaneous origin in a whorl around the slightly swollen apex of the sporangiophore. × 600. **e–g** Successive stages in the development of the sporocladium and pseudophialides prior to sporangiole formation. × 600. **h** Mature sporoclaclium showing disposition of pseudophialides and sporangiola on upper surface. × 600. **i** Mature sporocladium after sporangiola have fallen away; note furcate apical cell. × 600. **j**–**m** Four pseudophialides showing successive stages in the aerogenous development of the unispored sporangiole. × 1360. **n** Two mature sporangiola. × 1360 (redrawn from Benjamin 1958)

Notes: *Olpidiomycetes* was introduced by Doweld (2013a). *Olpidiomycetes* encompasses a single order *Olpidiales*. *Olpidiales* was introduced by Cavalier-Smith (2013) but it was invalid as per Article 42. Later, Doweld (2013a) effectively published the order and introduced a new class *Olpidiomycetes* to accommodate the order. While proposing the high-level classification of the fungi and a tool for evolutionary ecological analyses. Recently Chang et al. (2021) confirmed genome-scale phylogeny of *Olpidium* as the closest living zoosporic fungus to the non-flagellated, terrestrial fungi (whole-genome sequence of *Olpidium bornovanus* S191: JAEFCI000000000). Previously, Sekimoto et al. (2011) placed *Olpidium* under *Zygomycota* through molecular phylogenetic analyses of *tef2*, *rpb1*, *rpb2* and *ACT*.

Type order: ***Olpidiales*** Caval.-Sm., Eur. J. Protist. 49(2): 157 (2012) [2013].

Type family: ***Olpidiaceae*** J. Schröt. [as 'Olpidiacei'], in Cohn, Krypt.-Fl. Schlesien (Breslau) 3.1(1–8): 180 (1886) [1889].

Type genus: ***Olpidium*** (A. Braun) Rabenh., Flora Europaea algarum aquae dulcis et submarinae 3: 282 (1868) [1867].

Type species: not indicated

(*Olpidium endogenum* (A. Braun) J. Schröt. 1886 (Designated by Clements & Shear, Gen. fung., Edn 2 (Minneapolis): 234. 1931 *fide* Index Fungorum 2023).

ROZELLOMYCOTA Doweld, Index Fungorum 43: 1 (2013) emend. Tokarev & Nassonova.

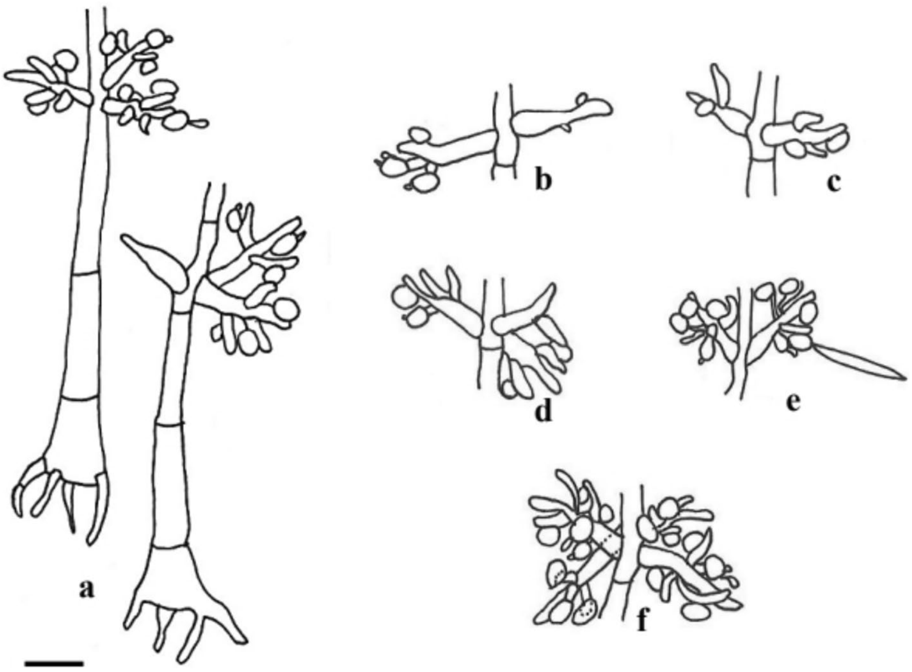


Fig. 50 *Ramicandelaber longisporus* PCNB-1157 (IFO 33179). **a** Habits. **b**–**f** Upper parts of sporangiophores showing the development of sporocladia (branchlets on branches of sporangiophores). Sporocladia produce subspherical pseudophialides. Scale bar **a**–**f** = 10 µm (redrawn from Ogawa et al. 2001)

Index Fungorum Registration Identifier 550328; Fig. 59

Intracellular obligate parasites parasitize host via phagocytosis of host organelles (in *Rozella*) or via osmotrophy (in all other known forms), penetration of the host via a polar tube. *Cells* amoeboid, multinucleate or uninucleate, covered by a single membrane, unwalled; pseudopodia-like extensions interdigitated between and partially extended around host organelles; microtubules underlie the plasma membrane in a random pattern and extend into cytoplasmic extensions. The most basal lineage of the phylum possesses bilaterally symmetrical posteriorly uniflagellate zoospores while other groups are non-motile. *Resting spores* thick-walled. With the exception of *Rozella*, *Mitosporidium,* and *Paramicrosporidium*, the mitochondria are reduced to mitosomes lacking the genetic apparatus (modified after Doweld 2013c).

NB: The phylum *Rozellomycota* sensu Wijayawardene et al. (2020a) in its current state lacks some important subdivisions (classes), which would incorporate a number of basal forms. This should be noted when dealing with its taxonomic framework, limited to two classes *Rudimicrosporea* and *Microsporidea,* which only cover the subphylum *Microsporidia,* leaving out a series of important taxa either as genera *incertae sedis* (*Mitosporidium*, *Morellospora*, *Nucleophaga*, *Paramicrosporidium*, *Rozella*) or as orders *incertae sedis* (*Chytridiopsida*).

Life modes and distribution: cosmopolitan obligate intracellular parasites of *Chytridiomycota*, *Blastocladiomycota*, *Monoblepharomycota*, and *Oomycota* (Karpov et al. 2014c), *Bacillariophyceae* (Chambouvet et al. 2019), *Ciliata*, *Apicomplexa*, *Amoebozoa*, *Paramyxea* and *Metazoa* (Corsaro et al. 2014; Nassonova et al. 2016; Stentiford et al. 2017).

Notes: Karpov et al. (2014a) introduced the superphylum *Opisthosporidia*, which accommodated the phyla *Cryptomycota/Rozellida, Microsporidia,* and the newly established *Aphelida*, the latter based upon the class *Aphelidea.* This taxonomic solution reflects the deep branching of this monophyletic group within *Holomycota* as a sister group to the kingdom *Fungi.* Further studies did not support the monophyly of Opisthosporidia (Torruella et al. 2018; Galindo et al. 2022), and Tedersoo et al. (2018), further supported by Wijayawardene et al. (2018b, 2020a, 2022a), placed *Cryptomycota/Rozellida* and *Microsporidia* as basal *Fungi*, bounded by the phylum *Rozellomycota* (Vávra and Lukeš 2013). In the frames of the current compendium, which represents “a mycologist’s view” of taxonomy, we are called upon using this affiliation, though we strongly believe it being debatable and requires further consideration. Meanwhile, the original diagnosis by Doweld (2013c) only described the *Rozella* part of the phylum, while nowadays a number of organisms included in the phylum has increased dramatically, which has provoked a need to modify the diagnosis. Since the new members of the phylum all parasitize host cells by importing nutrients from its cytoplasm and organelles (Vavra and Lukes 2013; Haag et al. 2014; Corsaro et al. 2014; Timofeev et al. 2020), not phagocytozing it, this part of diagnosis is also modified.

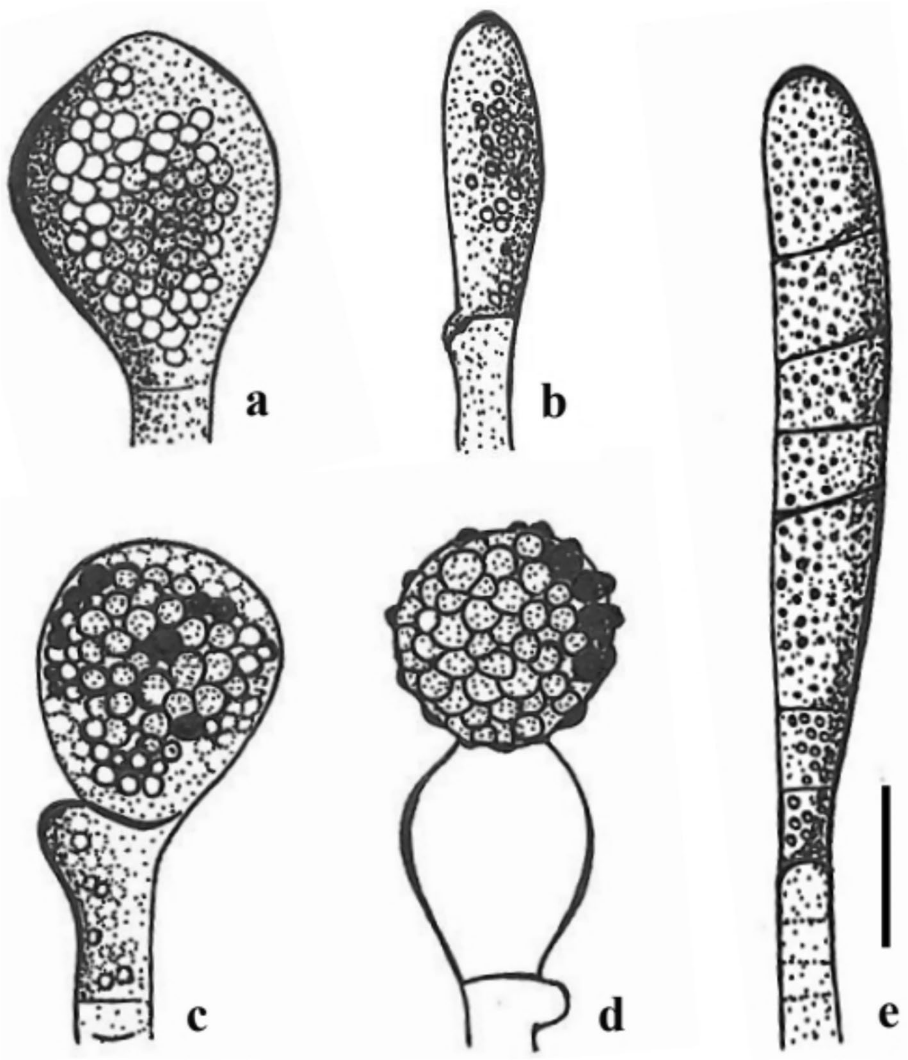


Fig. 51 *Monoblepharis macrandra.* Nomarski interference micrographs. **a** Solitary oogonium showing basal cross wall and the receptive papilla and lipid droplets of the egg. **b** Terminal antheridium cut off by basal cross wall prior to cleavage of sperms. **c** Oogonium with hypogynous antheridium. **d** Exogenous oospore showing bullations, thick wall, and attachment to mouth of empty oogonium. **e** Zoosporangium showing basal cross wall and cleavage planes of zoospores. Scale bar **a**–**f** = 10 μm (redrawn from Marek 1984)

Rudimicrosporea Sprague, Comp. Pathobiol. (New York, London): 1–31 (1977) emend. Tokarev & Nassonova.

Synonym: *Metchnikovellidea* Weiser, Vestnik Cesk. Spol. Zool. 41: 312 (1977).

Index Fungorum Registration Identifier 90611.

Minute, intracellular protozoan parasites. They are exclusively hyperparasites of gregarines, which are all (with one possible exception) in turn parasites of annelids, mostly marine. The spores have the essential characters of microsporidian spores, but differ sharply in having a highly simplified or rudimentary extrusion apparatus missing a polar sac/anchoring disk, a polaroplast and a posterior vacuole. The polar filament (tube) represented by a manubrium (instead of a long, coiled filament) that extends posteriorly from a polar sac and terminates in a tubulo-vesicular network. The sporoplasm, consisting of nucleus and cytoplasm, occupies the rest of the intrasporal cavity. The spore wall consists of the usual three layers (exospore, endospore, plasmalemma), but endospore is rather thin, almost undeveloped. The spores, having the simple extrusion apparatus, are roughly spherical or oval and quite small. In the vegetative sequence uninucleate and plasmodial forms have been reported. A dimorphism is exhibited in the occurrence of two sporulation (sporogonial) sequences. In one sequence the plasmodium divides and produces numerous sporoblasts which transform into free spores resided either directly in the cytoplasm or within a parasitophorous vacuole. In the other sequence small plasmodia become encysted and produce a small, often constant number of relatively small, uninucleate spores within a cystic wall (spore sac) (modified after Sprague et al. 1977).

Life mode and distribution: cosmopolitan obligate intracellular parasites of *Apicomplexa,* namely *Gregarinasina,* which predominately parasitize marine annelids (Nassonova et al. 2016).

Notes: The last paragraph of the diagnosis is omitted as it gives a synopsis of *Rudimicrosporea* as of 1977, mentioning

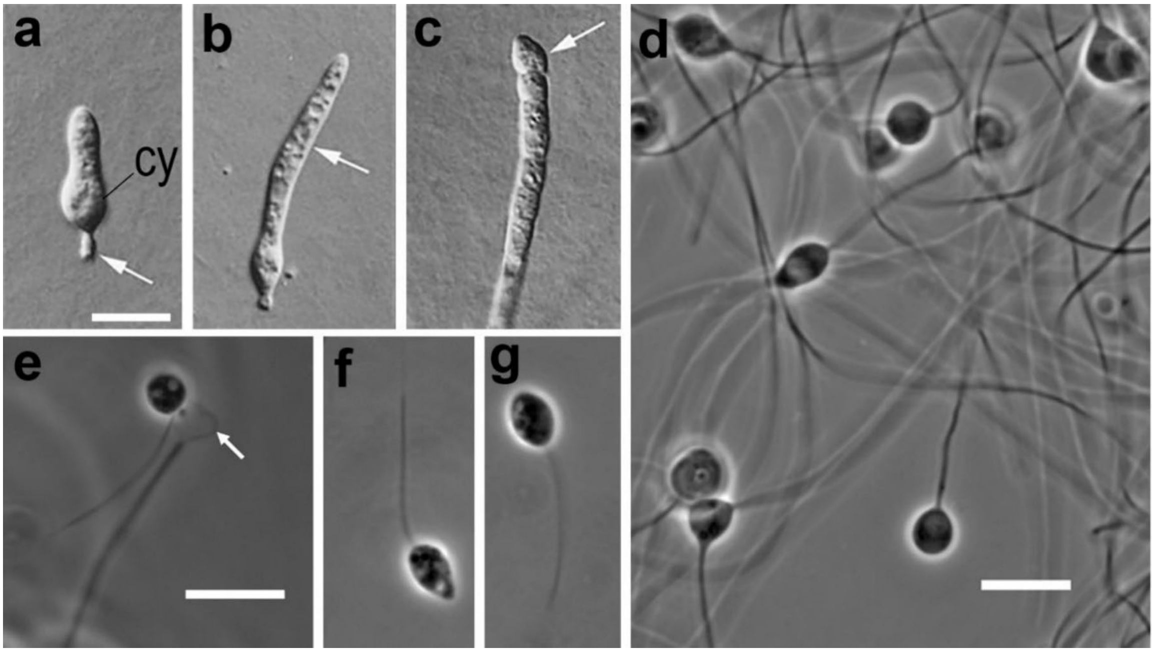


Fig. 52 Light microscopic images of *Monoblepharidomycetes*: **a**–**c** *Harpochytrium* sp. (after: Powell and Letcher 2014, modified), **d**–**g** *Telasphaerula gracilis* (after: J.E. Longcore in: Karpov et al. 2017a, modified). **a** Germination of zoospore cysts (cy) of *Harpochytrium* sp. in an uniaxial thallus with basal holdfast (arrow). **b** *Harpochytrium* sp. thallus with highly vacuolated, foamy appearing cytoplasm (arrow). **c** *Harpochytrium* sp. cleaving zoospores beginning at apex (arrow) of thallus. **d** polycentric thallus of *Telasphaerula gracilis* consisting of swellings connected by fine isodiametric tubes. **e** zoospore recently emerged from adjacent zoosporangium (arrow). **f**, **g** zoospores with typical shape for *Monoblepharidales*. Scale bars: **a**–**g** 10 µm

three genera with the respective number of species known by that time, and their geographical distribution. Since the taxonomic composition has been extended since then, including erection of one more family (Larsson 2000), the beginning of the diagnosis is also be the subject of change. The term *sporocyst* (as well as the term *cyst*) is not currently in use, and it is replaced by the term *spore sac* (Larsson 2014).

Type order: ***Metchnikovellida*** Vivier, Protistologica 11(2): 345–361 (1975).
Type family: ***Metchnikovellidae*** Caullery & Mesnil (1914) emend. Larsson 2014. Microsporidia: Pathogens of Opportunity. Ames, Iowa. 605–634. (2014).
Type genus: ***Metchnikovella*** Caullery & Mesnil C. R. Hebd. Seanc. Acad. Sci. Paris 125: 789 (1897).
Type species: ***Metchnikovella spionis*** Caullery & Mesnil C. R. Hebd. Seanc. Acad. Sci. Paris 125: 789 (1897).

Microsporidea Corliss & Levine, J. Protoozool. 10(Suppl.): 26–27 (1963) emend. Tokarev & Nassonova.

Index Fungorum Registration Identifier 90587.

Diagnosis: Obligate intracellular parasites with developmental sequences ended by formation of unicellular spores, containing uni- or binucleate germ (sporoplasm) and extrusion apparatus, unique in its structure, with the polar tube as its main part. The extrusion apparatus well developed. Flagella, centrioles, and lysosomes absent, mitochondria reduced to mitosomes, ribosomal RNA shortened highly contracted, providing giving the appearance of prokaryotic-type ribosomes molecules. Prespore developmental stages with uniform nuclei, either single or paired (diplokaryon). Nuclei haploid or diploid. Sexual process and intermediate host involvement possible. Infection performed via extrusion of polar tube which injects the germ into the host cell. Development either in direct contact with hyaloplasm and host cell organelles or within vacuole of host or parasite origin (modified after Issi et al. 2008.)

Life mode and distribution: cosmopolitan obligate intracellular parasites of *Ciliata, Paramyxea,* and *Metazoa* (Vavra and Lukes 2013; Stentiford et al. 2017).

Notes: The original diagnosis for the class *Microsporidea* is as following: "spore of unicellular origin; single sporoplasm; single valve; one or two long, tubular polar filaments through which sporoplasm escapes; cytozoic in invertebrates, especially arthropods, and lower (rarely higher) vertebrates" (Corliss and Levine 1963). It reflected the fact *Microsporidia* and *Myxozoa (Myxosporidia)* were referred to as the two respective classes of the subphylum *Cnidospora* of the protozoan phylum *Sporozoa*. Modern taxonomy, strongly supported by molecular phylogeny data, showed

Fig. 53 *Mortierella polycephala* (CBS 227.35, isolated by G. Linnemann). **a** Sporangia single, with irregular or with racemose branching. **b** Stalked chlamydospores (stylospores). **c** Smooth-walled chlamydospores among substrate hyphae, hyphae with oil drops and septa, tangle of hyphae. **d** Colony morphology on MEA and **e** on LcA after 1 week at 20 °C. Scale bars: **a** = 50 µm, **b**–**c** = 10 µm, **d**–**e** = 1 cm

polyphyletic origin of this group and made this affiliation obsolete. We therefore propose a redefinition of the class *Microsporidea*, based upon a more recent diagnosis of Issi and Voronin (2007) which was proposed in the frames of contemporary views of protistology (i.e., apart from *Fungi*). Those authors, however, preferred only to include one distinctive feature (well-developed extrusion apparatus), further indicating the diagnosis of the class corresponding to that of the phylum. Here, as the phylum *Microsporidia* is lowered to the subphylum rank in accordance with Wijayawardene et al. (2020a), the definition of the class *Microsporidea* lacks its important attributes and we introduce the main features of the class corresponding to those of the phylum, in the class diagnosis itself.

Type order: ***Nosematida*** Labbe (1899) emend. Tokarev & Issi in Wijayawardene et al., Mycosphere 11(1): 1060–1456 (2020).
Type family: ***Nosematidae*** Labbe (1899) emend. Tokarev, Huang, Solter, Malysh, Becnel & Vossbrinck, J. Invertebr. Pathol. 169:107279 (2020).
Type genus: ***Nosema*** Naegeli, Bot. Ztg. 15: 760 (1857).
Type species: ***Nosema bombycis*** Naegeli, Bot. Ztg. 15: 760 (1857).

SANCHYTRIOMYCOTA Galindo, López-García, Torruella, Karpov & Moreira, Nat. Commun. 12 (no. 4973): 9 (2021).
Index Fungorum Registration Identifier 558519; Fig. 60

Monocentric thallus, epibiotic; usually amoeboid zoospores with filopodia and immobile posterior pseudocilium

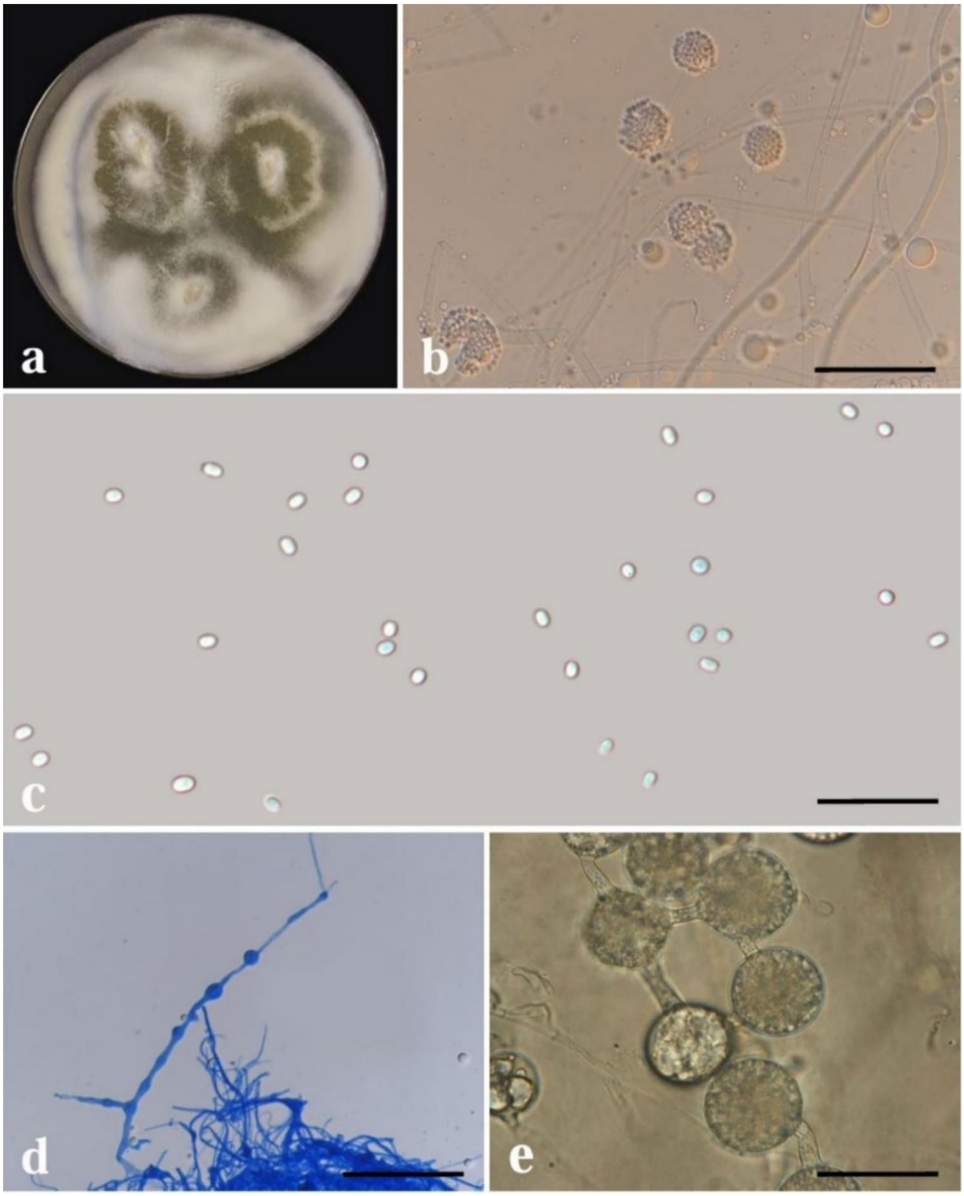


Fig. 54 Morphological and culture characteristics of *Mortierellomycetes* species. **a** Colony of *Mortierella alpina* on PDA plate. **b** Sporangiophore of *Entomortierella* sp. **c** Spores of *Entomortierella* sp. **d** Chain of gemmae of *Entomortierella* sp. stained in lactophenol cotton-blue. **e** Cluster of gemmae of *Entomortierella* sp. Scale bars: **b**–**e** 50 μm

with longest-known kinetosome in fungi (1–2 μm); centrosome in sporangium of two centrioles composed by nine microtubular singlets (adapted from Galindo et al. 2021).

Life mode and distribution: Obligate parasites of freshwater algae, cosmopolitan.

Notes: Galindo et al. (2021) introduced this phylum to accommodate two obligate parasites of freshwater algae (which are called as 'Sanchytrids') viz., *Sanchytrium* Karpov & Aleoshin 2017 (type: *Sanchytrium tribonematis* Karpov & Aleoshin 2017 *fide* Karpov et al. 2017a, b) and *Amoeboradix* Karpov et al. 2017a, b) (type species: *Amoeboradix gromovii* Karpov et al. 2017a, b *fide* Karpov et al. 2018). However, *Amoeboradix* 2017 and *Amoeboradix gromovii* 2017 are invalid (Art. F.5.1, Shenzhen) and thus validated in Index Fungorum (2024).

Ribosomal DNA molecular phylogenies placed *Sanchytrium* in *Monoblepharidomycetes* (Karpov et al. 2017a), and later among non-zoosporic fungi (Karpov et al. 2018). Based on these data Tedersoo et al. (2018) introduced *Sanchytriales* Tedersoo et al. and *Sanchytriomycetes* Tedersoo et al. to accommodate *Sanchytrium* (i.e., *Sanchytriaceae* Karpov & Aleoshin) and treated as a distinct clade in the phylum *Monoblepharomycota*. According to the multigene phylogeny (Galindo et al. 2021) both the *Sanchytrium* and *Amoeboradix* give a well-supported monophyletic lineage sister to the *Blastocladiomycota*.

Below we introduce new subphylum *Sanchytriomycotina*. Hence, the phylum consists of one subphylum and one class.

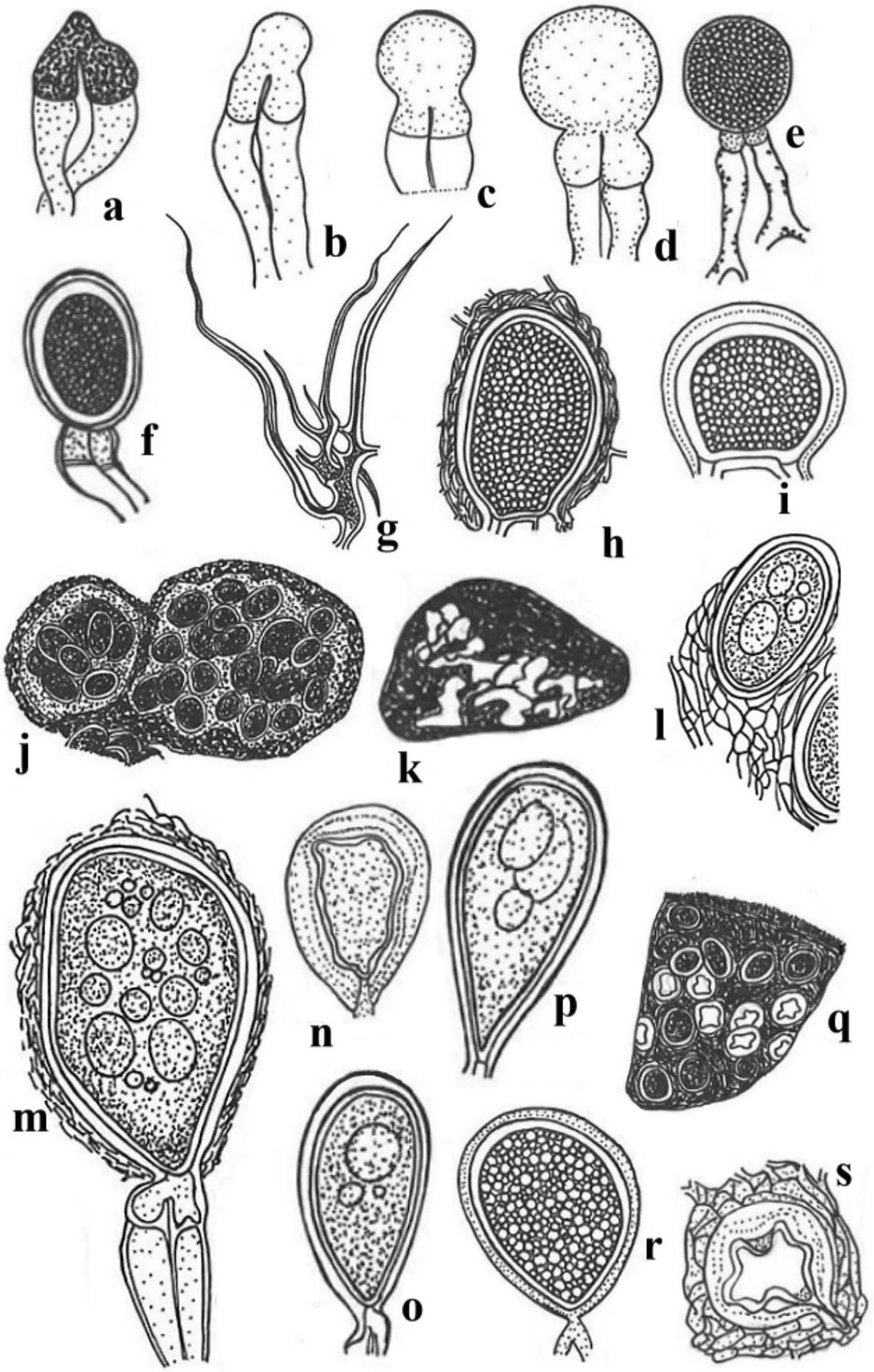


Fig. 55 *Endogone* spp. and different stages of the life cycle. *Endogone pisiformis*: **a**–**e** Successive stages in the formation of zygospores. **f** Mature spores with gametes attached. **g** Peculiarly differentiated hypha forming the superficial tomentum of a young individual. ***Endogone multiplex*****: h** Mature spore showing hyphal envelope. **i** Mature spore with discrete gamete attachments, treated with KOH. **j** Larger and smaller spore-groups surrounded by envelope with incorporated humus-material. ***Endogone tuberculosa*****: k** Section of sporocarp showing disposition of sporogenous areas, (light), with surrounding and penetrating earthy envelope (dark): magnified about seven times as reduced. **l** Portion of gleba showing spores and pseudoparenchymtous hyphal tissue. **m** Spore showing envelope and origin from gametes. **n** Fully matured spore with greatly thickened exospore. **o**, **p** Spores of more elongate type. ***Endogone incrassate*****: q** Section of a portion of sporocarp, showing peridium and gleba with fully mature and more immature spores. **r** Spore showing characteristic fatty contents and probably sexual origin. **s** Fully mature spore with greatly thickened exospore and compacted surrounding hyphae (Redrawn from Thaxter 1922)

Sanchytriomycotina Karpov ***subphylum nov.***

Index Fungorum Identifier IF 558746.

The description is similar to the description of the phylum.

Sanchytriomycetes (Tedersoo et al.) Galindo, López-García, Torruella, Karpov & Moreira, Nat. Commun. 12 (no. 4973): 9 (2021).

Index Fungorum Registration Identifier 554005; Fig. 60

The description is similar to the description of the subphylum.

Type order: ***Sanchytriales*** (Tedersoo et al.) Galindo, López-García, Torruella, Karpov & Moreira, Nat. Commun. 12 (no. 4973): 9 (2021).

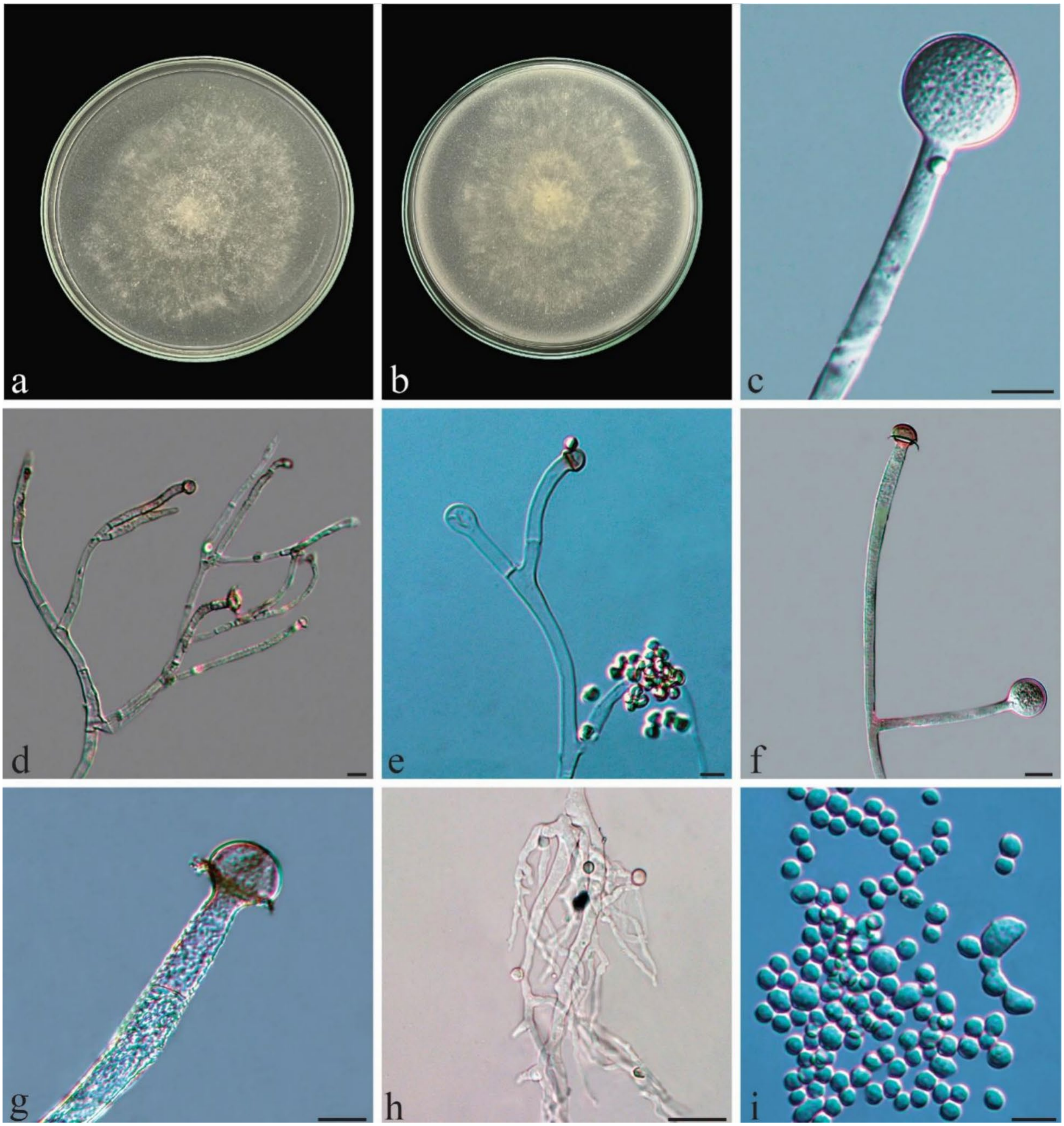


Fig. 56 *Mucor septatiphorus*. **a** Colony surface on PDA at 25 °C. **b** Colony reverse on PDA at 25 °C. **c** Sporangiophore with sporangium. **d**, **e** Branched sporangiophore with columellae. **f** Branched sporangiophore with terminal columella and lateral sporangium. **g** Sporangiophore with columella. **h** Rhizoids. **i** Sporangiospores. Scale bars **a**–**i** = 20 μm

Type family: ***Sanchytriaceae*** Karpov & Aleoshin, in Karpov, Mamanazarova, Popova, Aleoshin, James, Mamkaeva, Tcvetkova, Vishnyakov & Longcore, Fungal Biol. 121(8): 735 (2017).

Type genus: ***Sanchytrium*** Karpov & Aleoshin, in Karpov, Mamanazarova, Popova, Aleoshin, James, Mamkaeva, Tcvetkova, Vishnyakov & Longcore, Fungal Biol. 121(8): 735 (2017).

Type species: ***Sanchytrium tribonematis*** Karpov & Aleoshin, in Karpov, Mamanazarova, Popova, Aleoshin, James, Mamkaeva, Tcvetkova, Vishnyakov & Longcore, Fungal Biol. 121(8): 735 (2017).

ZOOPAGOMYCOTA Gryganskyi, M.E. Sm., Spatafora & Stajich, in Spatafora, Chang, Benny, Lazarus, Smith, Berbee, Bonito, Corradi, Grigoriev, Gryganskyi, James, O'Donnell,

Table 22 Economical and ecological significances of *Mucoromycetes*, examples:

Species name	Host	References
Choanephora cucurbitarum	Aubergine (*Solanun melogena*), cucumber (*Cucumis sativus*), green pea (*Pisum sativum*), lettuce (*Lactuca sativa*), and papaya (*Carica papaya*),	Das et al. (2017a,b,c), Sangeeta et al. (2018), and Ryu et al. (2023)
	Acerola (*Malpighia emarginata*), Barbados cherry (*Malpighia glabra*), breadfruit (*Arto-carpus altilis*), cashew (*Anacardium occidentale*), eggplant (*Solanun melongena*), papaya (*Carica papaya*), peach (*Prunus persica*), and strawberry (*Fragaria* × *ananassa*)	Cruz-Lachica et al. (2015), Vieira et al. (2018), Takushi et al. (2020), Zhang et al. (2020), and Souza et al. (2023)
Rhizopus arrhizus	Peach pumpkin (*Cucurbita moschata*), garlic (*Allium sativum*), grape (*Vitis vinifera*), sweet potato (*Ipomoea batatas*)	Quintieri et al. (2022), Li et al. (2023a,b), and Zhang et al. (2023)
Rhizopus stolonifer	Almond hull, peach (*Prunus persica*), jackfruit (*Artocarpus heterophyllus*), strawberry, sweet potato (*Ipomoea batatas)*	Sweany et al. (2019), Ventura-Aguilar et al. (2021), Li et al. (2023c), and Haque et al. (2023)
Mucor inaequisporus	Persimmon (*Diospyros kaki*), strawberry (*Fragaria* × *ananassa*)	Lee and Jung (2020) and Ren et al. (2023)
Mucor irregularis	Mangosteen (*Garcinia mangostana*)	Wang et al. (2022)
Mucor piriformis	Strawberry, kiwifruit (*Actinidia deliciosa*)	Thomidis et al. (2019) and Agyare et al. (2020)

Table 23 Medicinally/clinical significances of *Mucoromycetes*, examples:

Species name	Human/ animal	References (major refs in last 5 years)
Rhizopus homothallicus	Human	Gupta et al. (2023)
Rhizopus azygosporus	Human	Wang et al. (2023b)
Rhizopus microsporus	Human	Peng et al. (2023)
Rhizopus arrhizus	Human	Osório-Aragon et al. (2023)
Lichtheimia ramosa	Human	Zhang et al. (2022b) and Shen et al. (2023)
Lichtheimia corymbifera	Human	Chandran et al. (2022)
Mucor irregularis	Human	Zhang et al. (2022b)
Cunninghamella bertholletiae	Human	Harada et al. (2023)
Saksenaea vasiformis	Human	Singh et al. (2023)
Rhizomucor miehei	Human	Maatallah et al. (2022)

Roberson, Taylor, Uehling, Vilgalys & White, Mycologia 108(5): 1035 (2016).

Index Fungorum Registration Identifier 816300.

Haustoria are produced by some of the animal pathogens and mycoparasites. *Zoopagomycota* hyphae may be compartmentalized by septa that may be complete or uniperforate; in the latter, bifurcate septa contain electron opaque lenticular plugs. *Zygospore* formation typically involves modified hyphal tips, thallus cells, or hyphal bodies (yeast-like cells) that function as gametangia. The hyphal diameter is characteristically narrow in thalli that are branched or unbranched; sometimes specialized haustoria are produced in association with hosts. Only a handful of species have been successfully maintained in axenic culture. Sexual reproduction, where known, is by gametangial conjugation, forming globose zygospores on apposed differentiated or undifferentiated suspensor cells. **Asexual reproduction** is by arthrospores, chlamydospores, conidia, or multispored merosporangia that may be simple or branched (extracted from Spatafora et al. 2016).

Life mode and distribution: Associations with animals (e.g. pathogens, commensals, mutualists) and mycoparasites.

Notes: Spatafora et al. (2016) introduced the phylum *Zoopagomycota* after molecular evidence showed it formed a paraphyletic clade with *Mucoromycota*. The phylogenetic placement was confirmed by Wang et al. (2023c). Since Hibbett et al. (2007), *Zygomycota* was formally abandoned and the subphylum *Zoopagomycotina* Benny was proposed; the subphylum was originally identified as belonging to the "zygomycetes" (James et al. 2006b; White et al. 2006; Sekimoto et al. 2011; Ebersberger et al. 2012; Chang et al. 2015), a group created to accommodate basal fungi exclusively characterized by associations with animals and fungi. The class *Zoopagomycetes* was introduced by Dowell (2014 k)

Table 24 Industrial applications of *Mucoromycetes*

Species name	Industry	References (major refs in last 5 years)
Cunninghamella elegans	Production of surfactants, chitin and chitosan	Medeiros et al. (2022) and Silva et al. (2022a)
Absidia glauca, *Cunninghamella blakesleeana*, *C. echinulata*, *C. elegans*, *Mucor fragilis*, *M. flavus*	Production of fatty acids	Kosa et al. (2018), Alasmary et al. (2020), and Song et al. (2022)
Rhizopus arrhizus	Production of fumaric acid	Fan et al. (2020)
Actionomucor elegans, *Mucor racemosus*, *Rhizopus arrhizus*, *R. microsporus*, *R. stolonifer*	Production of fermented food	Shukla et al. (2020), Yao et al. (2021), Aoki et al. (2023), and Xie et al. (2023)
Cunninghamella echinulata, Lichtheimia ramosa, Mucor circinelloides, M. hiemalis, M. racemosus, *Rhizopus arrhizus*, *Rhizomucor pusillus*	Production of enzymes: amylases, cellulases, lipases, pectinase, phytases, proteases, xylanase	Benabda (2019), Ezeilo et al. (2019), Reis et al. (2019), López-Fernández et al. (2020), Volfold et al. (2021), Al Mousa et al. (2022), Abdel-Mageed et al. (2022), and Cavalheiro et al. (2023)
Actinomucor elegans, Mucor circinelloides, *Blakeslea trispora*	Beta-carotene, lycopene, zeaxanthin	Sevgili and Erkmen (2019), Naz et al. (2020), and Dulf et al. (2023)

and comprises *Zoopagales.* The order's monophyletic nature was confirmed by Davis et al. (2019) however the authors could not confirm their relationships with other subphyla due to the scarcity of available taxa.

Zoopagomycetes Doweld, Index Fungorum 60: 1. 2014.

Index Fungorum Registration Identifier 550358; Figs. 61, 62

Thallus simple, branched or none, or hyphal system extensively branched. Ectoparasites forming haustoria inside the host. Arthrospores, chlamydospores or uni- or multi-spored sporangiola (asexual reproduction); sporangiospores produced in simple or branched merosporangia. *Zygospores* globose, produced on differentiated, straight or coiled suspensors. Endo- or ectoparasites, predaceous.

Notes: Currently, the class comprises one order *Zoopagales* (families *Cochlonemataceae*, *Helicocephalidaceae*, *Piptocephalidaceae*, *Sigmoideomycetaceae* and *Zoopagaceae*).

Type order: ***Zoopagales*** Bessey ex R.K. Benj., in Kendrick, The Whole Fungus 2: 590 (1979).
Type family: ***Zoopagaceae*** Drechsler ex Drechsler emend. Duddington, Mycologia 27(1): 30 (1935).
Type genus: ***Zoopage*** Drechsler Mycologia 27(1): 30 (1935).
Type species: ***Zoopage phanera*** Drechsler, Mycologia 27(1): 30 (1935).

Placements of fossil fungi in higher ranks

Fungi are eukaryotic, uni- or multi-cellular, parasitic/saprobic, omnipresent organisms. Fossil fungi have been recorded in the form of dispersed spores, mycelia, sporocarps and mycorrhiza and are commonly observed in the palynological preparations or in thin sections of sedimentary rocks. These have been sporadically reported since long (Williamson 1878, 1880; Kidston and Lang 1921; Edwards 1922) but their study received major attention with the amplification of palynological studies since the 1950s. Although fungal remains are encountered in the sediments of all ages, their fossil records indicate that *Fungi* got well established during the Cretaceous and became conspicuously abundant in the Tertiary Period (Jain 1974; Jansonius 1976; Jain and Kar 1979; Ramanujam 1982; Kalgutkar and Jansonius 2000; Tripathi 2009; Saxena and Tripathi 2011; Saxena et al. 2021), suggesting that their proliferation is linked with diversification of angiosperms. Being fragmentary, fossil fungi generally lack characteristic features that are diagnostic of extant taxa, hampering their classification with extant fungi. However, a good number of fossil fungal taxa (other than spores) can be related to their extant counterpart (up to order/ family or even genus level). Here, only such legitimate genera, which could be related to extant taxa, have been considered, see below. Holotypes of type species of 27 genera are illustrated (Fig. 61).

1. Phylum: ***Ascomycota*** Caval.-Sm.

Ascomycota taxa are known as the sac fungi, is the largest and most diversified phylum of *Fungi* and is characterised by having septate hyphae with simple septal pores. The most important feature of this fungal group is the 'ascus' (pl. asci), a microscopic sexual structure in which non-motile spores, called ascospores, are formed. Asci are often housed in a fruiting body or ascocarp. However, a large number of species of *Ascomycota* are asexual, i.e. they do not have a sexual cycle and thus do not form asci or ascospores. As evident from the study of fossil fungi, the majority of dispersed fungal spores found in palynological preparations are

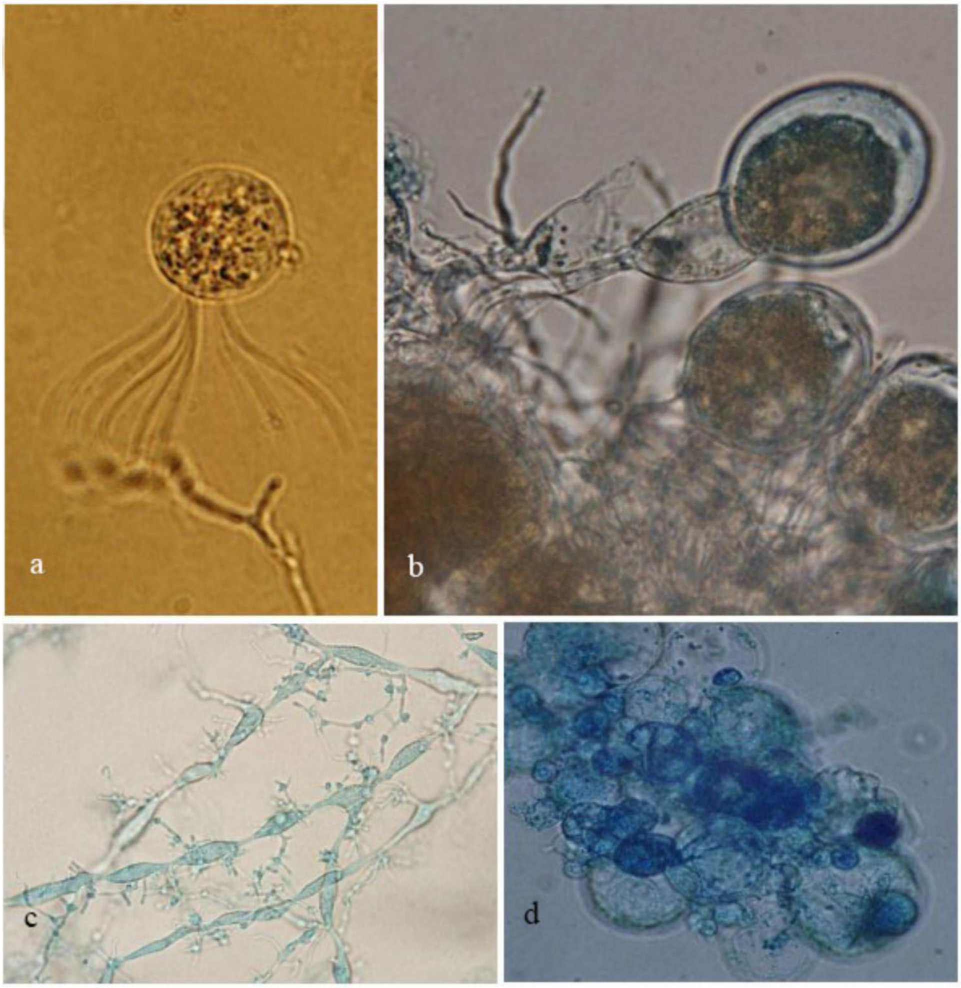


Fig. 57 Taxa of *Neocallimastigaceae*. **a**, **b** Zoospores and sporangia of *Neocallimastix frontalis*: (**a** Phase contrast microscopic illustration showing the *Neocallimastix frontalis* polyflagellated zoospores. **b** Phase contrast microscopic illustration showing the *Neocallimastix frontalis* sporangia. *Neocallimastix frontalis* produces globose shaped sporangia. Sporangiophores in *Neocallimastix frontalis* are short and often display an egg-cup like morphology). **c** *Anaeromyces contortus* Phase contrast microscopy showing hyphal structure. The genus *Anaeromyces* is characterized by displaying multiple constrictions, usually occurring at regular intervals resulting in a distinctive and taxonomically informative sausage-shaped morphology. **d** *Caecomyces communes*. Phase contrast microscopy showing hyphen structure. The genus *Caecomyces* does not produce atypical filamentous hyphae. Rather, *Caecomyces* spp. produces bulbous rhizoidal growth pattern. Only the genera *Caecomyces* and *Cyllamyces* display this characteristic bulbous rhizoidal growth pattern

produced by the *Ascomycota*. Ascospores are produced, usually in groups of four or eight, inside a sac (ascus) by the so-called 'perfect (sexual) stage' of these fungi. The 'imperfect (asexual) stage' may produce several types of asexual spores, named as conidiospores (or conidia).

The following fossil genera exhibit affinity with *Ascomycota*, but their resemblance with taxa of lower ranks could not be established: *Adendorfia* G.Woroviec et al., *Appianoporites* S.Y. Sm. et al., *Asteromites* Poinar, *Aureofungus* Hibbett et al., *Cashhickia* T.N. Taylor et al., *Casparyotorula* Rikkinen et al., *Cephalothecoidomyces* G. Worobiec et al., *Chlorolichenomycites* Honegger et al., *Entropezites* Poinar & R. Buckley, *Eomelanomyces* Beimforde et al., *Galloea* Alstrup & Søchting, *Honeggeriella* Matsunaga et al., *Jimwhitea* M. Krings & T.N. Taylor, *Palaeoanellus* A.R. Schmidt et al. and *Spheciophila* Poinar. Fossil ascomycetus fungi are represented by the following eight classes: *Dothideomycetes* O.E. Erikss. & Winka, *Eurotiomycetes* O.E. Erikss. & Winka, *Laboulbeniomycetes* Engl., *Lecanoromycetes* O.E. Erikss. & Winka, *Leotiomycetes* O.E. Erikss. & Winka, *Pezizomycetes* O.E. Erikss. & Winka, *Sordariomycetes* O.E. Erikss. & Winka and *Taphrinomycetes* O.E. Erikss. & Winka, as given below.

1.1. Class: ***Dothideomycetes*** O.E. Erikss. & Winka

Class *Dothideomycetes* constitutes one of the most abundant classes of fossil *Ascomycota*. This class is represented by the following genera: *Alternaria* Nees, *Appendicisporonites* R.K. Saxena & S. Khare 1992 (Fig. 63-a), *Asterina* Lév., *Asterinites* Doub. & D. Pons, *Asterothyrites* Cookson, *Brefeldiellites* Dilcher, *Caldesites* Puri, *Callimothallus* Dilcher 1965 (Fig. 63-b), *Cribrites* R.T. Lange, *Cryptodidymosphaerites* Currah et al., *Cucurbitariaceites* R.K. Kar et al. 1972 (Fig. 63-c), *Dictyosporiuminites* Debi Mukh., *Dictyotopileos* Dilcher, *Epicoccum* Link, *Euthythyrites* Cookson, *Haplopeltis* Theiss., *Hysterites* Göpp., *Kalviwadithyrites* M.R. Rao in R.K. Saxena 2012 (Fig. 63-d), *Koshalia* S. Sarkar & V. Prasad 2003 (Fig. 63-e), *Leptosphaerites* Richon, *Mariusia* D. Pons & Boureau, *Melanosporites* Pampal., *Microthallites* Dilcher, *Microthyriacites* Cookson, *Microthyrites* Pampal., *Molinea* Doub. & D. Pons, *Palaeoasterina* S. Mitra et al. *Palaeocercospora* S. Mitra & M. Banerjee 2000

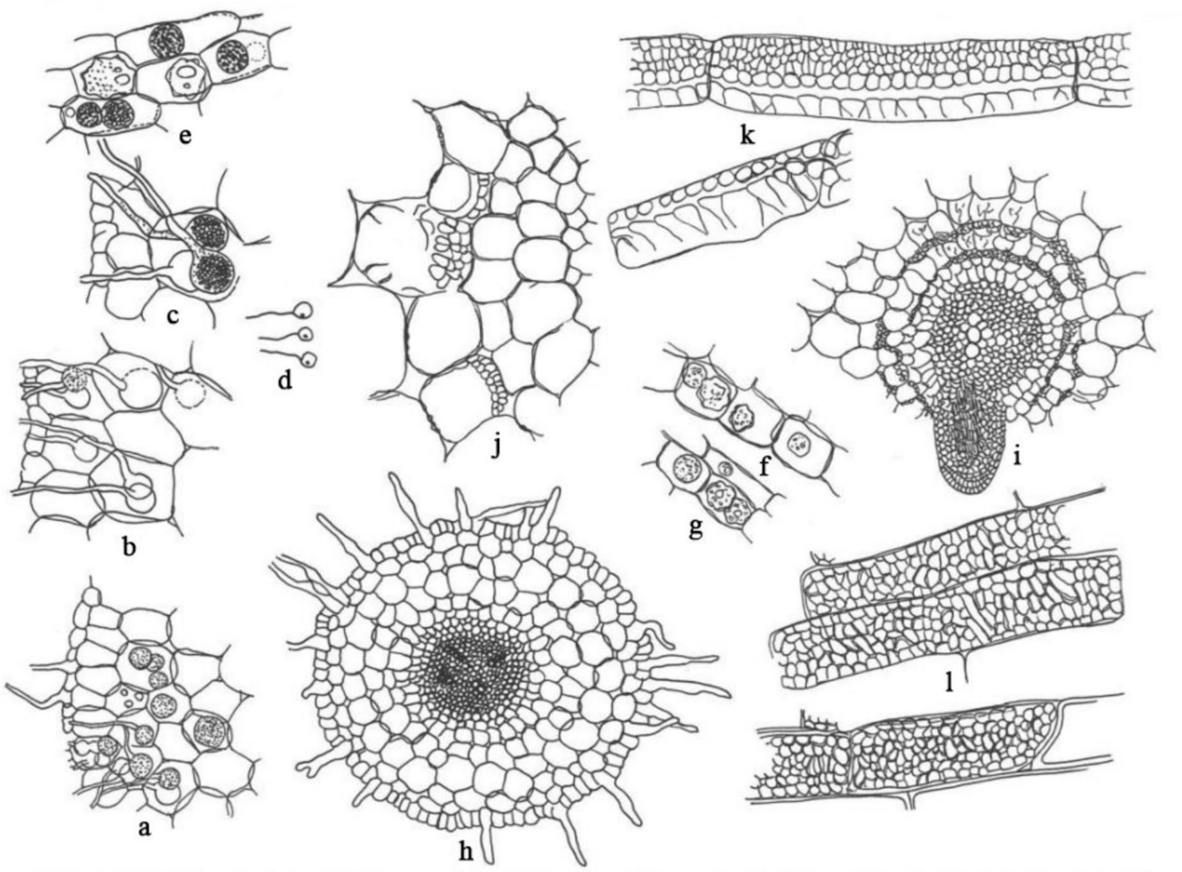


Fig. 58 *Olpidium brassicae* (=*Chytridium brassicae*) (Redrawn from Lay et al. (2018) who accepted the name *Olpidium brassicae* and they used Woronin (1878) to illustrate the taxon). **a**, **b**, **c** the zoosporangia of *Chytridium brassicae* in various developmental stages. **d** zoospores of *C. brassicae*. **e**, **f**, **g** showed resting spores or spores of *C. brassicae*. **h** a cross section of a completely healthy root of a young cabbage seedling. **i**, **j**, **k** and **l** showed the root cells of cabbage

(Fig. 63-f), *Palaeoleptosphaeria* Barlinge & Paradkar 1982 (Fig. 63-g), *Palmellathyrites* Locq. et al., *Parmathyrites* K.P. Jain & R.C. Gupta 1970 (Fig. 63-h), *Pelicothallos* Dilcher, *Perisporiacites* Félix *Phragmothyrites* W.N. Edwards 1922 (Fig. 63-i), *Pleosporites* Y. Suzuki and *Torula* Pers., *Plochmopeltinites* Cookson, *Polyhyphaethyrites* R. Srivast. & R.K. Kar 2004 (Fig. 63-j), *Ratnagiriathyrites* R.K. Saxena & N.K. Misra 1990 (Fig. 63-k), *Rhytidhysteriumites* Debi Mukh., *Spinosporonites* R.K. Saxena & S. Khare, *Sporidesmium* Link, *Stomiopeltites* Alvin & M.D. Muir, *Trichopeltina* Theiss., *Trichopeltinites* Cookson, *Trichothyrites* F. Rosend., *Ussurithyrites* Krassilov and *Vizella* Sacc.

1.2. Class: ***Eurotiomycetes*** O.E. Erikss. & Winka

This class is represented by the following genera: *Chaenothecopsis* Vain., *Coleocarpon* Stubblef. et al., *Cryptocolax* R.A. Scott, *Memnonillasporonites* Debi Mukh., *Roannaisia* T.N. Taylor et al., *Sporocarpon* Will. and *Traquairia* Carruth.

1.3. Class: ***Laboulbeniomycetes*** Engl.

This class is represented by two genera, viz., Columnomyces R.K. Benj. and *Stigmatomyces* H. Karst.

1.4. Class: ***Lecanoromycetes*** Erikss. & Winka

This class is represented by *Sphaerophorus* Pers.

1.5. Class: ***Leotiomycetes*** O.E. Erikss. & Winka

This class is represented by the following genera: *Erisiphites* Pampal., *Lithouncinula* N. Sharma, et al., *Palaeosclerotium* G.W. Rothwell, *Perisporites* Pampal., *Protoerysiphe* N. Sharma et al. and *Trimmatostroma* Corda.

1.6. Class: ***Pezizomycetes*** O.E. Erikss. & Winka:

This class is represented by the following genera: *Ascodesmisites* Trivedi et al., *Paleomorchella* Poinar and *Pezizites* Göpp. & Berendt.

1.7. Class: ***Sordariomycetes*** O.E. Erikss. & Winka:

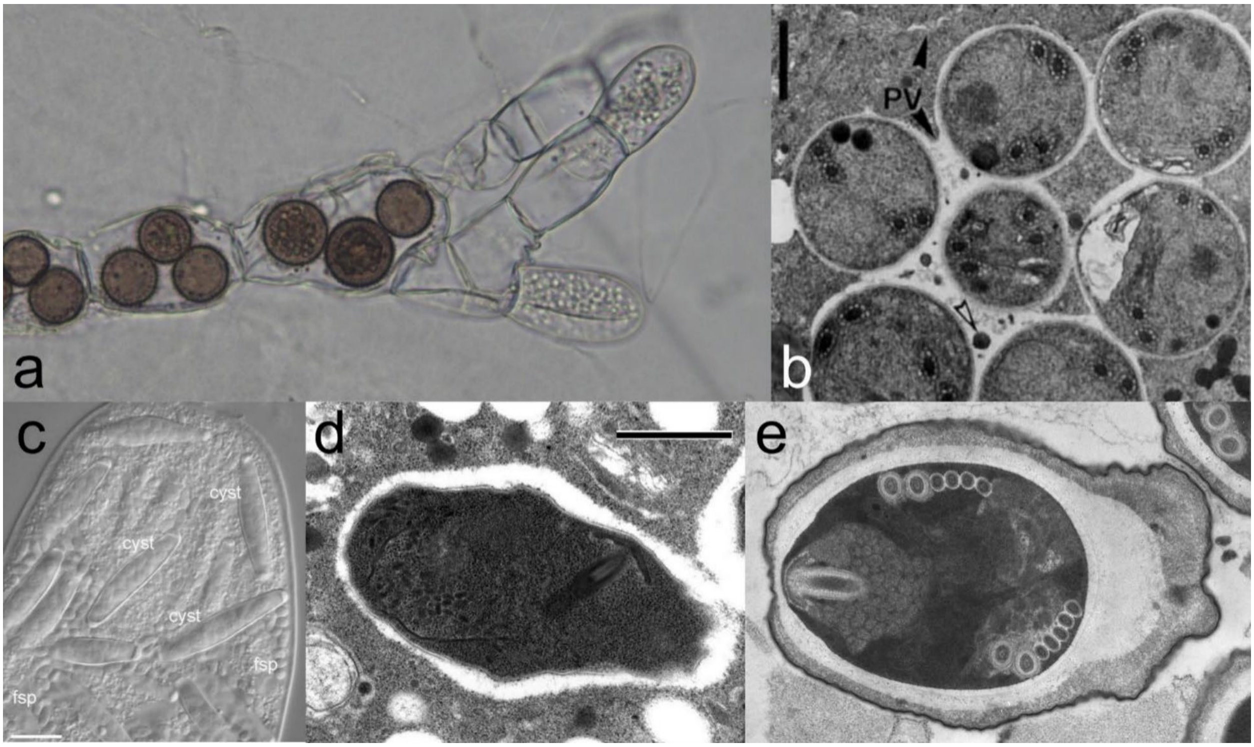


Fig. 59 The representatives of *Rozellomycota*. **A** *Rozella allomycis* parasitizing the blastocladiomycete *Allomyces* sp. (light microscopic photo by Timothy James CC BY-SA 3.0, https://commons.wikimedia.org/w/index.php?curid=8727738). **B** *Chytridiopsis trichopterae* from the caddisfly *Polycentropus flavomaculatus*, mature spores in parasitophorous vacuole (PV), arrowheads indicate remnants of plasmodium (transmission electron microscopic photo reprinted from Larsson (1993) under license 5622170021648 granted by John Wiley & Sons). **C** *Metchnikovella incurvata*, a hyperparasite of gregarines *Polyrhabdina pygospionis* from the *polychaete Pygospio* elegans. Infected gregarine cell filled with the spore sacs (cyst) and free spores (fsp) (light microscopic photo reprinted from Galindo et al. 2018 CC B Y 4 .0). **d** Mature spore of *Metchnikovella incurvate* (transmission electron microscopic photo reproduced with a kind permission of Yuliya Y. Sokolova, Institute of Cytology RAS, St. Petersburg, Russia). **e** Mature spore of *Crepidulospora beklemishevi* from the mosquito *Anopheles beklemishevi* (transmission electron microscopic photo reproduced w ith a k ind p ermission o f Anastasia V. S imakova, Tomsk S tate University, Tomsk, Russia). Scale bars: **b** = 1 µm; **c** = 5 µm; **d** = 0.5 µm.

Class *Sordariomycetes* constitutes one of the most abundant classes of fossil *Ascomycota*. This class is represented by the following genera: *Acremonium* Link, *Botryodiplodia* Sacc., *Brachysporisporites* Lange & Smith 1971 (Fig. 63-l) and *Brachysporium* Sacc., *Chaethomites* Pampal., *Chaetosphaeria* Tul. & C. Tul., *Clasterosporium* Schwein., *Diploneurospora* K.P. Jain & R.C. Gupta 1970 (Fig. 63-m), *Hypoxylonites* Elsik 1990 (Fig. 63-n), *Melanospora* Corda, *Meliola* Fr., *Meliolinites* Selkirk 1975 (Fig. 63-o) and *Meliostroma* R. Kar et al., *Palaeoamphisphaerella* Ramanujam & Srisailam (Fig. 63-p), *Palaeocirrenalia* Ramanujam & Srisailam 1980 (Fig. 63-q), *Palaeoclaviceps* Poinar et al., *Palaeocolletotrichum* S. Mitra & M. Banerjee 2000 (Fig. 63-r), *Palaeosordaria* Sahni & H.S. Rao 1943 (Fig. 63-s), *Paleoophiocordyceps* G.H. Sung et al., *Paleoserenomyces* Currah et al., *Petrosphaeria* Stopes & H. Fujii, *Spataporthe* Bronson et al., *Sphaerites* Unger, *Valsarites* Puri and *Zopfiella* G. Winter.

1.8. Class: ***Taphrinomycetes*** O.E. Erikss. & Winka

This class is represented by a single genus, viz., *Protomyces* Unger.

2. Phylum: ***Basidiomycota*** R.T. Moore

Basidiomycota are filamentous fungi composed of hyphae (except for basidiomycota-yeast) and reproduce sexually via the formation of specialized club-shaped end cells called basidia. They normally bear external meiospores (usually four). These specialized spores are called basidiospores. However, some *Basidiomycota* are obligate asexual reproducers. *Basidiomycota* that reproduces asexually can typically be recognized as members of this division by gross similarity to others, by the formation of a distinctive anatomical feature (the clamp connection) and cell wall components. The following fossil genera exhibit affinity with *Basidiomycota*, but their resemblance with taxa of lower ranks could not be established: *Lycoperdites* Poinar and *Mycetophagites* Poinar & Buckley. Fossil basidiomycetus fungi are represented by the following four classes: *Agaricomycetes* Doweld, *Agaricostilbomycetes* R. Bauer et al.,

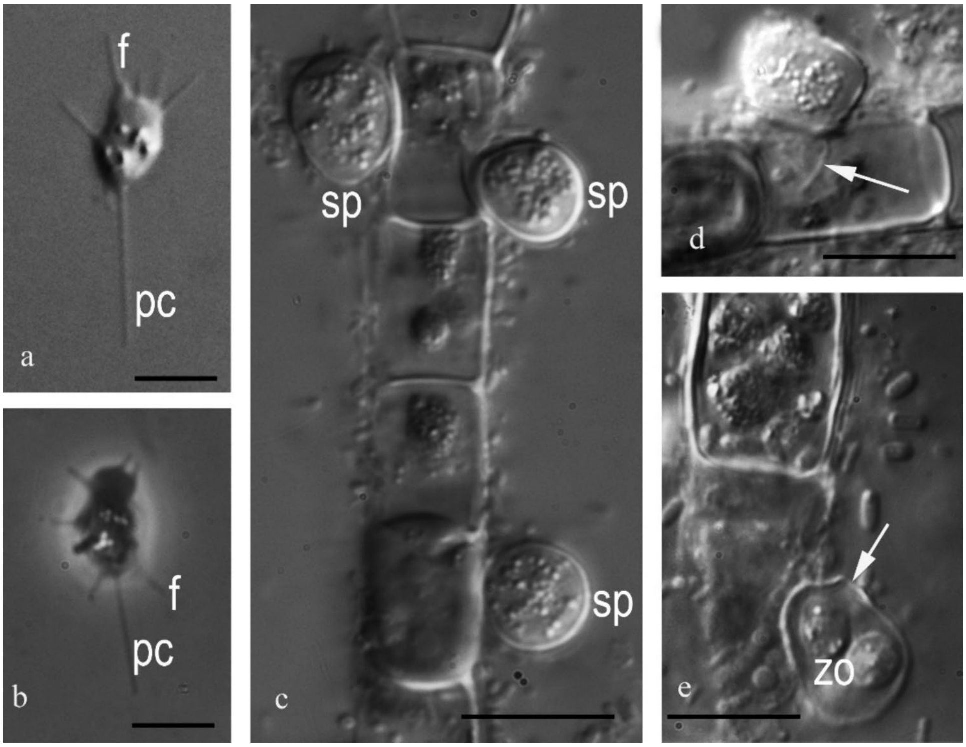


Fig. 60 Light microscopic images of *Sanchytrium tribonematis.* **a**, **b** amoeboid zoospores with filopodia (f) and posterior pseudocilium (pc). **c** sporangia (sp) on the *Tribonema* filament. **d** rhizoid (arrow) of sporangium. **e** zoospores (zo) releasing sporangium through the discharge pore (arrow). Scale bars: **a**, **b** = 3.5 µm, **c**–**e** = 10 µm

Pucciniomycetes R. Bauer et al. and *Ustilaginomycetes* R. Bauer et al.

2.1. Class: ***Agaricomycetes*** Doweld

This class is represented by the following genera: *Archaeomarasmius* Hibbett et al., *Coprinites* Poinar & Singer, *Cyathus* Haller, *Eopolyporoides* Rigby in G. Playford et al., *Fomes* (Fr.) Fr., *Ganodermites* A. Fleischm. et al., *Geastrum* Pers., *Gerontomyces* Poinar, *Gondwanagaricites* Heads et al., *Hydnum* L., *Nidula* V.S. White, *Lithopolyporales* R. Kar et al. 2003 (Fig. 63-t), *Palaeoagaricites* Poinar & Buckley, *Palaeoclavaria* Poinar & A.E. Br., *Palaeogaster* Poinar et al., *Phellinites* Singer & S. Archang., *Protomycena* Hibbett et al., *Pseudopolyporus* Hollick, *Scleroderma* Pers. and *Trametites* Mesch.

2.2. Class: ***Agaricostilbomycetes*** R. Bauer et al.

This class is represented by a single genus, viz., *Stilbum* Tode.

2.3. Class: ***Pucciniomycetes*** R. Bauer et al.

This class is represented by the following genera: *Aecidites* Debey & Ettingsh., *Aeciosporonites* Debi Mukh. *Hapalophragmites* Ramanujam & Ramachar 1980 (Fig. 63-u), *Milesites* Ramanujam & Ramachar 1980 (Fig. 63-v), *Pucciniasporonites* Ramanujam & Ramachar and *Shuklania* J.N. Dwivedi.

2.4. Class: ***Ustilaginomycetes*** R. Bauer et al.

This class is represented by the following genera: *Chlamydosporites* Paradkar 1975 (Fig. 63-w), *Mundkurella* Thirum., *Teliosporites* R. Kar et al. 2010 (Fig. 63-x), *Thecaphora* Fingerh. and *Ustilago* (Pers.) Roussel.

3. Phylum: ***Blastocladiomycota*** T.Y. James

Retesporangicus Strullu-Derr. is assignable to phylum *Blastocladiomycota*.

4. Phylum: ***Chytridiomycota*** Doweld

The following genera have affinity with phylum *Chytridiomycota* but their resemblance with taxa of lower ranks could not be established: *Brijax* M. Krings & C.J. Harper, *Globicultrix* M. Krings et al., *Illmanomyces* M. Krings & T.N. Taylor, *Nimbosphaera* C.J. Harper & M. Krings, *Palaeozoosporites* Strullu-Derr., *Perexiflasca* M. Krings et al., *Rhizophydites* M. Krings et al. Fossil chytridiomycetus fungi are represented by only one class, viz., *Chytridiomycetes* M. Möbius.

4.1. Class: ***Chytridiomycetes*** M. Möbius

This class is represented by the following genera: *Cultoraquaticus* Strullu-Derr., *Entophlyctis* A. Fisch., *Grilletia* Renault & C.E. Bertrand, *Guizhounema* X. Mu, *Krispiromyces* T.N. Taylor et al., *Lyonomyces* T.N. Taylor et al.,

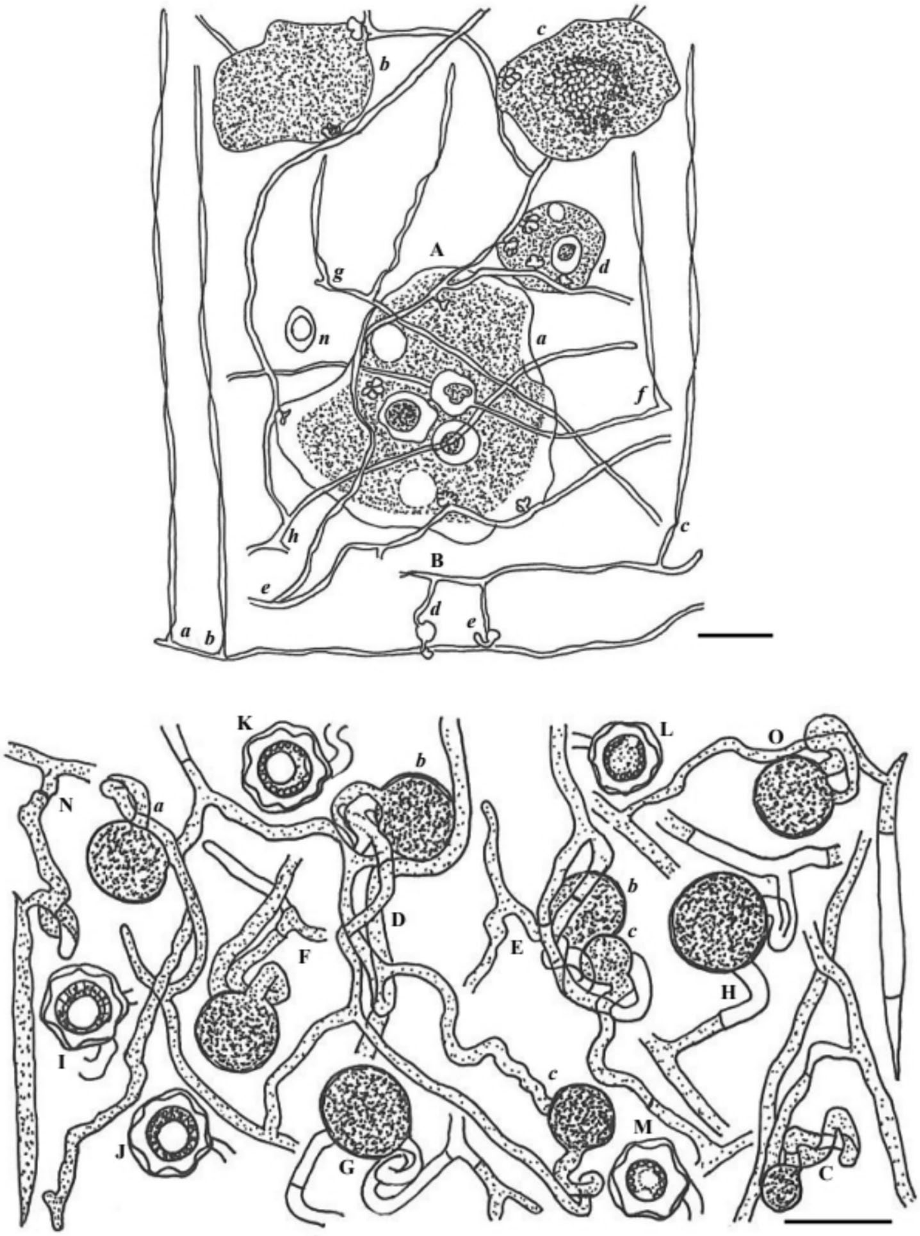


Fig. 61 *Zoopage phanera* Drechsler (redrawn from Drechsler 1935). **A** Four specimens: **a**, **b**, **c** and **d** of *Amocba terricola* III captured by the branched hyphae; **e** and **h** of *Zoopage phancra*, showing the stalked botryoid haustoria of the fungus; hyphae **f** and **g**, perhaps also adhering to animal but without having produced haustoria, bear respectively one and two erect conidiiferous branches with long chains of conidia of which from lack of space only the lowermost individuals are shown; in the animal, d is shown its nucleus, and the same structure from a healthy specimen is shown in n; × 500. **B** Two hyphae, bearing three conidial chains: **a**–**c** (shown only inpart from lack of space) and producing on diclinous sexual branches two zygosporangia, d and c, shown at early stages of development; × 500. **C**–**H** Sexual apparatus of *Zoopage phancra* showing diclinous origin of zygophore, inconstancy of septation during earlier stages in development of fusion product, and the frequently contorted condition of one of the zygophores; × 1000. **I**–**M** Approximately mature zygospores, each within its collapsing zygosporangial membrane; × 1000. **N**, **O** Sexual apparatus, with a germ tube from a conidium functioning directly as a zygophore; × 1000

Milleromyces T.N. Taylor et al., *Oochytrium* Renault, *Trewinomyces* M. Krings et al.

5. Phylum: ***Glomeromycota*** C. Walker & A. Schüßler

The following fossil genera exhibit affinity with *Glomeromycota*, but their resemblance with taxa of lower ranks could not be established: *Helmutella* M. Krings & T.N. Taylor, *Kryphiomyces* M. Krings et al., *Palaeomyces* D. Ellis and *Zwergimyces* M. Krings & T.N. Taylor. Fossil glomeromycetus fungi are represented by following two classes, viz., *Archaeosporomycetes* Sieverd et al. and *Glomeromycetes* Caval.-Sm.

5.1. Class: ***Archaeosporomycetes*** Sieverd et al.

This class is represented by *Archaeosporites* C. Walker et al.

5.2. Class: ***Glomeromycetes*** Caval.-Sm.

This class is represented by the following genera: *Gigasporites* Carlie J. Phipps & T.N. Taylor, *Glomites* T.N. Taylor et al., *Glomorphites* Garcia Mass., *Palaeogigaspora* R. Kar et al. 2010 (Fig. 63-**y**), *Palaeoglomus* R. Redecker et al. and Scutellosporites Dotzler et al.

6. Phylum: ***Mucoromycota*** Doweld

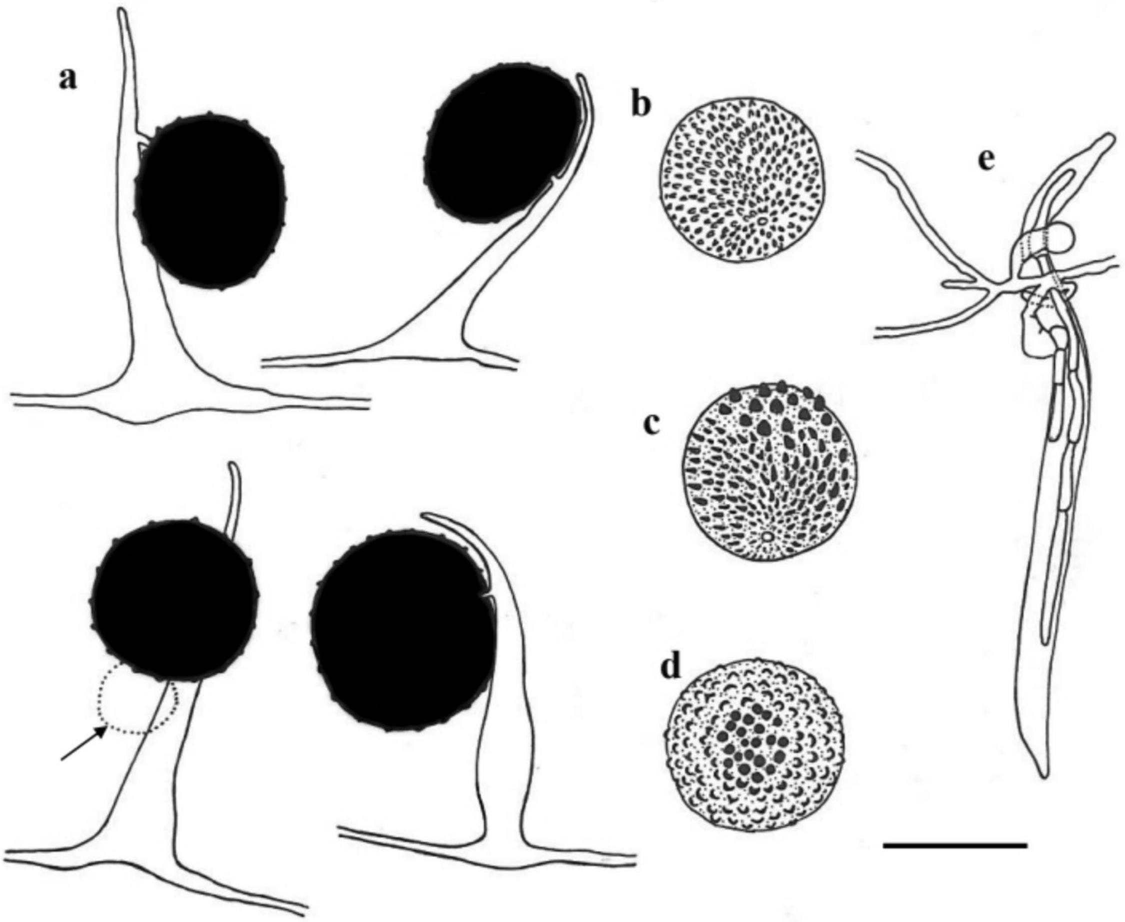


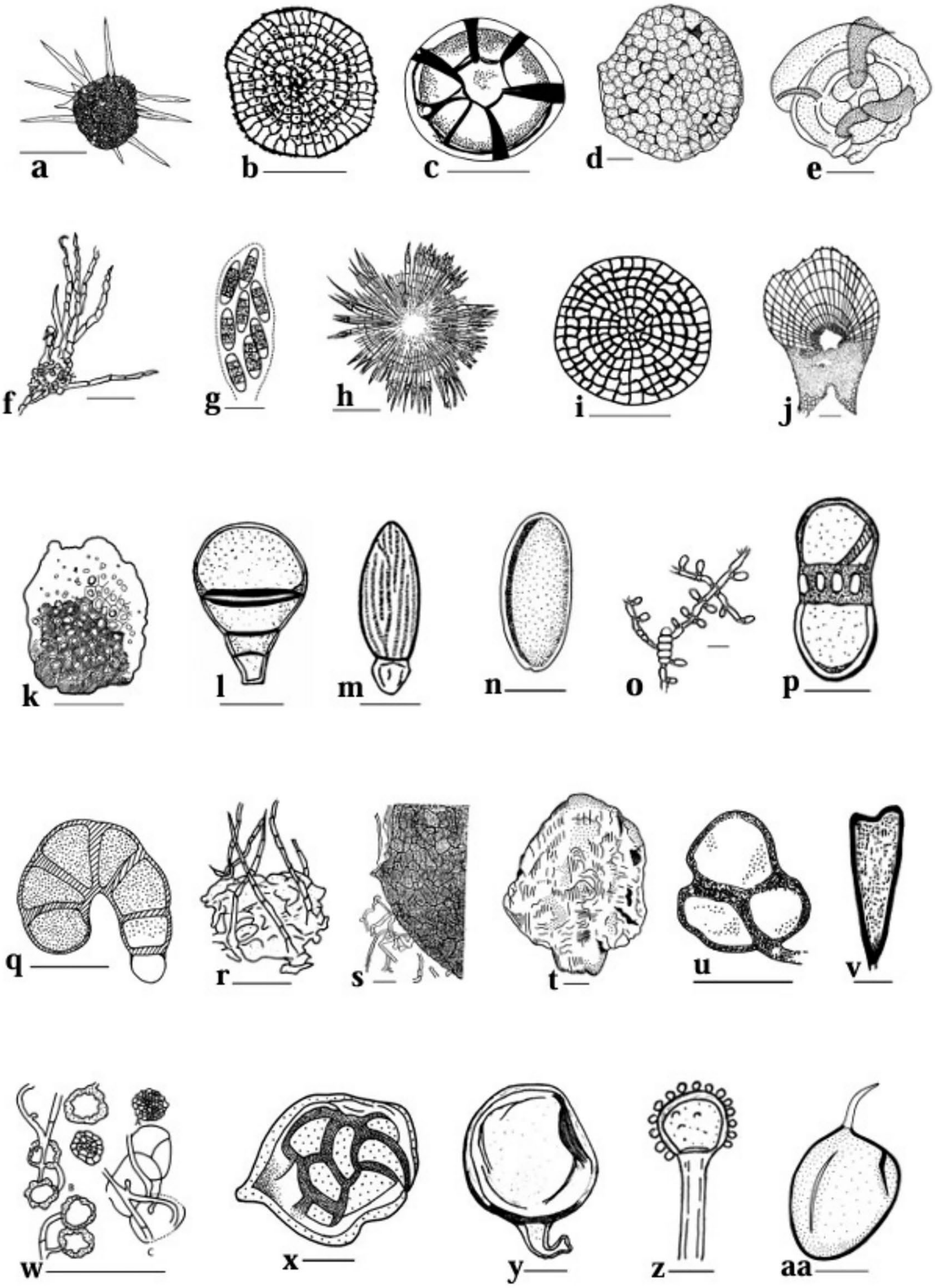
Fig. 62 *Verrucocephalum latericorvinisporum* (KPM-NC0016331). **a** Sporophores with matured black spores hanging on short side branchlets. One of the spores accompanying a water drop indicated by a dotted line (arrow). **b** The bottom view of a young hyaline spore with initial minute verrucae. **c** The bottom view of a maturing spore with darkly pigmented verrucae. **d** The top view of a maturing blackish spore with verrucose surface. **e** Whole figure of a trapped nematode with elongating haustorial assimilative hyphae from appressoria in a cavity of the nematode. Arrows indicate penetration parts with appressoria and post-penetration bulbs. Scale bar = **a**–**e** 50 µm (redrawn from Degawa 2013)

Stolophorites Wilh. Bock exhibits affinity with *Mucoromycota*, but its resemblance with taxa of lower ranks could not be established. Fossil mucoromycetus fungi are represented by a single class, viz., *Endogonomycetes* Doweld.

6.1. Class: ***Endogonomycetes*** Doweld

This class is represented by the following genera: *Chlamydospora* R. Kar et al., *Endochaetophora* J.F. White & T.N. Taylor (Doweld 2014e), *Lithomucorites* R. Kar et al. 2010 (Fig. 63-z)., *Palaeomycites* Mesch. and *Udaria* A. Gupta 1996 (Fig. 63-aa).

Fig. 63 Different morphologies of fossil spores. **a** *Appendicisporonites typicus*. **b** *Callimothallus pertusus*. **c** *Cucurbitariaceites bellus*. **d** *Kalviwadithyrites saxenae*. **e** *Koshalia enigmata*. **f** *Palaeocercospora siwalikensis*. **g** *Palaeoleptosphaeria intertrappeana*. **h** *Parmathyrites indicus*. **i** *Phragmothyrites eocaenicus*. **j** *Polyhyphaethyrites giganticus*. **k** *Ratnagiriathyrites hexagonalis*. **l** *Brachysporisporites pyriformis*. **m** *Diploneurospora tewarii*. **n** *Hypoxylonites brazosensis*. **o** *Meliolinites spinksii*. p *Palaeoamphisphaerella pirozynskii*. **q** *Palaeocirrenalia elegans*. **r** *Palaeocolletotrichum graminioides*. **s** *Palaeosordaria lagena*. **t** *Lithopolyporales zeerabadensis*. **u** *Hapalophragmites cumminsii*. **v** *Milesites irregularis*. **w** *Chlamydosporites gramineus* **a** Reticulate chlamydospore; **b**, **c** Mycelium and hyphae with haustoria and chlamydospores. **x** *Teliosporites globatus*. **y** *Palaeogigaspora excellensa*. **z** *Lithomucorites miocenicus*. **aa** *Udaria singhii*. Scale bars: **a**–**c**, **h**, **k**, **w** 50 µm, **d**, **g**, **r**, **t** 25 µm, **e**, **f**, **l**, **m**, **q**, **s**, **u** 20 µm, **i** 60 µm, **j** 500 µm, **n**–**p**, **v**, **x**–**z** 10 µm, aa 30 µm ▶



Acknowledgements The authors are grateful to the High-Level Talent Recruitment Plan of Yunnan Provinces (“Young Talents” Program and “High-End Foreign Experts” Program), the National Natural Science Foundation of China (Grant No. 32460002), the Key Laboratory of Yunnan Provincial Department of Education of the Deep-Time Evolution on Biodiversity from the Origin of the Pearl River, Mee-mann Chang Academician Workstation in Yunnan Province, (Grant No. 202205AF150002), and Yunnan Province Young and Middle-aged

Academic and Technical Leaders Reserve Talents Program (Grant No. 202305AC350252), and General Programs of the Provincial Department of Science and Technology (Grant No. 202101BA070001-076) for support. K.V. Mikhailov and O.A. Zverkov express gratitude to the Russian Science Foundation Grant No. 24-44-00099 for support of phylogenomic analysis. The authors like to thank Dr. Joyce E. Longcore, Dr. Bau Tolgor and Alexei O. Seliuk who provided photos of different taxa in Chytridiomycota, Neolecta and Sanchytrium species respectively. M.K. Wimalasena and T.C. Bamunuarachchige thank Science and Technology Human Resource Development Project, Ministry of Higher Education, Sri Lanka, funded by the Asian Development Bank (R3RJ2) and Tropical Microbiology Research Foundation. N.N. Wijayawardene thanks Maheshika Gunasekara, Geethanjana Perera and Kumuthu Jayakody for their help while preparing the manuscript. K.D. Hyde thanks the National Research Council of Thailand (NRCT) grant "Total fungal diversity in a given forest area with implications towards species numbers, chemical diversity and biotechnology" (Grant No. N42A650547). Bruno T. Goto thanks the Conselho Naional de Desenvolvimento Científico e Tecnológico (CNPq) for the research grant awarded to BT Goto (Proc. 306632/2022-5). A. L C. M. de A. Santiago thanks the Brazilian National Council for Scientific and Technological Development (CNPq) for providing the research grant, and the project 'Morphological and molecular approaches to understanding the communities of zygosporic fungi in the Atlantic Forest of Pernambuco and Paraíba, Brazil' (FACEPE –APQ-1346-2.12/22) for the financial support. Work in M. S. Elshahed and N. H. Youssef Laboratories was supported by the United States National Science Foundation (NSF) Grant number 2029478, and the United States National Institute of health (NIH) grant number 1P20GM152333-01. Martin Kukwa and Emilia A. Ossowska thank Adam Flakus (PAN, Kraków) for the help with the plate of Arthoniomycetes. K. Tanaka would like to thank the Japan Society for the Promotion of Science (JSPS, 23K05900). N. Suwannarach and J. Kumla would like to thank Chiang Mai University for partially support. M. Raza is grateful to the project of funds for stable support to agriculture sci-tech renovation (XJNKYWDZC–2022004). Qirui Li is thankful to the National Natural Science Foundation of China (31960005, 32000009 and 32170019). D. Haelewaters received support from the Research Foundation—Flanders (Senior Postdoctoral Fellowship 1206024N). G Péter thanks Bence Rácz who provided the TEM image of *Novakomyces olei*. Ramesh K. Saxena is grateful to the authorities of the Birbal Sahni Institute of Palaeosciences, Lucknow, India for library facilities. A. Menkis is grateful to Veera Tuovinen Nogerius for confocal laser scanning images of *Archaeorhizomyces*. U. Peintner thanks the FWF (P31038) for financial support, the Westerdijk Fungal Biodiversity Institute (WI-KNAW culture collection) for providing the original strain of *Mortierella polycephala*, and Anusha Telagathoti as well as Edoardo Mandolini for their help in the lab. Samantha Chandranath Karunarathna thanks the National Natural Science Foundation of China (Number NSFC 32260004) and the High-Level Talent Recruitment Plan of Yunnan Province "High-End Foreign Experts" programme) for their support. Julia Pawłowska received support from The National Centre for Research and Development, Poland, under grant no. Tango-IV-C/0005/2019. Dhanushka Wanasinghe thanks CAS President's International Fellowship Initiative (Number 2021FYB0005), the National Science Foundation of China (NSFC) under the project code 32150410362, and the Smart Yunnan Project (Young Scientists) under project code E13K281261. Armin Mešić is grateful to the Croatian Science Foundation for their financial support under the project grant HRZZ-IP-2022-10-5219 (FunMed). Elena S. Nassonova would like to thank the Russian Science Foundation (Grant Number 23-74-00071) for the financial support of research on microsporidia. Sergey A. Karpov thanks the RSF grant 21-74-20089 for support of writing and corrections, the Ministry of Science and Higher Education of the Russian Federation Grant 075-15-2021-1069 (rDNA sequencing of the aphelids and sanchytrids), and ZIN RAS Program 122031100260-0. Authors thank Yurong Yan and Gangya Xu for their help in references checking and formatting the manuscript. H.-M. Daniel is supported by the Belgian Science Policy Office (BELSPO) grantC5/00/BCCM.

Funding Funding was provide by National Natural Science Foundation of China (Nos. 32460002, 31960005, 32000009, 32170019, NSFC 32260004), Russian Science Foundation (Nos. 24-44-00099, 23-74-00071, 24-44-00099), National Research Council of Thailand (No. N42A650547), National Institute of Nursing Research (1P20GM152333-01), National Science Foundation (2029478), Japan Society for the Promotion of Science (JSPS, 23K05900), National Science Foundation of China (32150410362), Croatian Science Foundation (HRZZ-IP-2022-10-5219), RSF (21-74-20089), ZIN RAS (122031100260-0), Science and Technology Human Resource Development Project (R3RJ2), Asian Development Bank, Conselho Naional de Desenvolvimento Científico e Tecnológico (306632/2022-5), zygosporic fungi in the Atlantic Forest of Pernambuco and Paraíba, Brazil (FACEPE –APQ-1346-2.12/22), Agriculture Sci-Tech Renovation (XJNKY-WDZC–2022004), Research Foundation—Flanders (1206024N), FWF (P31038), Talent Recruitment Plan of Yunnan Province "High-End Foreign Experts, National Centre for Research and Development, Poland (Tango-IV-C/0005/2019), CAS President's International Fellowship Initiative (2021FYB0005), Smart Yunnan Project (E13K281261), High-Level Talent Recruitment Plan of Yunnan Provinces.

Declarations

Conflict of interest The authors declare no conflict of interest. The author list includes members of the Editorial Board of Fungal Diversity. They were not involved in the journal's review of, or decisions related to, this manuscript.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

References

Abdel-Mageed HM, Nada D, Radwan RA, Mohamed AS, Gohary NAEL (2022) Optimization of catalytic properties of *Mucorracemosus* lipase through immobilization in a biocompatible alginate gelatin hydrogel matrix for free fatty acid production: a sustainable robust biocatalyst for ultrasound-assisted olive oil hydrolysis. 3 Biotech 12:285. https://doi.org/10.1007/s13205-022-03319-8

Adl SM, Bass D, Lane CE, Luke J, Schoch CL, Smirnov A, Agatha S, Berney C, Brown MW, Burki F, Ardenas PC, Cepi I, Chistyakova L, del Campo J, Dunthorn M, Edvardsen B, Eglit Y, Guillou L, Hampl V, Heiss AA, Hoppenrath M, James TY, Karnkowska A, Karpov S, Kim E, Kolisko M, Kudryavtsev A, Lahr DJG, Lara E, Gall LL, Lynss DH, Mann DG, Massana R, Mitchell EAD, Morrow C, Park JS, Pawlowski JW, Powell MJ, Richter DJ, Rueckert S, Shadwick L, Shimano S, Spiegel FW, Torruella G, Youssef N, Zlatogursky V, Zhang Q (2019) Revisions to the classification, nomenclature and diversity of eukaryotes. J Eukaryot Microbiol 66:4–119. https://doi.org/10.1111/jeu.12691

Aghaei GS, Nasimi M, Agha Kuchak Afshari S, Ghasemi Z, Rezaie S (2017) First case of superficial infection due to *Naganishia albida* (formerly *Cryptococcus albidus*) in Iran: a review of the literature. Curr Med Mycol 3(2):33–37

Agyare S, Magan N, Xu X (2020) Conditions for infection of strawberry fruit by *M. piriformis* and *Rhizopus* spp. Eur J Plant Pathol 157:65–75. https://doi.org/10.1007/s10658-020-01981-3

Ahrendt SR, Quandt CA, Ciobanu D, Clum A, Salamov A, Andreopoulos B, Cheng JF, Woyke T, Pelin A, Henrissat B, Reynolds NK, Benny GL, Smith ME, James TY, Grigoriev IV (2018) Leveraging single-cell genomics to expand the fungal tree of life. Nat Microbiol 3(12):1417–1428. https://doi.org/10.1038/s41564-018-0261-0

Aime MC, Matheny PB, Henk DA, Frieders EM, Nilsson RH, Piepenbring M, McLaughlin DJ, Szabo LJ, Begerow D, Sampaio JP, Bauer R, Wei 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. https://doi.org/10.1080/15572536.2006.11832619

Aime MC, Toome M, David J, McLaughlin DJ (2014) Systematics and evolution. Mycota 2(10):271–294. https://doi.org/10.1007/978-3-642-55318-9_10

Aime MC, Urbina H, Liber JA, Bonito G, Oono R (2018a) Two new endophytic *Atractiellomycetes*, *Atractidochium hillariae* and *Proceropycnis hameedii*. Mycologia 110:136–146. https://doi.org/10.1080/00275514.2018.1446650

Aime MC, Castlebury LA, Abbasi M, Begerow D, Berndt R, Kirschner R, Marvanová L, Ono Y, Padamsee M, Scholler M, Thines M, Rossman AY (2018b) Competing sexual and asexual generic names in *Pucciniomycotina* and *Ustilaginomycotina* (*Basidiomycota*) and recommendations for use. IMA Fungus 9:75–89. https://doi.org/10.5598/imafungus.2018.09.01.06

Akinbobola AB, Kean R, Hanifi SMA, Quilliam RS (2023) Environmental reservoirs of the drug-resistant pathogenic yeast *Candida auris*. PLoS Pathog 19:e1011268. https://doi.org/10.1371/journal.ppat.1011268

Al Mousa AA, Amal A, Hassane AMA, Gomaa AEl-RF, Aljuriss JA, Dahmash ND, Abo-Dahab NF (2022) Response-surface statistical optimization of submerged fermentation for pectinase and cellulase production by *Mucor circinelloides* and *M. hiemalis*. Ferment 8:205. https://doi.org/10.3390/fermentation8050205

Alasmary FA, Awaad AS, Alqahtani SM, El-Meligy RM, Abdullah DA, Alqasoumi SI (2020) Evaluation of the chemical constituents and potential biological activities of *Cunninghamella blakesleeana*. Saudi Pharm J 28(10):1197–1202. https://doi.org/10.1016/j.jsps.2020.08.009

Alexopoulos CJ, Mims CW, Blackwell M (1996) Introductory mycology, 4th edn. Wiley, New York

Altschul SF, Madden TL, Schaffer AA, Zhang J, Zhang Z, Miller W, Lipman DJ (1997) Gapped BLAST and PSI-BLAST: a new generation of protein database search programs. Nucleic Acids Res 25(17):3389–3402. https://doi.org/10.1093/nar/25.17.3389

Ameen F, Al-Homaidan AA, Al-Sabri A, Almansob A, AlNAdhari S (2023) Anti-oxidant, anti-fungal and cytotoxic effects of silver nanoparticles synthesized using marine fungus *Cladosporium halotolerans*. Appl Nanosci 13:623–631. https://doi.org/10.1007/s13204-021-01874-9

Ametrano CG, Grewe F, Crous PW, Goodwin SB, Liang C, Selbmann L, Lumbsch HT, Leavitt SD, Muggia L (2019) Genome-scale data resolve ancestral rock-inhabiting lifestyle in *Dothideomycetes* (*Ascomycota*). IMA Fungus 10:19. https://doi.org/10.1186/s43008-019-0018-2

Amo de Paz G, Cubas P, Divakar PK, Lumbsch HT, Crespo A (2011) Origin and diversification of major clades in parmelioid lichens (*Parmeliaceae*, *Ascomycota*) during the Paleogene inferred by Bayesian analysis. PLoS ONE 6(12):e28161

Ann Chai LY, Denning DW, Warn P (2010) *Candida tropicalis* in human disease. Crit Rev Microbiol 36:282–298. https://doi.org/10.3109/1040841x.2010.489506

Aoki H, Nakatsuka-Mori T, Ueno Y, Nabeshima Y, Oyama H (2023) Analysis of functional ingredients of tempe-like fermented *Moringa oleifera* seeds (*Moringa tempe*) prepared with *Rhizopus* species. J Biosci Bioeng 135(4):306–312. https://doi.org/10.1016/j.jbiosc.2023.01.011

Arendrup MC, Boekhout T, Akova M, Meis JF, Cornely OA, Lortholary O (2014) ESCMID and ECMM joint clinical guidelines for the diagnosis and management of rare invasive yeast infections. Clin Microbiol Infect 3:76–98. https://doi.org/10.1111/14690691.12360

Arpin N, Fiasson J-L (1971) The pigments of *Basidiomycetes*: their chemo-taxonomic interest. In: Petersen RH (ed) Evolution in the higher *basidiomycetes*. University of Tennessee Press, Knoxville, pp 63–98

Ashwin R, Bagyaraj DJ, Raju BM (2023) Dual inoculation with *Bradyrhizobium liaoningense* and *Ambispora leptoticha* improves drought stress tolerance and productivity in soybean cultivars, MAUS 2 and DSR 12. Biologia 78(2):331–348. https://doi.org/10.1007/s11756-022-01196-3

Avis TJ, Caron SJ, Boekhout T, Hamelin RC, Bélanger RR (2001) Molecular and physiological analysis of the powdery mildew antagonist *Pseudozyma flocculosa* and related fungi. Phytopathology 91:249–254. https://doi.org/10.1094/PHYTO.2001.91.3.249

Baar J, Paradi I, Lucassen EC, Hudson-Edwards KA, Redecker D, Roelofs JG, Smolders AJ (2011) Molecular analysis of AMF diversity in aquatic macrophytes: a comparison of oligotrophic and utra-oligotrophic lakes. Aquat Bot 94:53–61. https://doi.org/10.1016/j.aquabot.2010.09.006

Bacigálová K (2008) *Protomyces buerenianus* (*Protomycetaceae*) a new species for Slovakia. Biologia 63:40–43. https://doi.org/10.2478/s11756-008-0015-1

Baker GE (1936) A study of the genus *Helicogloea*. Ann Mo Bot Gard 23(1):69–128

Bandoni RJ (1998) On some species of mycogloea. Mycoscience 39(1):31–36. https://doi.org/10.1007/BF02461575

Bandoni RJ, Krug J, Ginns J (2002) On some *Colacogloea* species from Canada. Czech Mycol 54:31–43

Baral HO (1994) Comments on 'Outline of the *ascomycetes*—1993'. Syst Ascomycetum 13:113–128

Baral HO (2004) The European and North-American species of *Sarcoscypha*. http://www.gbif-mycology.de/HostedSites/Baral/Sarcoscypha.htm

Baral HO, Haelewaters D, Pärtel K (2015) A new attempt to classify the families of the *Helotiales*. In: The second international workshop on *ascomycete* systematics. CBS symposium 22–24 April, AmsterdamBaral HO, Weber E, Gams W, Hagedorn G, Liu B, Liu XZ, Marson G, Marvanová L, Stadler M, Weiß M (2017b[2018]) Generic names in the *Orbiliaceae* (*Orbiliomycetes*) and recommendations on which names should be protected or suppressed. Mycol Prog 17:5–31. https://doi.org/10.1007/s11557-017-1300-6

Baral HO, Weber E, Marson G, Quijada L (2017) A new connection between wood saprobism and beetle endosymbiosis: the rarely reported saprobic discomycete *Tromeropsis* is congeneric with the symbiotic yeast *Symbiotaphrina* (*Symbiotaphrinales*, *Xylonomycetes*) and two asexual morphs misplaced in *Hyphozyma*. Mycol Progr 17: 215–254. – https://doi.org/10.1007/s11557-017-1340-y

Baral HO, Weber E, Gams W, Hagedorn G, Liu B, Liu X, Marson G, Marvanová L, Stadler M, Weiß M (2017) Generic names in the *Orbiliaceae* (*Orbiliomycetes*) and recommendations on which names should be protected or suppressed. Mycol Prog 17:5–31. https://doi.org/10.1007/s11557-017-1300-6

Baral HO, Weber E, Gams W, Hagedorn G, Liu B, Liu X, Marson G, Marvanová L, Stadler M, Weiß M (2018) Generic names in the *Orbiliaceae* (*Orbiliomycetes*) and recommendations on which names should be protected or suppressed. Mycol Prog 17:5–31. https://doi.org/10.1007/s11557-017-1300-6

Baral HO, Weber E, Marson G (2020) Monograph of *Orbiliomycetes* (*Ascomycota*) based on vital taxonomy. National Museum of Natural History Luxembourg, Luxembourg

Barr DJ (1980) An outline for the reclassification of the *Chytridiales*, and for a new order, the *Spizellomycetales*. Can J Bot 58(22):2380–2394

Barr ME (1983) The ascomycetes connection. Mycologia 75:1–13

Barr ME (1987) Prodromus to class loculoascomycetes. Newell, Amherst

Barr ME (1990) Prodromus to nonlichenized, pyrenomycetous members of class *Hymenoascomycetes*. Mycotaxon 39:43–184

Barr ME (1991) Notes on and additions to North American members of the *Herpotrichiellaceae*. Mycotaxon 41:419–436

Barreto GG, Bezerra JD, Costa-Rezende DH, Gusmão LF (2023) A multigene phylogeny of Umbellidion revealed a novel lineage in *Leotiomycetes*. Mycol Prog 22(7):48. https://doi.org/10.1007/s11557-023-01896-3

Bartnicki-Garcia S, Nickerson WJ (1962) Induction of yeast-like development in *Mucor* by carbon dioxide. J Bacteriol 84:829–840. https://doi.org/10.1128/jb.84.4.829-840.1962

Basiru S, Hijri M (2022) The potential applications of commercial arbuscular mycorrhizal fungal inoculants and their ecological consequences. Microorg 10(10):1897. https://doi.org/10.3390/microorganisms10101897

Bauer R (2004) *Basidiomycetous* interfungal cellular interactions a synopsis. In: Agerer R, Piepenbring M, Blanz P (eds) Frontiers in basidiomycote mycology. IHW-Verlag, Eching, pp 325–337

Bauer R, Oberwinkler F (1991a) The symplechosome: a unique cell organelle of some basidiomycetes. Botanica Acta 104(2):93–97

Bauer R, Oberwinkler F (1991b) The Colacosomes: New Structures at the Host-parasite Interface of a Mycoparasitic Basidiomycete. Botanica Acta 104(1):53–57. https://doi.org/10.1111/j.1438-8677.1991.tb00193.x

Bauer R, Oberwinkler F, Vánky K (1997) Ultrastructural markers and systematics in smut fungi and allied taxa. Can J Bot 75:1273–1314. https://doi.org/10.1139/b97-842

Bauer R, Vánky K, Begerow D, Oberwinkler F (1999) *Ustilaginomycetes* on *Selaginella*. Mycologia 91(3):475–484

Bauer R, Begerow D, Oberwinkler F, Piepenbring M, Berbee ML (2001) *Ustilaginomycetes*. In: Carter D, Chowdhary A, Heitman J, Kück U (eds) Systematics and evolution. The mycota, vol 7. Springer, Berlin, pp 57–83

Bauer R, Begerow D, Oberwinkler F, Marvanová L (2003) *Classicula*: the teleomorph of *Naiadella fluitans*. Mycologia 95:756–764. https://doi.org/10.2307/3761949

Bauer R, Lutz M, Oberwinkler F (2004) *Tuberculina*-rusts: a unique basidiomycetous interfungal cellular interaction with horizontal nuclear transfer. Mycologia 96(5):960–967. https://doi.org/10.1080/15572536.2005.11832896

Bauer R, Begerow D, Sampaio JP, Weiß M, Oberwinkler F (2006) The simple-septate *basidiomycetes*: a synopsis. Mycol Prog 5:41–66. https://doi.org/10.1007/s11557-006-0502-0

Bauer R, Garnica S, Oberwinkler F, Riess K, Weiß M, Begerow D (2015) *Entorrhizomycota*: a new fungal phylum reveals new perspectives on the evolution of fungi. PLoS ONE 10(7):1–19

Beaudet D, Chen ECH, Mathieu S, Yildirir G, Ndikumana S, Dalpé Y, Séguin S, Farinelli L, Stajich JE, Corradi N (2018) Ultra-low input transcriptomics reveal the spore functional content and phylogenetic affiliations of poorly studied arbuscular mycorrhizal fungi. DNA Res 25:217–227. https://doi.org/10.1093/dnares/dsx051

Begerow D, Stoll M, Bauer R (2006) A phylogenetic hypothesis of *Ustilaginomycotina* based on multiple gene analyses and morphological data. Mycologia 98:906–916. https://doi.org/10.1080/15572536.2006.11832620

Begerow D, Schafer AM, Kellner R, Yurkov A, Kemler M, Oberwinkler F, Bauer R (2014) *Ustilaginomycotina*. In: McLaughlin DJ, Spatafora JW (eds) Systematics and evolution, Part A, Part 1, Springer, New York. https://doi.org/10.1007/978-3-642-55318-9_11

Begerow D, McTaggart A, Agerer R (2018) 1/3 *Basidiomycota* and *Entorrhizomycota*. In: Frey W (ed) A. Engler's syllabus der pflanzenfamilien. Bontraeger Science Publishers, Germany

Beguin H (2010) *Tritirachium egenum*, a thiamine- and siderophore-auxotrophic fungal species isolated from a *Penicillium rugulosum*. FEMS Microbiol Ecol 74:165–171. https://doi.org/10.1111/j.1574-6941.2010.00929.x

Beimforde C, Feldberg K, Nylinder S, Rikkinen J, Tuovila H, Dörfelt H, Gube M, Jackson DJ, Reitner J, Seyfullah LJ, Schmidt AR (2014) Estimating the Phanerozoic history of the *Ascomycota* lineages: combining fossil and molecular data. Mol Phylogenet Evol 78:386–398. https://doi.org/10.1016/j.ympev.2014.04.024

Benabda O (2019) M'hir S, Kasmi M, Mnif W, Hamdi M (2019) Optimization of protease and amylase production by *Rhizopus oryzae* cultivated on bread waste using solid-state fermentation. J Chem 3:1–9. https://doi.org/10.1155/2019/3738181

Benjamin RK (1958) Sexuality in the *Kickxellaceae*. Aliso 4(1):149–169

Benjamin RK (1959) The merosporangiferous *Mucorales*. Aliso 4:321–453

Benjamin RK (1965) Addenda to "The Merosporangiferous *Mucorales*" III Dimargaris. Aliso 6(1):1–10

Benjamin RK (1979) *Zygomycetes* and their spores. Whole Fungus 2:573–262

Benkert D (1993) Bryoparasitic *Pezizales*: ecology and systematics. In: Pegler DN, Boddy I, Ing B, Kirk PM (eds) Fungi of Europe: investigation, recording and conservation. Royal Botanical Gardens, Kew, pp 147–156

Bennett AE, Bever JD, Deane BM (2009) *Arbuscular mycorrhizal* fungal species suppress inducible plant responses and alter defensive strategies following herbivory. Oecol 160:771–779. https://doi.org/10.1007/s00442-009-1338-5

Benny GL (2005) *Zygomycetes*. https://www.zygomycetes.org. Accessed 26 Dec 2023

Benny GL (2008) Methods used by Dr. R.K. Benjamin, and other mycologists, to isolate Zygomycetes.Aliso 26:37–61. https://doi.org/10.5642/aliso.20082601.08

Benny GL (2012) Current systematics of *Zygomycota* with a brief review of their biology. In: Misra JK, Tewari JP, Deshmukh SK (eds) Systematics and evolution of Fungi. Science Publishers, Enfield, p 412

Benny GL, Humber RA, Voigt K (2014) Zygomycetous fungi: phylum *Entomophthoromycota* and subphyla *Kickxellomycotina*, *Mortierellomycotina*, *Mucoromycotina*, and *Zoopagomycotina*. In: McLaughlin DJ, Spatafora JW (eds). Systematics and evolution. The Mycota, Vol. 7A. New York, Springer, pp 209–250

Benny GL, Smith ME, Kirk PM, Tretter ED, White MM (2016) Challenges and future perspectives in the systematics of *Kickxellomycotina*, *Mortierellomycotina*, *Mucoromycotina*, and *Zoopagomycotina*. In: Li D-W (ed) Biology of microfungi, fungal biology. Springer International Publishing, Switzerland, pp 65–126

Bensch K, Braun U, Groenewald JZ, Crous PW (2012) The genus *Cladosporium*. Stud Mycol 72:1–401. https://doi.org/10.3114/sim0003

Berbee ML (1996) *Loculoascomycete* origins and evolution of filamentous *ascomycete* morphology based on 18S rRNA gene sequence data. Mol Biol Evol 13:462–470. https://doi.org/10.1093/oxfordjournals.molbev.a025607

Berbee ML, James TY, Strullu-Derrien C (2017) Early diverging fungi: diversity and impact at the dawn of terrestrial life. Annu Rev Microbiol 71(1):41–60. https://doi.org/10.1146/annurev-micro-030117-020324

Berthet P (1964) Essai biotaxinomique sur les *discomycètes*. Université de Lyon, Thèse de Doctorat es Sciences Naturelles

Bezerra JD, Santos MG, Barbosa RN, Svedese VM, Lima DM, Fernandes MJS, Bruno SG, Laura MP, Almeida-Cortez JS, Cristina M, Souza-Motta CM (2013) Fungal endophytes from cactus *Cereus jamacaru* in Brazilian tropical dry forest: a first study. Symbiosis 60:53–63. https://doi.org/10.1007/s13199-013-0243-1

Bezerra JDP, Felipe MTDC, Paiva LM, Magalhães OMC, Silva-Nogueira EBD, Silva GAD, Souza-Motta CMD (2020) Phylogenetic placement of *Tritirachium* strains from the URM culture collection originally founded by Augusto Chaves Batista (1916–1967) in Brazil, and the description of *T. batistae* sp. nov. Acta Bot Bras 34:290–300. https://doi.org/10.1590/0102-33062019abb0356

Bhuiyan SA, Magarey RC, McNeil MD, Aitken KS (2021) Sugarcane smut, caused by *Sporisorium scitamineum*, a major disease of sugarcane: a contemporary review. Phytopathology 111(11):1905–1917. https://doi.org/10.1094/PHYTO-05-21-0221-RVW

Bidartondo MI, Read DJ, Trappe JM, Merckx V, Ligrone R, Duckett JG (2011) The dawn of symbiosis between plants and fungi. Biol Lett 7:574–577. https://doi.org/10.1098/rsbl.2010.1203

Blackwell M, Haelewaters D, Pfister DH (2020) *Laboulbeniomycetes*: evolution, natural history, and Thaxter's final word. Mycologia 112(6):1048–1059. https://doi.org/10.1080/00275514.2020.1718442

Blakeslee AF (1904) Sexual reproduction in the *Mucorineae*. Proc Am Acad Arts Sci 40:205–319. https://doi.org/10.2307/20021962

Błaszkowski J, Kozłowska A, Crossay T, Symanczik S, Al-Yahya'ei MN (2017) A new family, *Pervetustaceae* with a new genus, *Pervetustus*, and *P. simplex* sp. nov. (*Paraglomerales*), and a new genus, *Innospora* with *I. majewskii* comb. nov. (*Paraglomeraceae*) in the *Glomeromycotina*. Nova Hedwig 105(3–4):397–410. https://doi.org/10.1127/nova_hedwigia/2017/0419

Błaszkowski J, Niezgoda P, Meller E, Milczarski P, Zubek S, Malicka M, Magurno F (2021) New taxa in *Glomeromycota*: *Polonosporaceae* fam. nov., *Polonospora* gen. nov., and *P. polonica* comb. nov. Mycol Prog 20:941–951. https://doi.org/10.1007/s11557-021-01726-4

Błaszkowski J, Sánchez-García M, Niezgoda P, Zubek S, Fernández F, Vila A, Al-Yahya'ei MN, Symanczik S, Milczarski P, Malinowski R, Cabello M, Goto BT, Casieri L, Malicka M, Bierza W, Magurno F (2022) A new order, *Entrophosporales*, and three new *Entrophospora* species in *Glomeromycota*. Front Microbiol 13:962856. https://doi.org/10.3389/fmicb.2022.962856

Boekhout T (1995) *Pseudozyma* Bandoni emend. Boekhout, a genus for yeast-like anamorphs of *Ustilaginales*. J Gen Appl Microbiol Tokyo 41:359–366. https://doi.org/10.2323/jgam.41.359

Boekhout T (2011) *Pseudozyma* Bandoni emend. Boekhout 1985 and a comparison with the yeast state of *Ustilago maydis* (De Candolle) Corda (1842). In: Kurtzman CP, Fell JW, Boekhout T (eds) The yeasts, a taxonomic study. Elsevier, New York. pp 1857–1868. https://doi.org/10.1016/B978-0-444-52149-1.00153-1

Boekhout T, Fonseca A, Sampaio JP, Bandoni RJ, Kwon-Chung KJ (2011) Discussion of teleomorphic and anamorphic basidiomycetous yeasts. In: Kurtzman CP, Fell JW, Boekhout T (eds) The yeasts: a taxonomic study. Elsevier, London, pp 1339–1372

Bollen GJ, van der Pol-Luiten B (1975) Mesophilic heat-resistant fungi (Abstract). Acta Bot Neerl 24:254–255

Bonito G, Hameed K, Toome-Heller M, Healy R, Reid C, Liao HL, Aime MC, Schadt C, Vilgalys R (2017) Atractiella rhizophila, sp. Nov., an endorrhizal fungus isolated from the *Populus* root microbiome. Mycologia 109:18–26. https://doi.org/10.1080/00275514.2016.1271689

Boone CK, Six DL, Zheng Y, Raffa KF (2008) Parasitoids and dipteran predators exploit volatiles from microbial symbionts to locate bark beetles. Environ Entomol 37:150–161. https://doi.org/10.1093/ee/37.1.150

Borling Welin J, Lyberg K, Passoth V, Olstorpe M (2015) Combined moist airtight storage and feed fermentation of barley by the yeast *Wickerhamomyces anomalus* and a lactic acid bacteria consortium. Front Plant Sci 6:270. https://doi.org/10.3389/fpls.2015.00270

Borse BD, Patil VR, Nemade LC, Chaudhari SA (2015) Freshwater *Basidiomycetes* from India. In: Patil VR (ed) Resrach *on Freshwter fungi*. Lulu Publications, Morrisville

Boudier E (1885) Nouvelle classification naturelle des Discomycètes charnus connus généralement sous le nom de Pézizes. Bulletin De La Société Mycologique De France 1:91–120

Bourdichon F, Casaregola S, Farrokh C, Frisvad JC, Gerds ML, Hammes WP, Harnett J, Huys G, Laulund S, Ouwehand A, Powell IB, Prajapati JB, Seto Y, Schure ET, Boven AV, Vankerckhoven V, Zgoda A, Tuijtelaars S, Hansen EB (2012) Food fermentations: microorganisms with technological beneficial use. Int J Food Microbiol 154:87–97. https://doi.org/10.1016/j.ijfoodmicro.2011.12.030

Brady BL, Sutton BC, Samson RA (1984) *Agaricostilbum pulcherrimum* (Berk. & Broome) comb. nov. Trans Br Mycol Soc 83(3):540–541

Brasfield TW (1938) The *Dacrymycetaceae* of temperate North America. Am Midl Nat 20:211–235. https://doi.org/10.2307/2485192

Breuer U, Harms H (2006) *Debaryomyces hansenii*—an extremophilic yeast with biotechnological potential. Yeast 23:415–437. https://doi.org/10.1002/yea.1374

Brewster MS (1952) A new species of *Physoderma*. Mycologia 44(1):97–100

Brysch-Herzberg M, Jia GS, Seidel M, Assali I, Du LL (2022) Insights into the ecology of *Schizosaccharomyces* species in natural and artificial habitats. Antonie Van Leeuwenhoek 115(5):661–695. https://doi.org/10.1007/s10482-022-01720-0

Brysch-Herzberg M, Jia GS, Sipiczki M, Seidel M, Li W, Assali I, Du LL (2023) *Schizosaccharomyces lindneri* sp. nov., a fission yeast occurring in honey. Yeast 40:237–253. https://doi.org/10.1002/yea.3857

Bunn RA, Simpson DT, Bullington LS, Lekberg Y, Janos DP (2019) Revisiting the 'direct mineral cycling' hypothesis: *arbuscular mycorrhizal* fungi colonize leaf litter, but why? ISME J 13:1891–1898. https://doi.org/10.1038/s41396-019-0403-2

Bush DA, Horisberger M, Horman I, Wursch P (1974) The wall structure of *Schizosaccharomyces* pombe. Microbiology 81(1):199–206

Buzzini P, Lachance M-A, Yurkov A (2017) Yeasts in natural ecosystems: diversity. Elsevier, Amsterdam

Cabrales E, Lopez-Hernández D, Toro M (2019) Effect of inoculation with *Glomeromycota* fungi and fertilization on maize yield in acid soils. In: González-Andrés F, Ormeño-Orrillo E (eds) Microbial probiotics for agricultural systems. Springer, New York, pp205–212

Čadež N, Dlauchy D, Tome M, Péter G (2021) *Novakomyces olei* sp. nov., the first member of a novel *Taphrinomycotina* lineage. Microorganisms 9(2):301

Cai HL, Shimada M, Nakagawa T (2021) The potential and capability of the methylotrophic yeast *Ogataea methanolica* in a "methanol bioeconomy." Yeast 39:440–448. https://doi.org/10.1002/yea.3807

Calabon MS, Hyde KD, Jones EG, Luo ZL, Dong W, Hurdeal VG, Gentekaki E, Rossi W, Leonardi M, Thiyagaraja V, Lestari AS (2022) Freshwater fungal numbers. Fungal Divers 114(1):3–235. https://doi.org/10.1007/s13225-022-00503-2

Campo S, Martín-Cardoso H, Olivé M, Pla E, Catala-Forner MC, Eixarch MM, Segundo BS (2020) Effect of root colonization by arbuscular mycorrhizal fungi on growth, productivity and blast resistance in rice. Rice 13:42. https://doi.org/10.1186/s12284-020-00402-7

Cannon PF, Kirk PM (2007) Fungal families of the world. Wallingford, Oxfordshire. https://doi.org/10.1017/S0024282908009158

Cao C, Xi L, Chaturvedi V (2019) *Talaromycosis* (*Penicilliosis*) Due to *Talaromyces* (*Penicillium*) *marneffei*: insights into the clinical trends of a major fungal disease 60 years after the discovery of the pathogen. Mycopathologia 184:709–720. https://doi.org/10.1007/s11046-019-00410-2

Cao B, Haelewaters D, Power N, Begerow D, Boekhout T, GiachiniAJ GSP, Gunde-Cimerman N, Hyde KV, Kemler M, Li GJ, Liu DM, Liu XZ, Nuytinck J, Papp V, Savchenko A, Savchenko K, Tedersoo L, Theelen B, Thines M, Tomšovský M, Toome-Heller M, Urón JP, Verbeken A, Vizzini A, Yurkov AM, Zamora JC, Zhao RL (2021) Delimiting species in *Basidiomycota*: a review. Fungal Divers 109:181–237. https://doi.org/10.1007/s13225-021-00479-5

Cavalheiro GF, Costa AC, Garbin AP, Silva GA, Garcia NFL, Paz MF, Fonseca GG, Leite RSR (2023) Catalytic properties of amylases produced by *Cunninghamella echinulata* and *Rhizopus microspo*rus. An Acade Bras Ciênc 95(3):e20230187. https://doi.org/10.1590/0001-3765202320230187

Cavalier-Smith T (1998) A revised six-kingdom system of life. Biol Rev 73:203–266. https://doi.org/10.1017/s0006323198005167

Cavalier-Smith T (2013) Early evolution of eukaryote feeding modes, cell structural diversity, and classification of the protozoan phyla *Loukozoa*, *Sulcozoa*, and *Choanozoa*. Eur J Protistol 49(2):115–178

Cavallari LG, Fernandes AM, Mota LHSO, Leite HMF, Piroli VLB (2021) Growth and phosphorus uptake by cassava in P-deficient soil in response to mycorrhizal inoculation. Rev Bras Cienc Solo. https://doi.org/10.36783/18069657rbcs20210060

Cazabonne J, Bartrop L, Dierickx G, Gafforov Y, Hofmann TA, Martin TE, Piepenbring M, Rivas-Ferreiro M, Haelewaters D (2022) Molecular-based diversity studies and field surveys are not mutually exclusive: on the importance of integrated methodologies in mycological research. Front Fungal Biol 3:860777. https://doi.org/10.3389/ffunb.2022.860777

Celio GJ, Padamsee M, Dentinger BTM, Bauer R, McLaughlin DJ (2006) Assembling the fungal tree of life: constructing the structural and biochemical database. Mycologia 98:850–859. https://doi.org/10.3852/mycologia.98.6.850

Chambouvet A, Monier A, Maguire F, Itoïz S, Del Campo J, Elies P, Edvardsen B, Eikreim W, Richards TA (2019) Intracellular infection of diverse diatoms by an evolutionary distinct relative of the fungi. Curr Biol 29(23):4093–1401. https://doi.org/10.1016/j.cub.2019.09.074

Chamroensakchai T, Kleebchaiyaphum C, Tatiyanupanwong S, Eiam-Ong S, Kanjanabuch T (2021) *Tinea nigra* palmaris-associated peritonitis, caused by *Hortaea werneckii*: the first case report in a peritoneal dialysis patient. Perit Dial Int 41:333–336. https://doi.org/10.1177/0896860820944778

Chandran VA, Koka K, Therese L, Mukherjee B (2022) A rare fungal orbital infection in an immunocompetent young male caused by *Lichtheimia corymbifera* (*Absidia corymbifera*). Ocul Immunol Inflamm 30(7–8):1970–1973. https://doi.org/10.1080/09273948.2021.1909735

Chang Y, Wang S, Sekimoto S, Aerts AL, Choi C, Clum A, LaButti KM, Lindquist EA, Ngan CY, Ohm RA, Salamov AA, Grigoriev IV, Spatafora JW, Berbee ML (2015) Phylogenomic analyses indicate that early fungi evolved digesting cell walls of algal ancestors of land plants. Genome Biol Evol 7(6):1590–1601. https://doi.org/10.1093/gbe/evv090

Chang Y, Desirò A, Na H, Sandor L, Lipzen A, Clum A, Barry K, Grigoriev IV, Martin FM, Stajich JE, Smith ME (2019) Phylogenomics of *Endogonaceae* and evolution of mycorrhizas within *Mucoromycota*. New Phytol 222(1):511–525. https://doi.org/10.1111/nph.15613

Chang Y, Rochon DA, Sekimoto S, Wang Y, Chovatia M, Sandor L, Salamov A, Grigoriev LV, Stajich JE, Spatafora JW (2021) Genome-scale phylogenetic analyses confirm *Olpidium* as the closest living zoosporic fungus to the non-flagellated, terrestrial fungi. Sci Rep 11(1):321–327. https://doi.org/10.1038/s41598-021-82607-4

Chanyachailert P, Leeyaphan C, Bunyaratavej S, Chongtrakool P (2019) Subcutaneous phaeohyphomycosis from *Medicopsis romeroi* in a diabetic patient. Med Mycol Case Rep 26:69–72. https://doi.org/10.1016/j.mmcr.2019.07.006

Chanyachailert P, Leeyaphan C, Bunyaratavej S (2023) Cutaneous fungal infections caused by *Dermatophytes* and Non-*Dermatophytes*: an updated comprehensive review of epidemiology, clinical presentations, and diagnostic testing. J Fungi 9:669. https://doi.org/10.3390/jof9060669

Chen CJ, Oberwinkler F, Chen ZC (2001) Restudy of some type specimens of *Tremella* (I). Mycotaxon77:215–224. https://doi.org/10.1016/j.ympev.2011.05.014

Chen Z, Hu B, Hu S, Vogel-Mikuš K, Pongrac P, Vymazal J (2022) Immobilization of chromium enhanced by arbuscular mycorrhizal fungi in semi-aquatic habitats with biochar addition. J Hazard Mater. https://doi.org/10.1016/j.jhazmat.2022.129562

Chen DY, Long CL, He RJ, Dong RH, Jiang L (2023a) *Cetraspora huaxica*, a new species of *arbuscular mycorrhizal* fungi (*Glomeromycotina*) from Guiyang, China. Mycosystema 42(8):1661–1672

Chen YP, Su PW, Hyde KD, Maharachchikumbura SSN (2023b) Phylogenomics and diversification of *Sordariomycetes*. Mycosphere 14(1):414–451. https://doi.org/10.5943/mycosphere/14/1/5

Chenchouni H, Mekahlia MN, Beddiar A (2020) Effect of inoculation with native and commercial *Arbuscular mycorrhizal* fungi on growth and mycorrhizal colonization of olive (*Olea europaea* L.). Sci Horticult. https://doi.org/10.1016/j.scienta.2019.108969

Chethana KT, Jayawardena RS, Chen YJ, Konta S, Tibpromma S, Phukhamsakda C, Abeywickrama PD, Samarakoon MC, Senwanna C, Mapook A, Tang X (2021) Appressorial interactions with host and their evolution. Fungal Divers 110(1):75–107. https://doi.org/10.1007/s13225-021-00487-5

Chowdhary A, Sharada K, Singh PK, Bhagwani DK, Kumar N, de Groot T, Meis JF (2020) Outbreak of *Dirkmeia churashimaensis* fungemia in a neonatal intensive care unit, India. Emerg Infect Dis 26:764–768. https://doi.org/10.3201/eid2604.190847

Chuang SC, Ho HM, Benny GL, Lee CF (2013) Two new *Ramicandelaber* species from Taiwan. Mycologia 105(2):320–334. https://doi.org/10.3852/11-219

Chuang SC, Ho HM, Reynolds N, Smith ME, Benny GL, Chien CY, Tsai JL(2017) Preliminary phylogeny of *Coemansia* (*Kickxellales*), with descriptions of four new species from Taiwan. Mycologia 109(5):815–831. https://doi.org/10.1080/00275514.2017.1401892

Claudiu Chinan V, Hewitt D (2012) *Neolecta vitellina*, first record from Romania, with notes on habitat and phenology. Mycotaxon 118(1):197–201. https://doi.org/10.5248/118.197

Cole GT, Kendrick B (1981) Biology of conidial fungi, vol 1. Academic Press, New York, p 504

Cole GT, Samson RA (1979) Patterns of development in conidial fungi. Pitman Publ. Co., London

Comitini F, Canonico L, Agarbati A, Ciani M (2023) Biocontrol and probiotic function of non-*Saccharomyces* yeasts: new insights in agri-food industry. Microorg 11:1450. https://doi.org/10.3390/microorganisms11061450

Cooper CR (2011) Yeasts pathogenic to humans. In: Kurtzman CP, Fell JW, Boekhout T (eds) The yeasts: a taxonomic study. Elsevier, London, pp 1339–1372

Corazon-Guivin MA, Cerna-Mendoza A, Guerrero-Abad JC, Vallejos-Tapullima A, Rios-Ramires O, Vallejos-Torres G, Sota-Ricaldi AM, Santos VM, Silva GA, Oehl F (2020) *Paraglomus occidentale*, a new arbuscular mycorrhizal fungus from the sources of the Amazon river in Peru, with a key to the *Paraglomeromycetes* species. Sydowia 72:85–94

Corazon-Guivin MA, Vallejos-Tapullima A, Valles-Coral MÁ, Mendiola-Céspedes AR, Ascón-Dionicio GU, Corrêa RX, Oehl F (2023) *Viscospora peruviscosa*, a new fungus in the *Glomeraceae* from a plantation of *Theobroma cacao* in Peru. J Food Qual 96:117–122. https://doi.org/10.5073/JABFQ.2023.096.015

Cordier T, Robina C, Capdeviellea X, Desprez-Loustaua ML, Vachera C (2012) Spatial variability of phyllosphere fungal assemblages: genetic distance predominates over geographic distance in a European beech stand (*Fagus sylvatica*). Fungal Ecol 5:509–520. https://doi.org/10.1016/j.funeco.2011.12.004

Corsaro D, Walochnik J, Venditti D, Steinmann J, Müller KD, Michel R (2014) Microsporidia-like parasites of amoebae belong to the early fungal lineage *Rozellomycota*. Parasitol Res 113:1909–1918. https://doi.org/10.1007/s00436-014-3838-4

Corsaro D, Wylezich C, Venditti D, Michel R, Walochnik J, Wegensteiner R (2019) Filling gaps in the microsporidian tree: rDNA phylogeny of *Chytridiopsis typographi* (*Microsporidia*: *Chytridiopsida*). Parasitol Res 118:169–180. https://doi.org/10.1007/s00436-018-6130-1

Crous PW, Summerell BA, Carnegie AJ, Wingfield MJ, Hunter GC, Burgess TI, Andjic V, Barber PA, Groenewald J (2009) Unravelling *Mycosphaerella*: do you believe in genera? Persoonia 23:99–118. https://doi.org/10.3767/003158509X479487

Crous PW, Wingfield MJ, Burgess TI, Carnegie AJ, Hardy GESJ, Smith D, Summerell BA, Cano-Lira JF, Guarro J, Houbraken J, Lombard L, Martín MP, Sandoval-Denis M, Alexandrova AV, Barnes CW, Baseia IG, Bezerra JDP, Guarnaccia V, May TW, Hernández-Restrepo M, Stchigel AM, Miller AN, Ordoñez ME, Abreu VP, Accioly T, Agnello C, Agustin Colmán A, Albuquerque CC, Alfredo DS, Alvarado P, Araújo-Magalhães GR, Arauzo S, Atkinson T, Barili A, Barreto RW, Bezerra JL, Cabral TS, Camello Rodríguez F, Cruz RHSF, Daniëls PP, da Silva BDB, de Almeida DAC, de Carvalho Júnior AA, Decock CA, Delgat L, Denman S, Dimitrov RA, Edwards J, Fedosova AG, Ferreira RJ, Firmino AL, Flores JA, García D, Gené J, Giraldo A, Góis JS, Gomes AAM, Gonçalves CM, Gouliamova DE, Groenewald M, Guéorguiev BV, Guevara-Suarez M, Gusmão LFP, Hosaka K, Hubka V, Huhndorf SM, Jadan M, Jurjević Ž, Kraak B, Kučera V, Kumar TKA, Kušan I, Lacerda SR, Lamlertthon S, Lisboa WS, Loizides M, Luangsa-Ard JJ, Lysková P, Mac Cormack WP, Macedo DM, Machado AR, Malysheva EF, Marinho P, Matočec N, Meijer M, Mešić A, Mongkolsamrit S, Moreira KA, Morozova OV, Nair KU, Nakamura N, Noisripoom W, Olariaga I, Oliveira RJV, Paiva LM, Pawar P, Pereira OL, Peterson SW, Prieto M, Rodríguez-Andrade E, Rojo De Blas C, Roy M, Santos ES, Sharma R, Silva GA, Souza-Motta CM, Takeuchi-Kaneko Y, Tanaka C, Thakur A, Smith MT, Tkalčec Z, Valenzuela-Lopez N, van der Kleij P, Verbeken A, Viana MG, Wang XW, Groenewald JZ (2017) Fungal planet description sheets 625–715. Persoonia 39:270–467. https://doi.org/10.3767/persoonia.2017.39.11

Cruz-Lachica I, Marquez-Zequera I, Garcia-Estrada RS, Carrillo-Fasio JA, Leon-Felix J, Allende-Molar R (2015) First report of *Gilbertella persicaria* causing papaya fruit rot. Plant Dis 100(1):150812113038002. https://doi.org/10.1094/PDIS-05-15-0607-PDN

Czeczuga B (1980) Badania nad karotenoidami u grzybów. IX. *Dacrymycetaceae*. Acta Mycol 16:115–120

da Silva GA, Corazon-Guivin MA, de Assis DMA, Oehl F (2023) *Blaszkowskia*, a new genus in *Glomeraceae*. Mycol Prog 22:74. https://doi.org/10.1007/s11557-023-01919-z

Dai YC, Cui BK (2011) *Fomitiporia ellipsoidea* has the largest fruiting body among the fungi. Fungal Biol 115:813–814. https://doi.org/10.1016/j.funbio.2011.06.008

Dai YC, Yang ZL, Cui BK, Wu G, Yuan HS, Zhou LW, He SH, Ge ZW, Wu F, Wei YL, Yuan SJ (2021) Diversity and systematics of the important macrofungi in Chinese forests. Mycosystema 40(4):770–805

Daniel HM, Moons MC, Huret S, Vrancken G, De Vuyst L (2011) *Wickerhamomyces anomalus* in the sourdough microbial ecosystem. Antonie Van Leeuwenhoek 99:63–73. https://doi.org/10.1007/s10482-010-9517-2

Daniel HM, Lachance MA, Kurtzman CP (2014) On the reclassification of species assigned to *Candida* and other anamorphic ascomycetous yeast genera based on phylogenetic circumscription. Antonie Van Leeuwenhoek 106:67–84. https://doi.org/10.1007/s10482-014-0170-z

Das S, Dutta S, Barman AR (2017a) First report of leaf blight of papaya caused by *Choanephora cucurbitarum* in India. Indian J Plant Prot 45(4):393–395

Das S, Dutta S, Kuiry SP, Mandal B (2017b) First report of twig blight of green pea caused by *Choanephora infundibulifera* in India. Indian Phytopathol 70(3):400–402

Das S, Dutta S, Mandal B (2017c) First report on blossom and leaf blight of Aubergine (*Solanum melongena* L.) caused by *Choanephora infundibulifera* (Currey) Sacc., in India. J Mycol Plant Pathol 47(1):69–73

Dave R, Madamwar D (2010) Preparations for the use of *Candida rugosa* lipase in non-conventional solvents. Biocatal Biotransform 28(3):157–166. https://doi.org/10.3109/10242422.2010.489152

Davis WJ, Amses KR, Benny L, Carter-House D, Chang Y, Grigoriev I, Smith ME, Spatafora JW, Stajich JE, James TY (2019) Genome-scale phylogenetics reveals a monophyletic *Zoopagales* (*Zoopagomycota*, *Fungi*). Mole Phylogenet Evol 133:152–163. https://doi.org/10.1016/j.ympev.2019.01.006

Davison J, Moora M, Semchenko M, Adenan SB, Ahmed T, Akhmetzhanova AA, Anslan S (2021) Temperature and pH define the realized niche space of *arbuscular mycorrhizal* fungi. New Phytol 231(2):763–776. https://doi.org/10.1111/nph.17240

Dayarathne MC, Maharachchikumbura SSN, Jones EBG, Dong W, Devadatha B, Yang J, Ekanayaka AH, De Silva W, Sarma VV, Al-Sadi AM, Khongphinitbunjong K, Hyde KD, Zhao RL (2019) Phylogenetic revision of *Savoryellaceae* and evidence for its ranking as a subclass. Front Microbiol 10:840. https://doi.org/10.3389/fmicb.2019.00840

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 70:3711–3717. https://doi.org/10.1099/ijsem.0.004223

de Hoog GS (1974) The genera *Blastobotrys*, *Sporothrix*, *Calcarisporium* and *Calcarisporiella* gen. nov. Stud Mycol 7:1–84

de Hoog GS (1979) The taxonomic position of *Moniliella*, *Trichosporonoides* and *Hyalodendron*—an essay. Stud Mycol 19:81–90

de Hoog GS, Smith MTh (2004) Ribosomal gene phylogeny and species delimitation in *Geotrichum* and its teleomorphs. Stud Mycol 50:489–515

de Hoog GS, Guarro J, Gene´ J, Figueras MJ (2000) Atlas of clinical fungi, 2nd edn. Centraal bureauvo or Schimmel cultures/Universitat Rovirai Virgili, Utrecht/Reus

de Hoog GS, Gottlich E, Platas G, Genilloud O, Leotta G, van Brummelen J (2005) Evolution, taxonomy and ecology of the genus *Thelebolus* in Antarctica. Stud Mycol 51:33–76 de Hoog GS, Smith MT, 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 Hoog GS, Dukik K, Monod M, Packeu A, Stubbe D, Hendrickx M, Kupsch C, Stielow JB, Freeke J, Gräser Y(2017) Toward a novel multilocus phylogenetic taxonomy for the *Dermatophytes*. Mycopathologia 182:5–31. https://doi.org/10.1007/s11046-016-0073-9

de Hoog GS, Guarro J, Gené J, Ahmed S, Al-Hatmi AMS, Figueras MJ (2020) Atlas of clinical fungi, 4th edn. Foundation Atlas of Clinical Fungi, Hilversum

de la Providencia IE, de Souza FA, Fernandez F, Delmas NS, Declerck S (2005) *Arbuscular mycorrhizal* fungi reveal distinct patterns of anastomosis formation and hyphal healing mechanisms between different phylogenetic groups. New Phytol 165:261–271. https://doi.org/10.1111/j.1469-8137.2004.01236.x

de Menezes GCA, Godinho VM, Porto BA, Gonçalves VN, Rosa LH (2017) *Antarctomyces pellizariae* sp. nov., a new, endemic, blue, snow resident psychrophilic *ascomycete* fungus from Antarctica. Extremophiles 21:259–269. https://doi.org/10.1007/s00792-016-0895-x

de Mora JF, Valentín E, Herrero E, Sentandreu R (1990) Glycoprotein molecules in the walls of *Schizosaccharomyces pombe* wild-type cells and a morphologically altered mutant resistant to papulacandin B. Microbiology 136(11):2251–2259

de Souza FA, Dalpé Y, Declerck S, de la Providencia I, Séjalon-Delmas N (2005) Life history strategies in *Gigasporaceae*: insight from monoxenic culture. Springer, Berlin

de Vuyst L, Harth H, Van Kerrebroeck S, Leroy F (2016) Yeast diversity of sourdoughs and associated metabolic properties and functionalities. Int J Food Microbiol 239:26–34. https://doi.org/10.1016/j.ijfoodmicro.2016.07.018

Dee JM, Mollicone M, Longcore JE, Roberson RW, Berbee ML (2015) Cytology and molecular phylogenetics of *Monoblepharidomycetes* provide evidence for multiple independent origins of the hyphal habit in the Fungi. Mycologia 107(4):710–728. https://doi.org/10.3852/14-275

Degawa Y (2013) *Verrucocephalum*, a new nematophagous genus in the *Helicocephalidaceae* (*Zoopagales*). Mycoscience 55(2):144–148. https://doi.org/10.1016/j.myc.2013.07.002

Deja-Sikora E, Kowalczyk A, Trejgell A, Szmidt-Jaworska A, Baum C, Mercy L, Hrynkiewicz K (2020) Arbuscular mycorrhiza changes the impact of potato virus Y on growth and stress tolerance of *Solanum tuberosum* L. *in vitro*. Front Microbiol 10:2971. https://doi.org/10.3389/fmicb.2019.02971

Delanoë P, Delanoë M (1912) Sur les rapports des kystes de Carini du poumon des rats avec le *Trypanosoma lewisi*. CR Acad Sci (paris) 155:658–660

Denchev CM, Denchev TT (2014) Nomenclatural novelties. *Malasseziomycetes* Denchev & T. Denchev, class. nov. Index Fungorum Index Fungorum 145:1–1

Deng S, Tsui CK, Gerrits van den Ende AH, Yang LY, Najafzadeh MJ, Hamid Badali H, Ruoyu Li RY, Hagen F, Meis JF, Sun JF, Dolatabadi S, Papierok B, Weihua Pan W, de Hoog GS, Liao WQ (2015) Global spread of human chromoblastomycosis is driven by recombinant *Cladophialophora carrionii* and predominantly clonal *Fonsecaea* species. PLoS Negl Trop Dis 9:e0004004. https://doi.org/10.1371/journal.pntd.0004004

Desirò A, Faccio A, Kaech A, Bidartondo MI, Bonfante P (2014) *Endogone*, one of the oldest plantassociated fungi, host unique Mollicutes-related endobacteria. New Phytol 205:1464–1472. https://doi.org/10.1111/nph.13136

Desirò A, Rimington WR, Jacob A, Pol NV, Smith ME, Trappe JM, Bidartondo MI, Bonito G (2017) Multigene phylogeny of *Endogonales*, an early diverging lineage of fungi associated with plants. IMA Fungus 8:245–257. https://doi.org/10.5598/imafungus.2017.08.02.03

Dias B, Lopes M, Ramôa R, Pereira AS, Belo I (2021) *Candida tropicalis* as a promising oleaginous yeast for olive mill wastewater bioconversion. Energies 14(3):640. https://doi.org/10.3390/en14030640

Díaz-Escandón D, Tagirdzhanova G, Vanderpool D, Allen CCG, Aptroot A, Češka O, Hawksworth DL, Huereca A, Knudsen K, Kocourková J, Lücking R, Resl P, Spribille T (2022) Genome-level analyses resolve an ancient lineage of symbiotic *ascomycetes*. Curr Biol 32:5209–5218. https://doi.org/10.1016/j.cub.2022.11.014

Díaz-Valderrama JR, Nguyen HDT, Aime MC (2017) *Wallemia peruviensis* sp. nov., a new xerophilic fungus from an agricultural setting in South America. Extremophiles 21:1017–1025. https://doi.org/10.1007/s00792-017-0960-0

Dib I, Nidetzky B (2008) The stabilizing effects of immobilization in D-amino acid oxidase from *Trigonopsis variabilis*. BMC Biotechnol 8:72–83. https://doi.org/10.1186/1472-6750-8-72

Dickie IA, Alexander I, Lennon S, Öpik M, Selosse MA, van der Heijden MGA, Martin FM (2015) Evolving insights to understanding mycorrhizas. New Phytol 205:1369–1374. https://doi.org/10.1111/nph.13290

Diederich P, Lawrey JD, Sikaroodi M, van den Boom PPG, Ertz D (2012) *Briancoppinsia*, a new coelomycetous genus of *Arthoniaceae* (*Arthoniales*) for the lichenicolous *Phoma cytospora*, with a key to this and similar taxa. Fungal Divers 52:1–12. https://doi.org/10.1007/s13225-011-0105-1

Diederich P, Lawrey JD, Ertz D (2018) The 2018 classification and checklist of lichenicolous fungi, with 2000 non-lichenized, obligately lichenicolous taxa. Bryologist 121:340–425. https://doi.org/10.1639/0007-2745-121.3.340

Diederich P, Millanes AM, Wedin M, Lawrey JD (2022) Flora of lichenicolous fungi, *Basidiomycota*, vol 1. National Museum of Natural History, Luxembourg

Dilcher DL (1965) Epiphyllous fungi from Eocene deposits in western Tennessee, U.S.A. Palaeontogr Abt B 116:1–54

Dix NJ, Webster J (1995) Fungal ecology. University Press, Cambridge

Döbbeler P (1979) Untersuchungen an moosparasitischen *Pezizales* aus der Verwandtschaft von *Octospora*. Nova Hedwig 31:817–864

Domsch KH, Gams W, Anderson TH (1980) Compendium of soil fungi. Academic Press, London

Dotzler N, Krings M, Taylor TN, Agerer R (2006) Germination shields in *Scutellospora* (*Glomeromycota*: *Diversisporales*, *Gigasporaceae*) from the 400 million-year-old Rhynie chert. Mycol Prog 5:178–184. https://doi.org/10.1007/s11557-006-0511-z

Douglass AP, Offei B, Braun-Galleani S, Coughlan AY, Martos AAR, Ortiz-Merino RA, Byrne KP, Wolfe KH (2018) Population genomics shows no distinction between pathogenic *Candida krusei* and environmental *Pichia kudriavzevii*: one species, four names. PLoS Pathog 14(7):e1007138. https://doi.org/10.1371/journal.ppat.1007138

Doweld AB (2001) Prosyllabus tracheophytorum. In: Tentamen systematis plantarum vascularium (Tracheophyta). Geos, Moscow

Doweld AB (2013a) Nomenclatural novelties. Index Fungorum 42:1–1

Doweld AB (2013b) Nomenclatural novelties. Index Fungorum 45:1–1

Doweld AB (2013c) Nomenclatural novelties. Index Fungorum 43:1–1

Doweld AB (2014a) Nomenclatural novelties. Index Fungorum 49:1–1

Doweld AB (2014b) Nomenclatural novelties. Index Fungorum 92:1–1

Doweld AB (2014c) Nomenclatural novelties. Index Fungorum 87:1–1

Doweld AB (2014d) Nomenclatural novelties. Index Fungorum 69:1–1

Doweld AB (2014e) Nomenclatural novelties. Index Fungorum 57:1–1

Doweld AB (2014f) Nomenclatural novelties. Index Fungorum 46:1–1

Doweld AB (2014g) Nomenclatural novelties. Index Fungorum 74:1–1

Doweld AB (2014h) Nomenclatural novelties. Index Fungorum 90:1–1

Doweld AB (2014i) Nomenclatural novelties. Index Fungorum 59:1–1

Doweld AB (2014j) Nomenclatural novelties. Index Fungorum 73:1–1

Dranguet P, Cosio C, Faucheur SL, Peter DH, Loizeau JL, Ungureanu VGH, Slaveykova VI (2017) Biofilm compositin in the Olt River (*Romania*) reservoirs impacted by a chlor-alkali production plant. Environ Sci 175:1–11. https://doi.org/10.1039/C7EM00033B

Drechsler CE (1935) Some conidial *Phycomycetes* destructive to terricolous amoebae. Mycologia 27(1):6–4

Drechsler C (1937) Some hyphomycetes that prey on free-living terricolous nematodes. Mycologia 29:447–552

Du H, Bing J, Hu T, Ennis CL, Nobile CJ, Huang G (2020) *Candida auris*: epidemiology, biology, antifungal resistance, and virulence. PLoS Pathog 16:e1008921. https://doi.org/10.1371/journal.ppat.1008921

Duell EB, Cobb AB, Wilson GWT (2022) Effects of commercial *arbuscular mycorrhizal* inoculants on plant productivity and intra-radical colonization in native grassland: unintentional decoupling of a symbiosis? Plants 11:2276. https://doi.org/10.3390/plants11172276

Dukik K, Muñoz JF, Jiang Y, Feng PY, Sigler L, Stielow JB, Freeke J, Jamalian A, van den Ende BG, McEwen JG, Clay OK, Schwartz IS, Govender NP, Maphanga TG, Cuomo GA, Moreno LF, Kenyon C, Borman AM, de Hoog S (2017) Novel taxa of thermally dimorphic systemic pathogens in the *Ajellomycetaceae* (*Onygenales*). Mycoses 60:296–309. https://doi.org/10.1111/myc.12601

Dulf FV, Vodnar DC, Dulf E-H (2023) Solid-state fermentation with *Zygomycetes* fungi as a tool for biofortification of apple pomace with γ-linolenic acid, carotenoid pigments and phenolic antioxidants. Food Res Int 173(2):113448. https://doi.org/10.1016/j.foodres.2023.113448

Ebersberger I, de Matos SR, Kupczok A, Gube M, Kothe E, Voigt K, Von Haeseler A (2012) A consistent phylogenetic backbone for the fungi. Mol Biol Evol 29(5):1319–1334. https://doi.org/10.1093/molbev/msr285

Eckblad FE (1968) The genera of the operculate *Discomycetes*. A reevaluation of their taxonomy, phylogeny and nomenclature. Nytt Magasin for Botanikk 15:1–191

Eddy SR (2011) Accelerated profile HMM searches. PLoS Comput Biol 7(10):e1002195. https://doi.org/10.1371/journal.pcbi.1002195

Edman JC, Kovacs JA, Masur H, Santi DV, Elwood HJ, Sogin ML (1988) Ribosomal RNA sequence shows *Pneumocystis carinii* to be a member of the fungi. Nat 334:519–522. https://doi.org/10.1038/334519a0

Edwards WN (1922) An Eocene microthyriaceous fungus from Mull. Scotland Trans Br Mycol Soc 8:66–72

Edwards Molina JP, Paul PA, Amorim L, Silva LHCP, Siqueri FV, Borges EP, Campos HD, Nunes Junior J, Meyer MC, Martins MC, Balardin RS, Carlin VJ, Grigolli JFJ, Belufi LMdR, Godoy CV (2019) Meta-analysis of fungicide efficacy on soybean target spot and cost–benefit assessment. Plant Pathol 68:94–106. https://doi.org/10.1111/ppa.12925

Ekanayaka AH, Ariyawansa HA, Hyde KD, Jones EBG, Daranagama DA, Phillips AJL, Hongsanan S, Jayasiri SC, Zhao Q (2017) Discomycetes: the apothecial representatives of the phylum *Ascomycota*. Fungal Divers 87:237–298. https://doi.org/10.1007/s13225-017-0389-x

Ekanayaka AH, Hyde KD, Jones EBG, Zhao Q (2018) Taxonomy and phylogeny of operculate *Discomycetes*: *Pezizomycetes*. Fungal Divers 90:161–243. https://doi.org/10.1007/s13225-018-0402-z

Ekanayaka AH, Hyde KD, Gentekaki E, McKenzie EHC, Zhao Q, Bulgakov TS, Camporesi E (2019) Preliminary classification of *Leotiomycetes*. Mycosphere 10(1):310–489. https://doi.org/10.5943/mycosphere/10/1/7

El-Gazzar N, Almaary K, Ismail A, Polizzi G (2020) Influence of *Funneliformis mosseae* enhanced with titanium dioxide nanoparticles (TiO_2NPs) on *Phaseolus vulgaris* L. under salinity stress. PLoS ONE 15(12):e0243491

Elsik WC (1990) *Hypoxylonites* and *Spirotremesporites* form genera for Eocene to Pleistocene fungal spores bearing a single furrow. Palaeontogr Abt B 216(1–6):137–169

Engler A (1989) Syllabus der Pflanzenfamilien, 2nd edn. Gebruder Borntraeger, Berlin

Eriksson OE (1982) Notes on ascomycete systematics. Syst Ascomycetum 11:49–82

Eriksson OE (1994) *Pneumocystis carinii*, a parasite in lungs of mammals, referred to a new family and order (*Pneumocystidaceae*, *Pneumocystidales*, *Ascomycota*). Syst Ascomycetum 13:165–180

Eriksson OE (2005) Outline of *Ascomycota* 2005. Myconet 11:1–113

Eriksson OE, Hawksworth DL (1986) Notes on ascomycete systematics. Nos 1–224. Syst Ascomycetum 5:113–174

Eriksson O, Hawksworth DL (1993) Outline of the ascomycetes—1993. Syst Ascomycetum 12:1–257

Eriksson OE, Winka K (1997) Supraordinal taxa of *Ascomycota*. Myconet 1:1–16

Eriksson OE, Svedskog A, Landvik S (1993) Molecular evidence for the evolutionary hiatus between *Saccharomyces cerevisiae* and *Schizosaccharomyces pombe*. Syst Ascomycetum11:119–162

Eriksson OE, Baral HO, Currah RS, Hansen K, Kurtzman CP, Læssøe T, Rambold G (2003) Notes on *ascomycete* systematics Nos 3580–3623. Myconet 9:91–103

Ertz D, Tehler A (2011) The phylogeny of *Arthoniales* (*Pezizomycotina*) inferred from nucLSU and *RPB2* sequences. Fungal Divers 49:47–71. https://doi.org/10.1007/s13225-010-0080-y

Ertz D, Miadlikowska J, Lutzoni F, Dessein S, Raspé O, Vigneron N, Hofstetter V, Diederich P (2009) Towards a new classification of the *Arthoniales* (*Ascomycota*) based on a three-gene phylogeny focussing on the genus *Opegrapha*. Mycol Res 113:141–152. https://doi.org/10.1016/j.mycres.2008.09.002

Ertz D, Bungartz F, Diederich P, Tibell L (2011) Molecular and morphological data place *Blarneya* in *Tylophoron* (*Arthoniaceae*). Lichenologist 43:345–356. https://doi.org/10.1017/S002428291100020X

Ertz D, Lawrey JD, Common RS, Diederich P (2014) Molecular data resolve a new order of *Arthoniomycetes* sister to the primarily lichenized *Arthoniales* and composed of black yeasts, lichenicolous and rock-inhabiting species. Fungal Divers 66:113–137. https://doi.org/10.1007/s13225-013-0250-9

Ertz D, Tehler A, Irestedt M, Frisch A, Thor G, van den Boom P (2015) A large-scale phylogenetic revision of *Roccellaceae* (*Arthoniales*) reveals eight new genera. Fungal Divers 70:31–53. https://doi.org/10.1007/s13225-014-0286-5

Ezeilo UR, Wahab RA, Mahat NA (2019) Optimization studies on cellulase and xylanase production by *Rhizupos oryzae* UC2 using raw oil palm frond leaves as substrate under solid state fermentation. Renew Energy 156:1301–1312. https://doi.org/10.1016/j.renene.2019.11.149

Falcão EL, Silva FSB (2023) *Arbuscular mycorrhizal* fungi acting as biostimulants of proanthocyanidins accumulation—what is there to know? Rhizosphere 27:100762. https://doi.org/10.1016/j.rhisph.2023.100762

Fan T, Liu X, Zhao R, Zhang Y, Liu H, Wang Z, Wang F, Nie K, Deng L (2020) Hydrolysis of food waste by hot water extraction and subsequent *Rhizopus* fermentation to fumaric acid. J Environ Manag 270:110954. https://doi.org/10.1016/j.jenvman.2020.110954

Field KJ, Pressel S, Duckett JG, Rimington WR, Bidartondo MI (2015) Symbiotic options for the conquest of land. Trends Ecol Evol 30:477–486. https://doi.org/10.1016/j.tree.2015.05.007

Fitzpatrick HM (1930) The lower fungi phycomycetes. McGraw-Hill, New York

Floudas D, Binder M, Riley R, Barry K, Blanchette RA, Henrissat B, Martínez AT, Otillar R, Spatafora JW, Ydav JS, Aerts A, Benoit I, Boyd A, Carlson A, Copeland A, Coutinho PM, de Vries RP, Ferreira P, Findley K, Boster F, Gaskell J, Glotzer D, Górecki P, Heitman J, Hesse C, Hori C, Igarashi K, Jurgens JA, Kallen N, Kersten P, Kohler A, Kües U, Arun Kumar TK, Kuo A, Labutti K, Larrondo LF, Lindquist E, Ling A, Lombard V, Lucas S, Lundell T, Martin R, Mclaughlin DJ, Morgenstern I, Morin E, Murat C, Nagy LG, Nolan M, Ohm RA, Patyshakuliyeva A, Rokas A, Ruiz-dueñas FJ, Sabat J, Salamov S, Samejima A, Schmutz A, Slot JC, John FS, Stenlid J, Sun H, Sun S, Syed K, Tsang A, Wiebenga A, Young D, Pisabarro A, Eastwood DC, Martin F, Cullen D, Grigoriev IV, Hibbett SD (2012) The Paleozoic origin of enzymatic lignin decomposition reconstructed from 31 fungal genomes. Science 336:1715–1719. https://doi.org/10.1126/science.1221748

Fonseca Á, Rodrigues MG (2011) *Taphrina* fries (1832). In: Kurtzma, CP, Fell JW, Boekhout T (eds) The yeasts A taxonomic study, 5th edn. Elsevier Amsterdam, pp 823–858

Fonseca Á, Sampaio JP, Inácio J, Fell JW (2000) Emendation of the basidiomycetous yeast genus *Kondoa* and the description of *Kondoa aeria* sp. nov. Antonie Van Leeuwenhoek 77:293–302

Francisco EC, de Jong AW, Colombo AL (2023) *Candida haemulonii* species complex: a mini-review. Mycopathol. https://doi.org/10.1007/s11046-023-00748-8

Freimoser FM, Rueda-Mejia MP, Tilocca B, Migheli Q (2019) Biocontrol yeasts: mechanisms and applications. World J Microbiol Biotechnol 35:154. https://doi.org/10.1007/s11274-019-2728-4

Fries EM (1815) Observationes mycologicae. 1:1–230 Mix, A.J. 1949. A monograph of the genus *Taphrina*. University of Kansas Science Bulletin 33:1–167

Frisch A, Thor G, Ertz D, Grube M (2014) The *Arthonialean* challenge: restructuring *Arthoniaceae*. Taxon 63:727–744

Frisch A, Ohmura Y, Ertz D, Thor G (2015) *Inoderma* and related genera in *Arthoniaceae* with elevated white pruinose pycnidia or sporodochia. Lichenologist 47:233–256. https://doi.org/10.1017/S0024282915000201

Galindo LJ, Torruella G, Moreira D, Timpano H, Paskerova G, Smirnov A, Nassonova E, López-García P (2018) Evolutionary genomics of *Metchnikovella incurvata* (*Metchnikovellidae*): an early branching microsporidium. Genome Biol Evol 10(10):2736–2748. https://doi.org/10.1093/gbe/evy205

Galindo LJ, López-García P, Torruella G, Karpov S, Moreira D (2021) Phylogenomics of a new fungal phylum reveals multiple waves of reductive evolution across *Holomycota*. Nat Commun 12(4973):1–14. https://doi.org/10.1038/s41467-021-25308-w

Galindo LJ, Torruella G, Lopez-Garcia P, Ciobanu M, Gutierrez-Preciado A, Karpov SA, Moreira D (2022) Phylogenomics supports the monophyly of aphelids and fungi and identifies new molecular synapomorphies. Syst Biol. https://doi.org/10.1093/sysbio/syac054

Gams W (1977) A key to the species of *Mortierella*. Persoonia 9:381–391

Gargas A, Taylor JW (1995) Phylogeny of the discomycetes and early radiations of the apothecial ascomycotina inferred from SSU rDNA sequence data. Exp Mycol 19:7–15. https://doi.org/10.1006/emyc.1995.1002

Garnault M, Duplaix C, Leroux P, Couleaud G, Carpentier F, David O, Walker AS (2019) Spatiotemporal dynamics of fungicide resistance in the wheat pathogen *Zymoseptoria tritici* in France. Pest Manag Sci 75:1794–1807. https://doi.org/10.1002/ps.5360

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. https://doi.org/10.1371/journal.pone.0149531

Gazis R, Miadlikowska J, Lutzoni F, Arnold AE, Chaverri P (2012) Culture-based study of endophytes associated with rubber trees in Peru reveals a new class of *Pezizomycotina*: *Xylonomycetes*. Mol Phylogenet Evol 65(1):294–304. https://doi.org/10.1016/j.ympev.2012.06.019

Geiser DM, LoBuglio KL (2001) The monophyletic *Plectomycetes*: *Ascosphaerales*, *Onygenales*, *Eurotiales*. In: McLaughlin DJ, McLaughlin EG, Lemke PA (eds) The mycota: systematics and evolution. Springer, Berlin, pp 201–220

Geiser DM, Gueidan C, Miadlikowska J, Lutzoni F, Kauff F, Hofstetter V, Fraker E, Schoch CL, Tibell L, Untereiner WA, Aptroot A (2006) *Eurotiomycetes*: *Eurotiomycetidae* and *Chaetothyriomycetidae*. Mycologia 98:1053–1064. https://doi.org/10.3852/mycologia.98.6.1053

Gernandt DS, Platt JL, Stone JK, Spatafora JW, Holst-Jensen A, Hamelin RC, Kohn LM (2001) Phylogenetics of *Helotiales* and *Rhytismatales* based on partial small subunit nuclear ribosomal DNA sequences. Mycologia 93(5):915–933

Gibson B, Geertman J-MA, Hittinger CT, Krogerus K, Libkind D, Louis EJ, Magalhães F, Sampaio JP (2017) New yeasts—new brews: modern approaches to brewing yeast design and development. FEMS Yeast Res 17:fox038. https://doi.org/10.1093/femsyr/fox038

Giordani P (2019) Lichen diversity and biomonitoring: a special issue. Diversity 11(9):171. https://doi.org/10.3390/d11090171

Gładkowski W, Mazur M, Białońska A, Wawrzeńczyk C (2011) Lactones 35 [1]. Metabolism of iodolactones with cyclohexane ring in *Absidia cylindrospora* culture. Enzym Microb Technol 48:326–333. https://doi.org/10.1016/j.enzmictec.2010.12.007

Goldmann L, Weir A (2018) Molecular phylogeny of the *Laboulbeniomycetes* (*Ascomycota*). Fungal Biol 122(2–3):87–100. https://doi.org/10.1016/j.funbio.2017.11.004

Gomes SR, Queiroz MB, Leroy JA, Lima JL, Freire FA, Jobim K, Souza FA, Goto BT (2022) Richness of arbuscular mycorrhizal fungi in a Brazilian tropical shallow lake: assessing an unexpected assembly in the aquatic-terrestrial gradient. Diversity 14(12):1046. https://doi.org/10.3390/d14121046

Gonzalez R, Morales P (2022) Truth in wine yeast. Microb. Biotechnol 15:1339–1356. https://doi.org/10.1111/1751-7915.13848

Gooday GW (1968) Hormonal control of sexual reproduction in *Mucor mucedo*. New Phytol 67:815–821. https://doi.org/10.1111/j.1469-8137.1968.tb06397.x

Goodwin TW (1953) Studies in carotenogenesis 8. The carotenoids present in the *basidiomycete Dacryomyces stillatus*. Biochem J 53:538–540. https://doi.org/10.1042/bj0530538

Grimm M, Grube M, Schiefelbein U, Zühlke D, Bernhardt J, Riedel K (2021) The lichens' microbiota, still a mystery? Front Microbiol 12:623839. https://doi.org/10.3389/fmicb.2021.623839

Groenewald M, Boekhout T, Neuvéglise C, Gaillardin C, van Dijck PWM, Wyss M (2014) *Yarrowia lipolytica*: safety assessment of an oleaginous yeast with a great industrial potential. Crit Rev Microbiol 40:187–206. https://doi.org/10.3109/1040841X.2013.770386

Groenewald M, Hittinger CT, Bensch K, Opulente DA, Shen XX, Li Y, Liu C, LaBella AL, Zhou X, Limtong S, Jindamorakot S, Gonçalves P, Robert V, Wolfe KH, Rosa CA, Boekhout T, Čadež N, Péter G, Sampaio JP, Lachance MA, Yurkov AM, Daniel HM, Takashima M, Boundy-Mills K, Libkind D, Aoki K, Sugita T, Rokas A (2023) A genome-informed higher rank classification of the biotechnologically important fungal subphylum *Saccharomycotina*. Stud Mycol 105:1–22. https://doi.org/10.3114/sim.2023.105.01

Gromov BV (2000) Algal parasites of the genera *Aphelidium*, *Amoeboaphelidium* and *Pseudoaphelidium* from the Cienkovski's '"Monadea"' group as representatives of a new class. Zool Zh 79:517–525 in Russian

Gruninger RJ, Puniya AK, Callaghan TM, Edwards JE, Youssef N, Dagar SS, Fliegerova K, Griffith GW, Forster R, Tsang A, McAllister T (2014) Anaerobic fungi (phylum

Neocallimastigomycota): advances in understanding their taxonomy, life cycle, ecology, role and biotechnological potential. FEMS Microbiol Ecol 90(1):1–7. https://doi.org/10.1111/1574-6941.12383

Gryganskyi AP, Humber RA, Smith ME, Hodge K, Huang B, Voigt K, Vilgalys R (2013) Phylogenetic lineages in *Entomophthoromycota*. Persoonia 30(1):94–105. https://doi.org/10.3767/003158513X666330

Gryganskyi AP, Nie Y, Hajek AE, Hodge KT, Liu XY, Aadland K, Voigt K, Anishchenko IM, Kutovenko VB, Kava L, Vuek A (2022) The early terrestrial fungal lineage of *Conidiobolus*—transition from saprotroph to parasitic lifestyle. J Fungi 8(8):789

Guarro J, Genéj SAM (1999) Developments in fungal taxonomy. Clin Microbiol Rev 12(3):454–500. https://doi.org/10.1128/CMR.12.3.454

Gueidan C, Villaseñor CR, De Hoog GS, Gorbushina AA, Untereiner WA, Lutzoni F (2008) A rock-inhabiting ancestor for mutualistic and pathogen-rich fungal lineages. Stud Mycol 61(1):111–119

Gueidan C, Ruibal C, De Hoog GS, Schneider H (2011) Rock-inhabiting fungi originated during periods of dry climate in the late Devonian and middle Triassic. Fungal Biol 115(10):987–996. https://doi.org/10.1016/j.funbio.2011.04.002

Gueidan C, Aptroot A, da Silva Cáceres ME, Badali H, Stenroos S (2014) A reappraisal of orders and families within the subclass *Chaetothyriomycetidae* (*Eurotiomycetes*, *Ascomycota*). Mycol Prog 13:1027–1039. https://doi.org/10.1007/s11557-014-0990-2

Gugnani HC (2022) *Ustilaginales* (Smut fungi) and their role in causing human infections, an update. Eur J Med Health Sci 4(2):64–69

Gupta AK, Batra R, Bluhm R, Boekhout T, Dawson TL (2004) Skin diseases associated with *Malassezia* species. J Am Acad Dermatol 51:785–798. https://doi.org/10.1016/j.jaad.2003.12.034

Gupta MK, Selvaraj S, Tilak R, Kumar N, Kumar R, Chakravarty J (2023) *Rhizopus homothallicus* rhino-orbital-cerebral mucormycosis: six cases from a tertiary care Centre, North India. Tropical Med Int Health 28(2):144–150

Haag KL, James TY, Pombert JF, Larsson R, Schaer TM, Refardt D, Ebert D (2014) Evolution of a morphological novelty occurred before genome compaction in a lineage of extreme parasites. Proc Natl Acad Sci USA 111(43):15480–15485. https://doi.org/10.1073/pnas.14104421

Habibi A, Banihashemi Z (2017) Dating divergence of *Polystigma* and other *Sordariomycetes*. Mycol Iranica 4(1):29–37

Haelewaters D, Zhao SY, De Kesel A, Handlin RE, Royer IR, Farrell BD, Pfister DH (2015) *Laboulbeniales* (*Ascomycota*) of the Boston Harbor Islands I: species parasitizing *Coccinellidae* and *Staphylinidae*, with comments on typification. Northeast Nat 22(3):459–477

Haelewaters D, Pfliegler WP, Gorczak M, Pfister DH (2019) Birth of an order: comprehensive molecular phylogenetic study excludes *Herpomyces* (*Fungi*, *Laboulbeniomycetes*) from *Laboulbeniales*. Mol Phylogenet Evol 133:286–301. https://doi.org/10.1016/j.ympev.2019.01.007

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, Power 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

Haelewaters D, Blackwell M, Pfister DH (2021a) *Laboulbeniomycetes*: intimate fungal associates of arthropods. Annu Rev Entomol 66:257–276. https://doi.org/10.1146/annurev-ento-013020-013553

Haelewaters D, Gorczak M, Kaishian P, DeKesel A, Blackwell M (2021b) *Laboulbeniomycetes*, enigmatic fungi with a turbulent taxonomic history. In: Zaragoza O, Casadevall A (eds) Encyclopedia of mycology, vol 1. Elsevier, Amsterdam, pp 263–283

Haelewaters D, Park D, Johnston PR (2021c) Multilocus phylogenetic analysis reveals that *Cyttariales* is a synonym of *Helotiales*. Mycol Prog 20(10):1323–1330. https://doi.org/10.1007/s11557-021-01736-2

Haelewaters D, Peterson RA, Nevalainen H, Aime MC (2021d) *Inopinafdgtum lactosum* gen & comb nov, the first yeast-like fungus in *Leotiomycetes*. Int J Syst Evol Microbiol 71(7):4862

Haelewaters D, Power N, Medina-van Berkum P, Martin TE, Verbeken A, Aime MC (2021e) Pioneering a fungal inventory at Cusuco National Park, Honduras. J Mesoam Biol 1(1):111–131

Hafellner J (1988) Principles of classification and main taxonomic groups. In: Galun M (ed) CRC handbook of lichenology, vol 3. CRC Press, Boca Raton, pp 41–52

Hagedorn G, Scholler M (1999) A reevaluation of predatory orbiliaceous fungi. I. Phylogenetic analysis using rDNA sequence data. Sydowia 51:27–48

Hahn RC, Hagen F, Mendes RP, Burger E, Nery AF, Siqueira NP, Guevara A, Rodrigues AM, de Camargo ZP (2022) Paracoccidioidomycosis: current status and future trends. Clin Microbiol Rev 35:e0023321. https://doi.org/10.1128/cmr.00233-21

Haïssam JM (2011) *Pichia anomala* in biocontrol for apples: 20 years of fundamental research and practical applications. Antonie Van Leeuwenhoek 99(1):93–105. https://doi.org/10.1007/s10482-010-9541-2

Hall TA (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucleic Acids Symp Ser 41(1):95–98

Hanafy RA, Dagar SS, Griffith GW, Pratt CJ, Youssef NH, Elshahed MS (2022) Taxonomy of the anaerobic gut fungi (*Neocallimastigomycota*): a review of classification criteria and description of current taxa. Int J Syst Evol Microbiol 72(7):005322. https://doi.org/10.1099/ijsem.0.005322

Hanhela R, Louhelainen K, Pasanen A (1995) Prevalence of microfungi in Finnish cow barns and some aspectsof the occurrence of *Wallemia sebi* and Fusaria. Sc J Work Environ Health 21:223–228. https://doi.org/10.5271/sjweh.31

Hansen K, Pfister DH (2006) Systematics of the *Pezizomycetes*-the operculate *discomycetes*. Mycologia 98:1029–1040. https://doi.org/10.3852/mycologia.98.6.1029

Hansen K, Perry BA, Dranginis AW, Pfister DH (2013) A phylogeny of the highly diverse cup-fungus family *Pyronemataceae* (*Pezizomycetes*, *Ascomycota*) clarifies relationships and evolution of selected life history traits. Mol Phylogenet Evol 67(2):311–335. https://doi.org/10.1016/j.ympev.2013.01.014

Haque MMU, Rahman MA, Ador MAH, Ahmed R (2023) First report of *Rhizopus stolonifer* causing premature soft rot of jackfruit in Bangladesh. Plant Dis 107(9):2843. https://doi.org/10.1094/PDIS-01-23-0056-PDN

Harada M, Yasuda K, Uruchida K, Yamashita R, Morikawa K, Ito Y, Mochizuki E, Matsuura S, Tsukui M, Koshimizu N (2023) An autopsy case of disseminated *Cunninghamella bertholletiae* infection in an immunocompetent patient: a case report. BMC Pulm Med 23:88. https://doi.org/10.1186/s12890-023-02382-y

Haridas S, Albert R, Binder M, Bloem J, LaButti K, Salamov A, Andreopoulos B, Baker SE, Barry K, Bills G, Bluhm BH, Cannon C, Castanera R, Culley DE, Daum C, Ezra D, González JB, Henrissat B, Kuo A, Liang C, Lipzen A, Lutzoni F, Magnuson J, Mondo SJ, Nolan M, Ohm RA, Pangilinan J, Park HJ, Ramírez L, Alfaro M, Sun H, Tritt A, Yoshinaga Y, Zwiers LH, Turgeon BG, Goodwin SB, Spatafora JW, Crous PW, Grigoriev IV (2020) 101 *Dothideomycetes* genomes: a test case for predicting lifestyles and emergence of pathogens. Stud Mycol 96:141–153. https://doi.org/10.1016/j.simyco.2020.01.003

Harper CJ, Walker C, Schwendemann AB, Kerp H, Krings M (2020) *Archaeosporites rhyniensis* gen. et sp. nov. (*Glomeromycota*, *Archaeosporaceae*) from the Lower Devonian Rhynie chert: a fungal lineage morphologically unchanged for more than 400 million years. Ann of Bot 126:915–928. https://doi.org/10.1093/aob/mcaa113

Hashimoto A, Masumoto H, Endoh R, Degawa Y, Ohkuma M (2021) Revision of *Xylonaceae* (*Xylonales*, *Xylonomycetes*) to include Sarea and Tromera. Mycoscience 62(1):47–63

Hawksworth DL, Eriksson OE (1986) The names of accepted orders of *Ascomycetes*. Systema Ascomycetum 5:175–184

Hawksworth DL, Lücking R (2017) Fungal diversity revisited: 2.2 to 3.8 million species. Microbiol Spectr. https://doi.org/10.1128/microbiolspec.FUNK-0052-2016

Hawksworth DL, Crous PW, Redhead SA, Reynolds DR, Samson RA, Seifert KA, Taylor JW, Wingfield MJ, Abaci O, Aime C, Asan A, Bai FY, de Beer ZW, Begerow D, Berikten D, Boekhout T, Buchanan PK, Burgess T, Buzina W, Cai L, Cannon PF, Crane JL, Damm U, Daniel HM, van Diepeningen AD, Druzhinina I, Dyer PS, Eberhardt U, Fell JW, Frisvad JC, Geiser DM, Geml J, Glienke C, Gräfenhan T, Groenewald JZ, Groenewald M, de Gruyter J, Guého-Kellermann E, Guo LD, Hibbett DS, Hong SB, de Hoog GS, Houbraken J, Huhndorf SM, Hyde KD, Ismail A, Johnston RP, Kadaifciler DG, Kirk PM, Kõljalg U, Kurtzman CP, Lagneau PE, Lévesque CA, Liu XZ, Lombard L, Meyer W, Miller A, Minter DW, Najafzadeh MJ, Norvell L, Ozerskaya SM, Öziç R, Pennycook SR, Peterson SW, Pettersson OV, Quaedvlieg W, Robert VA, Ruibal C, Schnürer J, Schroers HJ, Shivas R, Slippers B, Spierenburg H, Takashima M, Taşkoin E, Thines M, Thrane U, Uztan AH, van Raak M, Varga J, Vasco A, Verkley G, Videira SIR, de Vries RP, Weir BS, Yilmaz N, Yurkov A, Zhang N (2011) The amsterdam declaration on fungal nomenclature. IMA Fungus 2(1):105–112. https://doi.org/10.5598/imafungus.2011.02.01.14

Hayova VP, Tykhonenko YY (2017) The first records of *Bartheletia paradoxa* (*Bartheletiomycetes*, *agaricomycotina*) in Ukraine. Ukr Bot J 74(6):578–581

He MQ, Zhao RL, Hyde KD, Begerow D, Kemler M, Yurkov A, McKenzie EHC, Raspé O, Kakishima M, Sánchez-Ramírez S, Vellinga EC, Halling R, Papp V, Zmitrovich IV, Buyck B, Ertz D, Wijayawardene NN, Cui BK, Power N, Liu XZ, Li TH, Yao YJ, Zhu XY, Liu AQ, Li GJ, Zhang MZ, Ling ZL, Cao B, Antonín V, Boekhout T, da Silva BDB, De Crop E, Decock C, Dima B, Dutta AK, Fell JW, Geml J, Ghobad-Nejhad MG, Giachini AJ, Gibertoni TB, Gorjón SP, Haelewaters D, He SH, Hodkinson BP, Horak E, Hoshino T, Justo A, Lim YW, Menolli JN, Mešić A, Moncalvo JM, Mueller GM, Nagy LG, Nilsson RH, Noordeloos M, Nuytinck J, Orihara T, Ratchadawan C, Rajchenberg M, Silva-Filho AGS, Sulzbacher MA, Tkalčec Z, Valenzuela R, Verbeken A, Vizzini A, Wartchow F, Wei TZ, Wei M, Zhao CL, Kirk PM (2019) Notes, outline and divergence times of *Basidiomycota*. Fungal Divers 99:105–367. https://doi.org/10.1007/s13225-019-00435-4

He MQ, Zhao RL, Liu DM, Denchev TT, Begerow D, Yurkov A, Kemler M, Millanes AM, Wedin M, McTaggart AR, Shivas RG (2022a) Species Diversity of *Basidiomycota* 114(1):281–325. https://doi.org/10.1007/s13225-021-00497-3

He MQ, Wang MQ, Chen ZH, Deng WQ, Li TH, Vizzini A, Jeewon R, HydeKD ZRL (2022b) Potential benefits and harms: a review of poisonous mushrooms in the world. Fungal Biol Rev 42:56–68. https://doi.org/10.1016/j.fbr.2022.06.002

He MQ, Cao B, Liu F, Boekhout T, Denchev TT, Power N, Denchev CM, Kemler M, Gorjón SP, Begerow D, Valenzuela R, Davoodian N, Niskanen T, Vizzini A, Redhead SA, Ramírez-Cruz V, Papp V, Dudka VA, Dutta AK, García-Sandoval R, Liu XZ, Kijpornyongpan T, Savchenko A, Tedersoo L, Theelen B, Trierveiler-Pereira L, Wu F, Zamora JC, Zeng XY, Zhou LW, Liu SL, Ghobad-Nejhad M, Giachini AJ, Li GJ, Kakishima M, Olariaga I, Haelewaters D, Sulistyo B, Sugiyama J, Svantesson S, Yurkov A, Alvarado P, Antonín V, da Silva AF, Druzhinina I, Gibertoni TB, Guzmán-Dávalos L, Justo A, Karunarathna SC, Galappaththi MCA, Toome-Heller M, Hosoya T, Liimatainen K, Márquez R, Mešić A, Moncalvo JM, Nagy LC, Varga T, Orihara T, Raymundo T, Salcedo I, Silva-Filho AGS, Tkalčec Z, Wartchow F, Zhao CL, Bau T, Cabarroi-Hernández M, Cortés-Pérez A, Decock C, De Lange R, Weiss M, Menolli N, Nilsson RH, Fan YG, Verbeken A, Gafforov Y, Meiras-Ottoni A, Mendes-Alvarenga RL, Zeng NK, Wu Q, Hyde KD, Kirk PM, Zhao RL (2024) Phylogenomics, divergence times and notes of orders in *Basidiomycota*. Fungal Divers. https://doi.org/10.1007/s13225-024-00535-W

Healy R, Pfister DH, Rossman AY, Ludmila M, Hansen K (2016) Competing sexual-asexual generic names of *Pezizomycetes* and recommendations for use. IMA Fungus 7:285–288. https://doi.org/10.5598/imafungus.2016.07.02.08

Healy RA, Arnold AE, Bonito G, Huang YL, Lemmond B, Pfister DH, Smith ME (2021) Endophytism and endolichenism in *Pezizomycetes*: the exception or the rule? New Phytol 233:1974–1983. https://doi.org/10.1111/nph.17886

Hernández-Restrepo M, Gené J, Castañeda-Ruiz RF, Mena-Portales J, Crous PW, Guarro J (2017) Phylogeny of saprobic microfungi from Southern Europe. Stud Mycol 86(1):53–97. https://doi.org/10.1016/j.simyco.2017.05.002

Hesseltine CW (1965) A millennium of fungi, food, and fermentation. Mycologia 57:149–197. https://doi.org/10.2307/3756821

Hesseltine CW (1983) Microbiology of oriental fermented foods. Annu Rev Microbiol 37:575–601. https://doi.org/10.1146/annurev.mi.37.100183.003043

Hibbett DS, Donoghue MJ (1998) Integrating phylogenetic analysis and classification in fungi. Mycologia 90:347–356

Hibbett DS, Binder M, Bischoff JF, Blackwell M, Cannon PF, Eriksson OE, Huhndorf S, James T, Kirk PM, Lücking R, Lumbsch HT, Lutzoni F, Matheny PB, McLaughlin DJ, Powell MJ, Redhead S, Schoch CL, Spatafora JW, Stalpers JA, Vilgalys R, Aime MC, Aptroot A, Bauer R, Begerow D, Benny G, Castlebury LA, Crous PW, Dai YC, Gams W, Geiser DM, Griffith GW, Gueidan C, Hawksworth DL, Hestmark G, Hosaka K, Humber RA, Hyde KD, Ironside JE, Kõljalg U, Kurtzman CP, Larsson KH, Lichtwardt R, Longcore J, Miądlikowska J, Miller A, Moncalvo JM, Mozley-Standridge S, Oberwinkler F, Parmasto E, Reeb V, Rogers JD, Roux C, Ryvarden L, ampaio JP, Schüßler A, Sugiyama J, Thorn RG, Tibell L, Untereiner WA, Walker C, Wang Z, Weir A, Weiss M, White MM, Winka K, Yao YJ, Zhang N (2007) A higher level phylogenetic classification of the fungi. Mycol Res 111(5):509–547. https://doi.org/10.1016/j.mycres.2007.03.004

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, vol 7A. Springer, Berlin

Hibbett DS, Blackwell M, James TY, Spatafora JW, Taylor JW, Vilgalys R (2018) Phylogenetic taxon definitions for *Fungi, Dikarya, Ascomycota and Basidiomycota*. IMA Fungus 9:291–298. https://doi.org/10.5598/imafungus.2018.09.02.05

Hirose D, Degawa Y, Inaba S, Tokumasu S (2012) The anamorphic genus *Calcarisporiella* is a new member of the *Mucoromycotina*. Mycoscience 53(4):256–260

Hittinger CT, Rokas A, Bai FY, Boekhout T, Gonçalves P, Jeffries TW, Kominek J, Lachance MA, Libkind D, Rosa CA, Sampaio JP, Kurtzman CP (2015) Genomics and the making of yeast biodiversity. Curr Opin Genet Dev 35:100–109. https://doi.org/10.1016/j.gde.2015.10.008

Hoang DT, Chernomor O, von Haeseler A, Minh BQ, Vinh LS (2018) UFBoot2: improving the ultrafast bootstrap approximation. Mol Biol Evol 35(2):518–522. https://doi.org/10.1093/molbev/msx281

Hobbie EA, Weber NS, Trappe JM (2001) Mycorrhizal vs saprotrophic status of fungi: the isotopic evidence. New Phytol 150:601–610. https://doi.org/10.1046/j.1469-8137.2001.00134.x

Hoffmann K, Voigt K, Kirk PM (2011) *Mortierellomycotina* subphyl. nov., based on multi-gene genealogies. Mycotaxon 115:353–363. https://doi.org/10.5248/115.353

Hoffmann K, Pawłowska J, Walther G, Wrzosek M, de Hoog GS, Benny GL, Kirk PM, Voigt K (2013) The family structure of the *Mucorales*: a synoptic revision based on comprehensive multigene-genealogies. Persoonia 30(1):57–76. https://doi.org/10.3767/003158513X666259

Hongsanan S, Maharachchikumbura SS, Hyde KD, Samarakoon MC, Jeewon R, Zhao Q, Al-Sadi AM, Bahkali AH (2017) An updated phylogeny of *Sordariomycetes* based on phylogenetic and molecular clock evidence. Fungal Divers 84:25–41. https://doi.org/10.1007/s13225-017-0384-2

Hongsanan S, Hyde KD, Phookamsak R, Wanasinghe DN, McKenzie EHC, Sarma VV, Boonmee S, Lücking R, Bhat DJ, Liu NG, Tennakoon DS, Pem D, Karunarathna A, Jiang SH, Jones EBG, Phillips AJL, Manawasinghe IS, Tibpromma S, Jayasiri SC, Sandamali D, Jayawardena RS, Wijayawardene NN, Ekanayaka AH, Jeewon R, Lu YZ, Dissanayake AJ, Zeng XY, Luo ZL, Tian Q, Phukhamsakda C, Thambugala KM, Dai DQ, Chethana KWT, Samarakoon MC, Ertz D, Bao DF, Doilom M, Liu JK, Pérez-Ortega S, Suija A, Senwanna C, Wijesinghe SN, Konta S, Niranjan M, Zhang SN, Ariyawansa HA, Jiang HB, Zhang JF, Norphanphoun C, de Silva NI, Thiyagaraja V, Zhang H, Bezerra JDP, Miranda-González R, Aptroot A, Kashiwadani H, Harishchandra D, Sérusiaux E, Aluthmuhandiram JVS, Abeywickrama PD, Devadatha B, Wu HX, Moon KH, Gueidan C, Schumm F, Bundhun D, Mapook A, Monkai J, Chomnunti P, Suetrong S, Chaiwan N, Dayarathne MC, Yang J, Rathnayaka AR, Bhunjun CS, Xu JC, Zheng JS, Liu G, Feng Y, Xie N (2020a) Refined families of *Dothideomycetes*: *Dothideomycetidae* and *Pleosporomycetidae*. Mycosphere 11:1553–2107. https://doi.org/10.5943/mycosphere/11/1/13

Hongsanan S, Hyde KD, Phookamsak R, Wanasinghe DN, McKenzie EHC, Sarma VV, Lücking R, Boonmee S, Bhat DJ, Liu NG, Tennakoon DS, Pem D, Karunarathna A, Jiang SH, Jones EBG, Phillips AJL, Manawasinghe IS, Tibpromma S, Jayasiri SC, Sandamali D, Jayawardena RS, Wijayawardene NN, Ekanayaka AH, Jeewon R, Lu YZ, Dissanayake AJ, Zeng XY, Luo ZL, Tian Q, Phukhamsakda C, Thambugala KM, Dai DQ, Samarakoon MC, Chethana KWT, Ertz D, Doilom M, Liu JK, Pérez-Ortega S, Suija A, Senwanna C, Wijesinghe SN, Niranjan M, Zhang SN, Ariyawansa HA, Jiang HB, Zhang JF, Norphanphoun C, de Silva NI, Thiyagaraja V, Zhang H, Bezerra JDP, Miranda-González R, Aptroot A, Kashiwadani H, Harishchandra D, Sérusiaux E, Abeywickrama PD, Bao DF, Devadatha B, Wu HX, Moon KH, Gueidan C, Schumm F, Bundhun D, Mapook A, Monkai J, Bhunjun CS, Chomnunti P, Suetrong S, Chaiwan N, Dayarathne MC, Yang J, Rathnayaka AR, Xu JC, Zheng JS, Liu G, Feng Y, Xie N (2020b) Refined families of *Dothideomycetes*: orders and families *incertae sedis* in *Dothideomycetes*. Fungal Divers 105:17–318. https://doi.org/10.1007/s13225-020-00462-6

Houbraken J, Kocsubé S, Visagie CM, Yilmaz N, Wang XC, Meijer M, Kraak B, Hubka V, Bensch K, Samson RA, Frisvad JC (2020) Classification of *Aspergillus*, *Penicillium*, *Talaromyces* and related genera (*Eurotiales*): an overview of families, genera, subgenera, sections, series and species. Stud Mycol 95:5–169. https://doi.org/10.1016/j.simyco.2020.05.002

Hu J, Yang JY, Li J, Gao T, Yang GW, Ren HY (2018) First report of *Ustilago avenae* causing loose smut of oat (*Avena sativa*) in Shandong China. J Plant Pathol 100:123. https://doi.org/10.1007/s42161-018-0016-z

Hu F, Wang C, Wang P (2021) First case of subcutaneous mycosis caused by *D. churashimaensis* and a literature review of human *Ustilaginales* infections. Front Cell Infect Microbiol 11:711768. https://doi.org/10.3389/fcimb.2021.711768

Huang GM, Zou YN, Wu QS, Xu YJ, Kuča K (2020) Mycorrhizal roles in plant growth, gas exchange, root morphology, and nutrient uptake of walnuts. Plant Soil Environ 66(6):295–302

Hudson HJ, Ingold CT (1960) Aquatic *hyphomycetes* from Jamaica. Trans Br Mycol Soc 43:469–478. https://doi.org/10.1016/s0007-1536(60)80029-0

Humber RA (2012) *Entomophthoromycota*: a new phylum and reclassification for entomophthoroid fungi. Mycotaxon 120:477–492. https://doi.org/10.5248/120.477

Hurdeal VG, Gentekaki E, Hyde KD, Nguyen TTT, Lee HB (2021) Novel *Mucor* species (*Mucoromycetes*, *Mucoraceae*) from northern Thailand. MycoKeys 84:57–78. https://doi.org/10.3897/mycokeys.84.71530

Hustad VP, Miller AN, Dentinger BT, Cannon PF (2013) Generic circumscriptions in *Geoglossomycetes*. Persoonia 31:101–111. https://doi.org/10.3767/003158513X671235

Hyde KD (2022) The numbers of fungi. Fungal Divers 114(1):1. https://doi.org/10.1007/s13225-022-00507-y

Hyde KD, McKenzie EHC, KoKo TW (2011) Towards incorporating anamorphic fungi in a natural classification—checklist and notes for 2010. Mycosphere 2:1–88

Hyde KD, Jones EBG, Liu JK, Ariyawansa H, Boehm E, Boonmee S, Braun U, Chomnunti P, Crous PW, Dai DQ, Diederich P, Dissanayake A, Doilom M, Doveri F, Hongsanan S, Jayawardena R, Lawrey JD, Li YM, Liu YX, Lücking R, Monkai J, Muggia L, Nelsen MP, Pang KL, Phookamsak R, Senanayake IC, Shearer CA, Suetrong S, Tanaka K, Thambugala KM, Wijayawardene NN, Wikee S, Wu HX, Zhang Y, Aguirre-Hudson B, Alias SA, Aptroot A, Bahkali AH, Bezerra JL, Bhat DJ, Camporesi E, Chukeatirote E, Gueidan C, Hawksworth DL, Hirayama K, de Hoog S, Kang JC, Knudsen K, Li WJ, Li XH, Liu ZY, Mapook A, McKenzie EHC, Miller AN, Mortimer PE, Phillips AJL, Raja HA, Scheuer C, Schumm F, Taylor JE, Tian Q, Tibpromma S, Wanasinghe DN, Wang Y, Xu JC, Yacharoen S, Yan JY, Zhang M (2013) Families of *Dothideomycetes*. Fungal Divers 63:1313. https://doi.org/10.1007/s13225-013-0263-4

Hyde KD, Nilsson RH, Alias SA, Ariyawansa HA, Blair JE, Cai L, de Cock AWAM, Dissanayake AJ, Glockling SL, Goonasekara ID,Gorczak M, Hahn M, Jayawardena RS, van Kan JAL, Laurence MH, Lévesque CA, Li XH, Liu JK, Maharachchikumbura SSN, Manamgoda DS, Martin FN, McKenzie EHC, McTaggart AR, Mortimer PE, Nair PVR, Pawłowska J, Rintoul TL, Shivas RG, Spies CFJ, Summerell BA, Taylor PWJ, Terhem RB, Udayanga D, Vaghefi N, Walther G, Wilk M, Wrzosek M, Xu JC, Yan JY, Zhou N (2014) One stop shop: backbones trees for important phytopathogenic genera: I. Fungal Divers 67:21–125. https://doi.org/10.1007/s13225-014-0298-1

Hyde KD, Maharachchikumbura SS, Hongsanan S, Samarakoon MC, Lücking R, Pem D, Harishchandra D, Jeewon R, Zhao RL, Xu JC, Liu JK (2017) The ranking of fungi: a tribute to David L. Hawksworth on his 70th birthday. Fungal Divers 84:1–23

Hyde KD, Norphanphoun C, Chen J, Dissanayake AJ, Doilom M, Hongsanan S, Jayawardena RS, Jeewon R, Perera RH, Thongbai B, Wanasinghe DN (2018) Thailand's amazing diversity: up to

96% of fungi in northern Thailand may be novel. Fungal Divers 93:215–239. https://doi.org/10.1007/s13225-018-0415-7

Hyde KD, Norphanphoun C, Maharachchikumbura SSN, Bhat DJ, Jones EBG, Bundhun D, Chen YJ, Bao DF, Boonmee S, Calabon MS, Chaiwan N, Chethana KWT, Dai DQ, Dayarathne MC, Devadatha B, Dissanayake AJ, Dissanayake LS, Doilom M, Dong W, Fan XL, Goonasekara ID, Hongsanan S, Huang SK, Jayawardena RS, Jeewon R, Karunarathna A, Konta S, Kumar V, Lin CG, Liu JK, Liu NG, Luangsa-ard J, Lumyong S, Luo ZL, Marasinghe DS, McKenzie EHC, Niego AGT, Niranjan M, Perera RH, Phukhamsakda C, Rathnayaka AR, Samarakoon MC, Samarakoon SMBC, Sarma VV, Senanayake IC, Shang QJ, Stadler M, Tibpromma S, Wanasinghe DN, Wei DP, Wijayawardene NN, Xiao YP, Yang J, Zeng XY, Zhang SN, Xiang MM (2020) Refined families of *Sordariomycetes*. Mycosphere 11:305–1059. https://doi.org/10.5943/mycosphere/11/1/7

Imbusch F, Liebe S, Erven T, Varrelmann M (2021) Dynamics of Cercospora leaf spot disease determined by aerial spore dispersal in artificially inoculated sugar beet fields. Plant Pathol 70:853–861. https://doi.org/10.1111/ppa.13337

Inácio J, Daniel HM (2017) Commensalisms: the case of the human zymobiome. In: Buzzini P, Lachance MA, Yurkov A (eds) Yeasts in natural ecosystems: ecology, 1st edn. Springer, Cham, pp 211–228

Index Fungorum (2024) https://www.indexfungorum.org

Ingold CT (1979) Advances in the study of so-called aquatic hyphomycetes. Am J Bot 66:218–226. https://doi.org/10.2307/2442527

Irinyi L, Roper M, Malik R, Meyer W (2023) In silico environmental sampling of emerging fungal pathogens via big data analysis. Fungal Ecol 62:101212. https://doi.org/10.1016/j.funeco.2022.101212

Issi IV, Tokarev YS, Seliverstova EV, Nassonova ES (1987) Specified ultrastructural data on *Tubulinosema maroccanus* comb. nov. (*Nosema maroccanus* Krilova et Nurzhanov, 1987) (*Microsporidia*) from the Moroccan locust *Dociostaurus maroccanus* (Orthoptera). Acta Protozool 47(2):125

Jacobsen ID (2023) The role of host and fungal factors in the commensal-to-pathogen transition of *Candida albicans*. Curr Clin Micro Rpt 10:55–65. https://doi.org/10.1007/s40588-023-00190-w

Jain KP (1974) Fossil fungi. In: Surange KR et al (eds) Aspects and appraisal of Indian Palaeobotany. Birbal Sahni Institute of Palaeobotany, Lucknow, pp 38–46

Jain KP, Gupta RC (1970) Some fungal remains from the *Tertiaries* of Kerala Coast. Palaeobotanist 18(2):177–182

Jain KP, Kar RK (1979) Palynology of Neogene sediments around Quilon and Varkala, Kerala coast, South India–I. Fungal Remains. Palaeobotanist 26(2):105–118

Jaklitsch W, Baral HO, Lücking R, Lumbsch HT, Frey W (2016) Syllabus of plant families—A. Engler's syllabus der pflanzenfamilien part 1/2: *Ascomycota*, 13th edn. Borntraeger Science Publishers, Berlin. p 118

James TY, Kauff F, Schoch CL, Matheny PB, Hofstetter V, Cox CJ, Celio G, Gueidan C, Fraker E, Miadlikowska J, Lumbsch HT, Rauhut A, Reeb V, Arnold AE, Amtoft A, Stajich JE, Kentaro Hosaka K, Sung GH, Johnson D, O'Rourke B, Binder CM, M, Curtis JM, Slot JC, Wang Z, Wilson AW, Schüßler A, Longcore JE, O'Donnell K, Mozley-Standridge S, Porter D, Letcher PM, Powell MJ, Taylor JW, White MM, Griffith GW, Davies DR, Humber RA, Morton JB, Sugiyama J, Rossman AY, Rogers JD, Pfister DH, Hewitt D, Hansen K, Hambleton S, Shoemaker RA, Kohlmeyer J, Volkmann-Kohlmeyer B, Spotts RA, Serdani M, Crous PW, Hughes KW, Matsuura K, Langer E, Langer G, Untereiner WA, Lücking R, Büdel B, Geiser DM, Aptroot A, Diederich P, Schmitt I, Schultz M, Yahr R, Hibbett DS, François Lutzoni F, McLaughlin D, Spatafora JW, Vilgalys R (2006a) Reconstructing the early evolution of *Fungi* using a six-gene phylogeny. Nature 443:818–822. https://doi.org/10.1038/nature05110

James TY, Letcher PM, Longcore JE, Mozley-Standridge SE, Porter D, Powell MJ, Griffith G, Vilgalys R (2006b) A molecular phylogeny of the flagellated fungi (*Chytridiomycota*) and description of a new phylum (*Blastocladiomycota*). Mycologia 98(6):860–871. https://doi.org/10.3852/mycologia.98.6.860

James TY, Porter TM, Martin WW (2014) *Blastocladiomycota*. In: McLaughlin DJ, Spatafora JW (eds) The mycota VII—part A. Springer, New York, pp 177–207

Jančič S, Nguyen HD, Frisvad ZP, Schroers HJ, Seifert KA, Gunde-Cimerman N (2015) A taxonomic revision of the *Wallemia sebi* species complex. PLoS ONE 10(5):e0125933. https://doi.org/10.1371/journal.pone.0125933

Jansonius J (1976) Palaeogene fungal spores and fruiting bodies of the Canadian Arctic. Geosci Man 15:129–132

Jesus AL, Jerônimo GH, Pires-Zottarelli CLA (2021) Two new species of *Chytriomycetaceae*: morphological, phylogenetic, and ultrastructural characterization. Mycologia 113:312–325. https://doi.org/10.1080/00275514.2020.1843328

Jiang X, Yu H, Xiang M, Liu X, Liu X (2011) *Echinochlamydosporium variabile*, a new genus and species of *Zygomycota* from soil nematodes. Fungal Divers 46:43–51

Jiang YP, Dukik K, Muñoz JF, Sigler L, Schwartz IS, Govender NP, Kenyon C, Feng P, van den Ende BG, Stielow JB, Stchigel AM, de Hoog LuHG, S, (2018) Phylogeny, ecology and taxonomy of systemic pathogens and their relatives in *Ajellomycetaceae* (*Onygenales*): *Blastomyces*, *Emergomyces*, *Emmonsia*, *Emmonsiellopsis*. Fungal Divers 90:245–291. https://doi.org/10.1007/s13225-018-0403-y

Jiang Y-L, Bao W-J, Liu F, Wang G-S, Yurkov AM, Ma Q, Hu Z-D, Chen X-H, Zhao W-N, Li A-H, Wang Q-M (2024) Proposal of one new family, seven new genera and seventy new basidiomycetous yeast species mostly isolated from Tibet and Yunnan provinces, China. Stud Mycol 109:57–153. https://doi.org/10.3114/sim.2024.109.02

Jindamorakot S, Am-in S, Yukphan P, Yamada Y (2011) *Limtongia* gen. nov. for *Zygozyma smithiae* (*Lipomycetaceae*). Ann Microbiol 61:689–693

Jindamorakot S, Yukphan P, Yamada Y (2012) *Kockiozyma* gen. nov., for *Zygozyma suomiensis*: the phylogeny of the Lipomycetaceous yeasts. Ann Microbiol 62:1831–1840. https://doi.org/10.1007/s13213-012-0433-8

Jobim K, Goto BT (2016) Diversity of *Arbuscular mycorrhizal* fungi (*Glomeromycota*) in maritime sand dunes of Brazilian northeast. Stud Fungi 1(1):43–55. https://doi.org/10.5943/sif/1/1/4

Johnston PR, Minter DW (1989) Structure and taxonomic significance of the ascus in the *Coryneliaceae*. Mycol Res 92:422–430. https://doi.org/10.1016/S0953-7562(09)80683-7

Johnston PR, Quijada L, Smith CA, Baral HO, Hosoya T, Baschien C, Pärtel K, Zhuang WY, Haelewaters D, Park D, Carl S, López-Giráldez F, Wang Z, Townsend JP (2019) A multigene phylogeny toward a new phylogenetic classification of *Leotiomycetes*. IMA Fungus 10:1–22. https://doi.org/10.1186/s43008-019-0002-x

Johnston PR, Seifert KA, Stone JK, Rossman AY, Marvanová L (2014) Recommendations on generic names competing for use in *Leotiomycetes* (*Ascomycota*). IMA Fungus 5:91–120. https://doi.org/10.5598/imafungus.2014.05.01.11

Jumpponen A, Jones KL (2009) Seasonally dynamic fungal communities in the *Quercus macrocarpa* phyllosphere differ between urban and nonurban environment. New Phytol 186:496–513. https://doi.org/10.1111/j.1469-8137.2010.03197.x

Jumpponen A, Jones KL (2010) Massively parallel 454 sequencing indicates hyperdiverse fungal communities in temperate *Quercus macrocarpa* phyllosphere. New Phytol 184:438–448. https://doi.org/10.1111/j.1469-8137.2009.02990.x

Jumrani K, Bhatia VS, Kataria S, Alamri SA, Siddiqui MH, Rastogi A (2022) Inoculation with *arbuscular mycorrhizal* fungi alleviates the adverse effects of high temperature in Soybean. Plants 11(17):2210. https://doi.org/10.3390/plants11172210

Kachalkin A, Tomashevskaya M, Pankratov T, Yurkov A (2024) Endothallic yeasts in the terricolous lichens Cladonia. Mycol Prog 23:29. https://doi.org/10.1007/s11557-024-01966-0

Kalgutkar RM, Jansonius J (2000) Synopsis of fungal spores, mycelia and fructifications. AASP Contrib Ser 39:1–423

Kalsoom Khan F, Kluting K, Tångrot J, Urbina H, Ammunet T, Eshghi Sahraei S, Rydén M, Ryberg M, Rosling A (2020) Naming the untouchable—environmental sequences and niche partitioning as taxonomical evidence in fungi. IMA Fungus 11:23. https://doi.org/10.1186/s43008-020-00045-9

Kandemir H, Dukik K, de Melo TM, Stielow JB, Delma FZ, Al-Hatmi AMS, Ahmed SA, Ilkit M, de Hoog GS (2022) Phylogenetic and ecological reevaluation of the order *Onygenales*. Fungal Divers 115:1–72. https://doi.org/10.1007/s13225-022-00506-z

Kanouse BB (1927) A monographic study of special groups of the water molds I. *Blastocladiaceae*. Am J Bot 14:227–286

Kantarcioglu AS, Guarro J, de Hoog S, Apaydin H, Kiraz N (2017) An updated comprehensive systematic review of *Cladophialophora bantiana* and analysis of epidemiology, clinical characteristics, and outcome of cerebral cases. Med Mycol 55:579–604. https://doi.org/10.1093/mmy/myw124

Kar RK, Singh RY, Sah SCD (1972) On some algal and fungal remains from Tura Formation of Garo Hills. Assam Palaeobotanist 19(2):146–154

Kar RK, Sharma N, Agarwal A, Kar R (2003) Occurrence of fossil wood rotters (*Polyporales*) from Lameta Formation (Maastrichtian), India. Curr Sci 85:37–40

Kar R, Mandaokar BD, Kar RK (2010) Fungal taxa from the Miocene sediments of Mizoram, northeast India. Rev Palaeobot Palynol 158:240–249

Karaalioğlu O, Yüceer YK (2021) Nonconventional yeasts to produce aroma compounds by using agri-food waste materials. FEMS Yeast Res 21:foab063. https://doi.org/10.1093/femsyr/foab063

Karakehian JM, Quijada L, Friebes G, Tanney JB, Pfister DH (2019) Placement of *Triblidiaceae* in *Rhytismatales* and comments on unique ascospore morphologies in *Leotiomycetes* (*Fungi*, *Ascomycota*). MycoKeys 54:99–133

Karatygin IV, Snigirevskaya NS, Demchenko KN (2006) Species of the genus *Glomites* as plant mycobionts in early devonian ecosystems. Paleontol J 40:572–579. https://doi.org/10.1134/S0031030106050121

Karim A, Gerliani N, Aïder M (2020) *Kluyveromyces marxianus*: An emerging yeast cell factory for applications in food and biotechnology. Int J Food Microbiol 333:108818. https://doi.org/10.1016/j.ijfoodmicro.2020.108818

Karling JS (1977) Chytridiomycetarum iconographia. Lubrecht Cramer, Monticello

Karpov SA, Mikhailov KV, Mirzaeva GS, Mirabdullaev IM, Mamkaeva KA, Titova NN, Aleoshin VV (2013) Obligately phagotrophic aphelids turned out to branch with the earliest diverging fungi. Protist 164:195–205. https://doi.org/10.1016/j.protis.2012.08.001

Karpov SA, Mamkaeva MA, Aleoshin VV, Nassonova E, Lilje O, Gleason FH (2014a) Morphology, phylogeny, and ecology of the aphelids (*Aphelidea*, *Opisthokonta*) and proposal for the new superphylum *Opisthosporidia*. Front Microbiol 5:112. https://doi.org/10.3389/fmicb.2014.00112

Karpov SA, Mamkaeva MA, Benzerara K, Moreira D, López-García P (2014b) Molecular phylogeny and ultrastructure of *Aphelidium aff. melosirae* (*Aphelida*, *Opisthosporidia*). Protist 165:512–526

Karpov SA, Kobseva AA, Mamkaeva MA, Mamkaeva KA, Mikhailov KV, Mirzaeva GS, Aleoshin VV (2014c) *Gromochytrium mamkaevae* gen. & sp. nov. and two new orders: *Gromochytriales* and *Mesochytriales* (*Chytridiomycetes*). Persoonia 32:115–126. https://doi.org/10.3767/003158514X680234

Karpov SA, Mamanazarova KS, Popova OV, Aleoshin VV, James TY, Mamkaeva MA, Tcvetkova VS, Vishnyakov AE, Longcore JE (2017a) *Monoblepharidomycetes* diversity includes new parasitic and saprotrophic species with highly intronized rDNA. Fungal Biol 121(8):729–741. https://doi.org/10.1016/j.funbio.2017.05.002

Karpov SA, Torruella G, Moreira D, Mamkaeva MA, Lo´pez-Garcı ´a P (2017b) Molecular phylogeny of *Paraphelidium letcheri* sp. nov. (*Aphelida*, *Opisthosporidia*). J Eukaryot Microbiol 5:573–578. https://doi.org/10.1111/jeu.12389

Karpov SA, López-García P, Mamkaeva MA, Klimov VI, Vishnyakov AE, Tcvetkova VS, Moreira D (2018) The chytrid-like parasites of algae *Amoeboradix gromovi* gen. et sp. nov. and *Sanchytrium tribonematis* belong to a new fungal lineage. Protist 169(1):122–140. https://doi.org/10.1016/j.protis.2017.11.002

Karpov SA, Cvetkova VS, Annenkova NV, Vishnyakov AE (2019) Kinetid structure of *Aphelidium* and *Paraphelidium* (*Aphelida*) suggests the features of the common ancestor of *Fungi* and *Opisthosporidia*. J Euk Microbiol 66(6):911–924. https://doi.org/10.1111/jeu.12742

Katoh K, Standley DM (2013) MAFFT multiple sequence alignment software version 7: improvements in performance and usability. Mol Biol Evol 30(4):772–780. https://doi.org/10.1093/molbev/mst010

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 Prog 19(5):481–493. https://doi.org/10.1007/s11557-020-01571-x

Kendrick B (2000) [3rd edition]—the fifth kingdom. Micologue Publications, Ontario

Kendrick B (2017) Eumycotan fungi—the mainstream and others: Phylum 4 *Zygomycota*, phylum 5 *Glomeromycota*, phylum 6 *Microsporidia*. The fifth kingdom, 4th edn. Hackett Publishing Company, Indianapolis, pp 38–54

Kerrigan J, Smith MTh (2001) *Ascobotryozyma* J. Kerrigan, M.Th. Smith & J.D. Rogers. In: Kurtzman CP, Fell JW, Boekhout T (eds) The yeasts–a taxonomic study, 5th edn. Elsevier, Amsterdam, pp 319–323

Kidston R, Lang WH (1921) On Old Sandstone plants showing structure, from the Rhynie Chert Bed, Aberdeenshire. Part V. The thallophyta occurring in the peat-bed; the succession of the plants through a vertical section of the bed, and the conditions of accumulation and preservation of the deposit. Trans R Soc Edinb Earth Sci 52:855–902

Kijpornyongpan T, Mondo SJ, Barry K, Sandor L, Lee L, Lipzen A, Pangilinan J, LaButti K, Hainaut M, Henrissat B, Grigoriev IV, Spatafora JW, Aime MC (2018) Broad genomic sampling reveals a smut pathogenic ancestry of the fungal clade *Ustilaginomycotina*. Mol Biol Evol 35(8):1840–1854. https://doi.org/10.1093/molbev/msy072

Kim T, Choi Y, Choi JS, Park J (2022) A case of superficial fungal infection caused by *Naganishia diffluens*. J Mycol Infect 27:14–18

Kirchhoff L, Olsowski M, Rath PM, Steinmann J (2019) *Exophiala dermatitidis*: key issues of an opportunistic fungal pathogen. Virulence 10:984–998

Kirk PM, Cannon PF, Minter DW, Stalpers JA (2008) Ainsworth & Bisby's dictionary of the fungi, 10th edn. CABI, Wallingford, p 439

Kirkland TN, Stevens DA, Hung CY, Beyhan S, Taylor JW, Shubitz LF, Duttke SH, Heidari A, Johnson RH, Deresinski SC, Lauer A, Fierer J (2022) *Coccidioides* species: a review of basic research: 2022. J Fungi 8:859. https://doi.org/10.3390/jof8080859

Kirschner R (2004) Sporodochial anamorphs of species of *Helicogloea*. Front Basidiomycote Mycol 165–178

Kirschner R, Okuda T (2013) A new species of *Pseudocercospora* and new record of *Bartheletia paradoxa* on leaves of *Ginkgo biloba*. Mycol Prog 12:421–426. https://doi.org/10.1007/s11557-012-0849-3

Kirschner R, Begerow D, Oberwinkler F (2001) A new *Chionosphaera* species associated with conifer inhabiting bark beetles. Mycol Res 105(11):1403–1408

Kirschner R, Sampaio JP, Begerow D, Chen ZC, Oberwinkler F (2003) *Mycogloea nipponica*—the first known teleomorph in the heterobasidiomycetous yeast genus *Kurtzmanomyces*. Antonie Van Leeuwenhoek 84:109–114. https://doi.org/10.1023/A:1025484800974

Klinsukon C, Lumyong S, Kirkland KTW, Stevens DA, Hung CY, Beyhan S, Taylor JW, Shubitz LF, Duttke SH, Heidari A, Johnson RH, Deresinski SC, Lauer A, Fierer J (2021) Colonization by *arbuscular mycorrhizal* fungi improves salinity tolerance of eucalyptus (*Eucalyptus camaldulensis*) seedlings. Sci Rep 11:4362. https://doi.org/10.1038/s41598-021-84002-5

Kluge M (2002) A fungus eats a cyanobacterium: the story of the *Geosiphon pyriformis* endocyanosis. In: Biology and environment: proceedings of the Royal Irish Academy, vol 102, no 1, pp 11–14. Royal Irish Academy, Dublin

Kobayashi Y, Maeda T, Yamaguchi K (2018) The genome of *Rhizophagus clarus* HR1 reveals a common genetic basis for auxotrophy among Arbuscular mycorrhizal fungi. BMC Genom 19:465. https://doi.org/10.1186/s12864-018-4853-0

Korf RP (1972) Synoptic key to the genera of the *Pezizales*. Mycologia 64:937–994. https://doi.org/10.1080/00275514.1972.12019349

Kosa G, Zimmermann B, Kohler A, Ekeberg D, Afseth NK, Mounier J, Shapaval V (2018) High-throughput screening of *Mucoromycota* fungi for production of low- and high-value lipids. Biotechnol Biofuels 11:66. https://doi.org/10.1186/s13068-018-1070-7

Kottke I, Suárez JP, Herrera P, Cruz D, Bauer R, Haug I, Garnica S (2010) *Atractiellomycetes* belonging to the 'rust' lineage (*Pucciniomycotina*) form mycorrhizae with terrestrial and epiphytic neotropical orchids. Proc R Soc Lond Ser B 277(1685):1289–1298. https://doi.org/10.1098/rspb.2009.1884

Kourti M, Roilides E (2022) Invasive Trichosporonosis in neonates and pediatric patients with malignancies or hematologic disorders. Pathogens 11:242. https://doi.org/10.3390/pathogens11020242

Kraisitudomsook N, Healy RA, Pfister DH, Truong C, Nouhra E, Kuhar F, Mujic AB, Trappe JM, Smith ME (2020) Resurrecting the genus *Geomorium*: systematic study of fungi in the genera *Underwoodia* and *Gymnohydnotrya* (*Pezizales*) with the description of three new South American species. Persoonia 44:98–112. https://doi.org/10.3767/persoonia.2020.44.04

Kreger-van Rij NJW (1984) The yeasts—a taxonomic study, 3rd edn. Elsevier, Amsterdam

Kruse J, Doehlemann G, Kemen E, Thines M (2017) Asexual and sexual morphs of *Moesziomyces* revisited. IMA Fungus 8(1):117–129. https://doi.org/10.5598/imafungus.2017.08.01.09

Kuddus M, Aguilar CN (2022) Value-addition in food products and processing through enzyme technology. Elsevier Inc., California

Kumar S, Stecher G, Tamura K (2016) MEGA7: molecular evolutionary genetics analysis version 7.0 for bigger datasets. Mol Biol Evol 33(7):1870–1874. https://doi.org/10.1093/molbev/msw054

Kumar K, Singh E, Shrivastava S (2022) Microbial xylitol production. Appl Microbiol Biotechnol 106:971–979. https://doi.org/10.1007/s00253-022-11793-6

Kurihara Y, Degawa Y, Tokumasu S (2004) Two novel kickxellalean fungi, *Mycoëmilia scoparia* gen. sp. nov. and *Ramicandelaber brevisporus* sp. nov. Mycol Res 108(10):1143–1152. https://doi.org/10.1017/s0953756204000930

Kurihara Y, Park JY, Ando K, Sukarno N, Ilyas M, Yuniarti E, Saraswati R, Mangunwardoyo W, Widyastuti Y (2008) Indonesian *Kickxellales*: two species of *Coemansia* and *Linderina*. Mycoscience 49(4):241–249. https://doi.org/10.1007/S10267-008-0414-8

Kurtzman CP (2003) Phylogenetic circumscription of *Saccharomyces*, *Kluyveromyces* and other members of the *Saccharomycetaceae*, and the proposal of the new genera *Lachancea*, *Nakaseomyces*, *Naumovia*, *Vanderwaltozyma* and *Zygotorulaspora*. FEMS Yeast Res 4:233–245. https://doi.org/10.1016/S1567-1356(03)00175-2

Kurtzman CP (2011) *Trigonopsis* Schachner emend. Kurtzman & Robnett (2007). In: Kurtzman C, Fell JW, Boekhout T (eds) The yeasts—a taxonomic study, 5th edn. Elsevier, Amsterdam, pp 1331–1335

Kurtzman CP, de Hoog GS (2011) *Eremothecium* Borzi emend. Kurtzman. In: Kurtzman C, Fell JW, Boekhout T (eds) The yeasts—a taxonomic study, 5th edn. Elsevier, Amsterdam, pp 405–412

Kurtzman CP, Fell JW (1998) The yeasts—a taxonomic study, 4th edn. Elsevier, Amsterdam

Kurtzman CP, Robnett CJ (1997) Identification of clinical important ascomycetous yeasts based on nucleotide divergence in the 5'end of the large-subunit (26S) ribosomal DNA gene. J Clin Microbiol 35:1216–1223. https://doi.org/10.1128/jcm.35.5.1216-1223.1997

Kurtzman CP, Robnett CJ (1998) Identification and phylogeny of ascomycetous yeasts from analyses of nuclear large subunit (26S) ribosomal DNA partial sequences. Antonie Van Leeuwenhoek 73:331–371. https://doi.org/10.1023/a:1001761008817

Kurtzman CP, Robnett CJ (2003) Phylogenetic relationships among yeasts of the "*Saccharomyces* complex" determined from multigene sequence analyses. FEMS Yeast Res 3:417–432. https://doi.org/10.1016/S1567-1356(03)00012-6

Kurtzman CP, Robnett CJ (2007) Multigene phylogenetic analysis of the *Trichomonascus*, *Wickerhamiella* and *Zygoascus* yeast clades, and the proposal of *Sugiyamaella* gen.nov. and 14 new species combinations. FEMS Yeast Res 7:141–151. https://doi.org/10.1111/j.1567-1364.2006.00157.x

Kurtzman CP, Robnett CJ (2010) Systematics of methanol assimilating yeasts and neighboring taxa from multigene sequence analysis and the proposal of *Peterozyma* gen. nov. FEMS Yeast Res 10:353–361. https://doi.org/10.1111/j.1567-1364.2010.00625.x

Kurtzman CP, Robnett CJ (2013a) *Alloascoidea hylecoeti* gen. nov., comb. nov., *Alloascoidea africana* comb. nov., *Ascoidea tarda* sp. nov., and *Nadsonia starkeyi-henricii* comb. nov., new members of the *Saccharomycotina* (*Ascomycota*). FEMS Yeast Res 13:423–432. https://doi.org/10.1111/1567-1364.12044

Kurtzman CP, Robnett CJ (2013b) Relationships among genera of the *Saccharomycotina* (*Ascomycota*) from multigene phylogenetic analysis of type species. FEMS Yeast Res 13:23–33. https://doi.org/10.1111/1567-1364.12006

Kurtzman CP, Suzuki M (2010) Phylogenetic analysis of *ascomycete* yeasts that form coenzyme Q-9 and the proposal of the new genera *Babjeviella*, *Meyerozyma*, *Millerozyma*, *Priceomyces* and *Scheffersomyces*. Mycoscience 51:2–14. https://doi.org/10.1007/s10267-009-0011-5

Kurtzman CP, Albertyn J, Basehoar-Powers E (2007) Multigene phylogenetic analysis of the *Lipomycetaceae* and proposed transfer of *Zygozyma* species to *Lipomyces* and *Babjevia anomala* to *Dipodascopsis*. FEMS Yeast Res 7:1027–1034. https://doi.org/10.1111/j.1567-1364.2007.00246.x

Kurtzman CP, Robnett CJ, Basehoar-Powers E (2008) Phylogenetic relationships among species of *Pichia*, *Issatchenkia* and *Williopsis* determined from multigene phylogenetic analysis, and the proposal of *Barnettozyma* gen. nov., *Lindnera* gen. nov. and *Wickerhamomyces* gen. nov. FEMS Yeast Res 8:939–954. https://doi.org/10.1111/j.1567-1364.2008.00419.x

Kurtzman CP, Fell JW, Boekhout T (2011) The yeasts—a taxonomic study, 2, 5th edn. Elsevier, Amsterdam

Kuznetsov PA, Avchieva PB (2002) *Candida maltosa* used for the bio-degradation of petroleum product pollutants. US Patent US6444204B1

Lachance MA (2011a) *Metschnikowia* Kamienski (1899). In: Kurtzman C, Fell JW, Boekhout T (eds) The yeasts—a taxonomic study, 2, 5th edn. Elsevier, Amsterdam, pp 575–620

Lachance MA, (2011b) Sporopachydermia Rodrigues de Miranda, (1978b). In: Kurtzman C, Fell JW, Boekhout T (eds) The yeasts—a taxonomic study, 5th edn. Elsevier, Amsterdam, pp 799–803

Lachance MA, Kurtzman CP (2013) The yeast genus *Tortispora* gen. nov., description of *Tortispora ganteri* sp. nov., *Tortispora mauiana* f.a., sp. nov., *Tortispora agaves* f.a., sp. nov., *Tortispora sangerardii* f.a., sp. nov., *Tortisporacuajiniquilana* f.a., sp. nov., *Tortispora starmeri* f.a., sp. nov., and *Tortispora phaffii* f.a., sp. nov., reassignment of *Candida caseinolytica* to *Tortispora caseinolytica* f.a., comb. nov., emendation of *Botryozyma*, and assignment of *Botryozyma*, *Tortispora* gen. nov., and *Trigonopsis* to the family *Trigonopsidaceae* fam. nov. Int J Syst Evol Microbiol 63:3104–3114. https://doi.org/10.1099/ijs.0.052209-0

Lahue C, Madden AA, Dunn RR, Smukowski Heil C (2020) History and domestication of *Saccharomyces cerevisiae* in bread baking. Front Genet 11:584718. https://doi.org/10.3389/fgene.2020.584718

Lamit LJ, Romanowicz KJ, Potvin LR, Singh K, Lennon JT, Tringe SG, Kane ES, Lilleskov EA (2017) Patterns and drivers of fungal community depth stratification in *Sphagnum* peat. FEMS Microbiol Ecol. https://doi.org/10.1093/femsec/fix082

Landvik S, Egger K, Schumacher T (1997) Toward a subordinal classification of the *Pezizales* (*Ascomycota*): phylogenetic analyses SSU rDNA sequences. Nord J Bot 17:403–418. https://doi.org/10.1111/j.1756-1051.1997.tb00337.x

Landvik S, Kristiansen R, Schumacher T (1998) Phylogenetic and structural studies in the *Thelebolaceae* (*Ascomycota*). Mycoscience 39:49–56. https://doi.org/10.1007/BF02461578

Landvik S, Eriksson OE, Berbee ML (2001) *Neolecta*—a fungal dinosaur? Evidence from β-tubulin amino acid sequences. Mycologia 93(6):1151–1163. https://doi.org/10.1080/00275514.2001.12063248

Lange RT, Smith PH (1971) The Maslin Bay flora, South Australia. 3. Dispersed fungal spores. Neves Jahrb Geol Palaontol Monatsh 11:663–681

Langer E, Oberwinkler F (1998) *Spiculogloea occulta* (*Heterobasidiomycetes*) morphology and culture characteristics. Mycotaxon 69:249–254

Lantz H, Johnston PR, Park D, Minter DW (2011) Molecular phylogeny reveals a core clade of *Rhytismatales*. Mycologia 103(1):57–74. https://doi.org/10.3852/10-060

Lappalainen S, Pasanen AL, Reiman M, Kalliokoski P (1998) Serum IgG antibodies against *Wallemia sebi* and *Fusarium* species in Finnish farmers. Ann Alergy Astma Immunol 81:589–592. https://doi.org/10.1016/S1081-1206(10)62710-X

Lappalainen MHJ, Hyvärinen A, Hirvonen MR, Rintala H, Roivainen J, Renz H, Pfefferle PI, Nevalainen A, Roponen M, Pekkanen J (2012) High indoor microbial levels are associated with reduced Th1 cytokine secretion capacity in infancy. Int Arch Allergy Immunol 159:194–203. https://doi.org/10.1159/000335596

Larsson JIR (1993) Description of *Chytridiopsis trichopterae* n. sp. (Microspora, Chytridiopsidae), a microsporidian parasite of the caddis fly *Polycentropus flavomaculatus* (Trichoptera, Polycentropodidae), with comments on relationships between the families Chytridiopsidae and Metchnikovellidae. J Eukary Microbiol 40:37–48. https://doi.org/10.1111/j.1550-7408.1993.tb04880.x

Larsson JIR (2000) The hyperparasitic microsporidium *Amphiacantha longa* Caullery et Mesnil, 1914 (*Microspora*: *Metchnikovellidae*)-description of the cytology, redescription of the species, emended diagnosis of the genus *Amphiacantha* and establishment of the new family Amphiacanthidae. Folia Parasitol 47(4):241–256

Larsson JIR (2014) The primitive microsporidia. Microsporidia 9:605–634. https://doi.org/10.1002/9781118395264.ch24

Lartillot N, Philippe H (2004) A Bayesian mixture model for across-site heterogeneities in the amino-acid replacement process. Mol Biol Evol 21(6):1095–1109. https://doi.org/10.1093/molbev/msh112

Lartillot N, Rodrigue N, Stubbs D, Richer J (2013) PhyloBayes MPI: phylogenetic reconstruction with infinite mixtures of profiles in a parallel environment. Syst Biol 62(4):611–615. https://doi.org/10.1093/sysbio/syt022

Latef AAHA, Hashem A, Rasool S, Abd Allah EF, Alqarawi AA, Egamberdieva D, Jan S, Anjum NA, Ahmad P (2016) *Arbuscular mycorrhizal* symbiosis and abiotic stress in plants: a review. J Plant Biol 59:407–426. https://doi.org/10.1007/s12374-016-0237-7

Latinne A, Chen HW, Kuo CC, Lorica R, Singleton G, Stuart A, Malbas FF, Demanche C, Chabé M, Michaux J, Morand S (2021) Revisiting the pneumocystis host specificity paradigm andtransmission ecology in wild Southeast Asian rodents. Infect Genet Evol 93:104978. https://doi.org/10.1016/j.meegid.2021.104978

Lawrey J, Diederich P, Nelsen MP, Freebury C, Van den Broeck D, Sikaroodi M, Ertz D (2012) Phylogenetic placement of lichenicolous *Phoma* species in the *Phaeosphaeriaceae* (*Pleosporales*, *Dothideomycetes*). Fungal Divers 55:195–213. https://doi.org/10.1007/s13225-012-0166-9

Lay CY, Hamel C, St-Arnaud M (2018) Taxonomy and pathogenicity of *Olpidium brassicae* and its allied species. Fungal Biol 122(9):837–846. https://doi.org/10.1016/j.funbio.2018.04.012

Lee SY, Jung HY (2020) First report of persimmon (*Diospyros kaki*) fruit rot caused by *Mucor inaequisporu*s in South Korea. Dis Notes 104(7):2031. https://doi.org/10.1094/PDIS-01-20-0060-PDN

Lee JK, Lee SY, Lee SJ, Kim KH (2005) Fruiting body development of a root pathogenic fungus, *Rhizina undulata*, after forest fire in eastern coastal pine forests of Korea. Forest Sci Technol 1:33–37. https://doi.org/10.1080/21580103.2005.9656266

Lei X, Zheng J, Zhao D, Qiao Z, An M, Zhang X (2022) *Moniliella aeria* sp. nov., a novel yeast isolated from the air of a Wuliangye baijiu-making workshop. Int J Syst Evol Microbiol 72(7):005464. https://doi.org/10.1099/ijsem.0.005464

Leshem T, Letcher PM, Powell MJ, Sukenik A (2016) Characterization of a new chytrid species parasitic on the dinoflagellate, *Peridinium gatunense*. Mycologia 108:731–743. https://doi.org/10.3852/15-197

Letcher PM, Powell MJ (2014) Hypothesized evolutionary trends in zoospore ultrastructural characters in *Chytridiales* (*Chytridiomycota*). Mycologia 106:379–396. https://doi.org/10.3852/13-219

Letcher PM, Powell MJ (2018) Morphology, zoospore ultrastructure, and phylogenetic position of *Polyphlyctis willoughbyi*, a new species in *Chytridiales* (*Chytridiomycota*). Fungal Biol 122:1171–1183. https://doi.org/10.1016/j.funbio.2018.08.003

Letcher PM, Powell MJ, Churchill PF, Chambers JG (2006) Ultrastructural and molecular phylogenetic delineation of a new order, the *Rhizophydiales* (*Chytridiomycota*). Mycol Res 110:898–915. https://doi.org/10.1016/j.mycres.2006.06.011

Letcher PM, Powell MJ, Barr DJ, Churchill PF, Wakefield WS, Picard KT (2008a) *Rhizophlyctidales*—a new order in *Chytridiomycota*. Mycol Res 112(9):1031–1048

Letcher PM, Powell MJ, Viusent MC (2008b) Rediscovery ofan unusual chytridiaceous fungus new to the order *Rhizophydiales*. Mycologia 100:325–334. https://doi.org/10.3852/mycologia.100.2.325

Letcher PM, Longcore JE, Powell MJ, Picard KT (2012) Zoospore ultrastructure and phylogenetic position of *Phlyctochytrium* *aureliae* Ajello is revealed (*Chytridiaceae Chytridiales*, *Chytridiomycota*). Mycologia 104:410–418. https://doi.org/10.3852/11-153

Letcher PM, Lopez S, Schmieder R, Lee PA, Behnke C, Powell MJ, McBride RC (2013) Characterization of *Amoeboaphelidium protococcarum*, an algal parasite new to the *Cryptomycota* isolated from an outdoor algal pond used for the production of biofuel. PLoS ONE 8(2):e56232. https://doi.org/10.1371/journal.pone.0056232

Letcher PM, Powell MJ, Lopez S, Lee PA, McBride RC (2015) A new isolate of *Amoeboaphelidium protococcarum*, and *Amoeboaphelidium occidentale*, a new species in phylum *Aphelida* (*Opisthosporidia*). Mycologia 107(3):522–531. https://doi.org/10.3852/14-064

Letcher PM, Longcore JE, Quandt CA, da Silva LD, James TY, Powell MJ (2017) Morphological, molecular, and ultrastructural characterization of *Rozella rhizoclosmatii*, a new species in *Cryptomycota*. Fungal Biol 121:1–10. https://doi.org/10.1016/j.funbio.2016.08.008

Letcher PM, Powell MJ, Davis WJ (2018) Morphology, zoospore ultrastructure, and molecular position of taxa in the *Asterophlyctis* lineage (*Chytridiales*, *Chytridiomycota*). Fungal Biol 122:1109–1123. https://doi.org/10.1016/j.funbio.2018.09.002

Li JL, Heath IB, Packer L (1993) The phylogenetic relationships of the anaerobic *chytridiomycetous* gut fungi (*Neocallimasticaceae*) and the *Chytridiomycota*. II. Cladistic analysis of structural data and description of *Neocallimasticales* ord. nov. Canad J Bot 71(3):393–407. https://doi.org/10.1139/b93-044

Li AH, Yuan FX, Groenewald M, Bensch K, Yurkov AM, Li K, Han PJ, Guo LD, Aime MC, Sampaio JP, Jindamorakot S, Turchetti B, Inácio J, Fungsin B, Wang QM, Bai FY (2020) 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 Y, Steenwyk JL, Chang Y, Wang Y, James TY, Stajich JE, Spatafora JW, Groenewald M, Dunn CW, Hittinger CT, Shen XX, Rokas A (2021a) A genome-scale phylogeny of fungi. Curr Biol 31:1653–1665. https://doi.org/10.1016/j.cub.2021.01.074

Li Z, Wang Q, Sun K, Feng J (2021b) Prevalence of *Batrachochytrium dendrobatidis* in Amphibians from 2000 to 2021: a global systematic review and meta-analysis. Front Vet Sci 8:791237. https://doi.org/10.3389/fvets.2021.791237

Li YY, Wang MM, Groenewald M, Li AH, Guo YT, Wu F, Zhang BQ, Tanaka E, Wang QM, Bai FY, Begerow D (2022) 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 11(12):777338

Li W, Jiang Y, Hu C, Liu G, Li Y, Wang S (2023a) Identification, pathogenic mechanism and control of *Rhizopus oryzae* causing postharvest fruit rot in pumpkin. Postharvest Biol Technol 204:112460. https://doi.org/10.1016/j.postharvbio.2023.112460

Li Y, Ji N, Zuo X, Hou Y, Zhang J, Zou Y, Jin P, Zheng Y (2023b) PpMYB308 is involved in *Pichia guilliermondii*-induced disease resistance against *Rhizopus* rot by activating the phenylpropanoid pathway in peach fruit. Postharvest Biol Technol 195:112115. https://doi.org/10.1016/j.postharvbio.2022.112115

Li Y, Zuo X, Ji N, Zhang J, Wang K, Jin P, Zheng Y (2023c) PpMYB1 and PpNPR1 interact to enhance the resistance of peach fruit to *Rhizopus stolonifer* infection. Plant Physiol Biochem 198:107682. https://doi.org/10.1016/j.plaphy.2023.107682

Liang SM, Li QS, Liu MY, Hashem A, Arjani ABFA, Alenazi MM, Allah EFA, Muthuramalingam P, Wu QS (2022) Mycorrhizal effects on growth and expressions of stress-responsive genes (aquaporins and SOSs) of tomato under salt stress. J Fungi 8:1–10. https://doi.org/10.3390/jof8121305

Libkind D, Sampaio JP, van Broock M (2010) *Cystobasidiomycetes* yeasts from Patagonia (Argentina): description of *Rhodotorula meli* sp. nov. from glacial meltwater. Int J Syst Evol Microbiol 60:2251–2256. https://doi.org/10.1099/ijs.0.018499-0

Lichtwardt RW, Lichtwardt RW (1986) Taxonomic treatment. *Trichomycetes* 138–273

Lichtwardt RW, Manier JF (1978) Validation of the *Harpellales* and *Asellariales*. Mycotaxon 7(3):441–442

Lima JLR, Felix JRB, Vieira HS, Nobre CP, Leroy JAS, Fiuza PO, Goto BT (2023) Recovering *arbuscular mycorrhizal* fungi (AMF) from decomposing litter: an unusual approach. New Zealand J of Bot. https://doi.org/10.1080/0028825X.2023.2232332

Lima JLR, Jobim K, Jardim J, Goto BT (2022) Highlighting the species richness of *arbuscular mycorrhizal* fungi (*Glomeromycota*) in the Brazilian semi-arid. Nova Hedwig 114:107–139. https://doi.org/10.1127/nova_hedwigia/2022/0678

Limber DP (1940) A new form genus of the *Moniliaceae*. Mycologia 32:23–30. https://doi.org/10.1080/00275514.1940.12017391

Linder KA, Kauffman CA (2020) Current and new perspectives in the diagnosis of *Blastomycosis* and *Histoplasmosis*. J Fungi 7:12. https://doi.org/10.3390/jof7010012

Linnakoski R, Jyske T, Veteli ER, Cortina-Escribano M, Magalhães F, Magalhaes F, Järvenpää E, Heikkilä L, Hutzler, Gibson B (2023) Brewing potential of strains of the boreal wild yeast *Mrakia gelida*. Front Microbiol 14:1108961. https://doi.org/10.3389/fmicb.2023.1108961

Linnemann G (1941) Die Mucorineen-Gattung *Mortierella Coemans*. Pflanzenforschung 23, Berlin-Dahlem.

Liu YJ, Whelen S, Hall BD (1999) Phylogenetic relationships among *ascomycetes*: evidence from an RNA polymerse II subunit. Mol Biol Evol 16(12):1799–1808. https://doi.org/10.1093/oxfordjournals.molbev.a026092

Liu YJ, Hodson MC, Hall BD (2006) Loss of the flagellum happened only once in the fungal lineage: phylogenetic structure of kingdom *Fungi* inferred from RNA polymerase II subunit genes. BMC Evol Biol 6:74. https://doi.org/10.1186/1471-2148-6-74

Liu Y, Leigh JW, Brinkmann H, Cushion MT, Rodriguez-Ezpeleta N, Philippe H, Lang BF (2009) Phylogenomic analyses support the monophyly of *Taphrinomycotina*, including *Schizosaccharomyces* fission yeasts. Mol Biol Evol 26:27–34. https://doi.org/10.1093/molbev/msn221

Liu NG, Ariyawansa HA, Hyde KD, Maharachchikumbura SS, Zhao RL, Phillips AJ, Jayawardena RS, Thambugala KM, Dissanayake AJ, Wijayawardene NN, Liu JK (2016) Perspectives into the value of genera, families and orders in classification. Mycosphere 7(11):1649–1668

Liu JK, Hyde KD, Jeewon R, Phillips AJ, Maharachchikumbura SS, Ryberg M, Liu ZY, Zhao Q (2017) Ranking higher taxa using divergence times: a case study in *Dothideomycetes*. Fungal Divers 84:75–99

Liu JW, Ge ZW, Horak E, Vizzini A, Halling RE, Pan CL, Yang ZL (2021) *Squamanitacea*e and three new species of *Squamanita* parasitic on *Amanita* basidiomes. IMA Fungus 12:4. https://doi.org/10.1186/s43008-021-00057-z

LoBuglio KF, Pfister DH (2010) Placement of *Medeolaria farlowii* in the *Leotiomycetes*, and comments on sampling within the class. Mycol Prog 9:361–368.https://doi.org/10.1007/s11557-009-0644-y

Lodder J (1970) The yeasts—a taxonomic study, 2nd edn. Elsevier, Amsterdam

Lodder J, Kreger-van Rij NJW (1952) The yeasts—a taxonomic study, 1st edn. Elsevier, Amsterdam

Londero MR, Zanrosso CD, Corso LL, Michelin L, Soldera J (2019) Catheter-related infection due to *Papiliotrema laurentii* in an oncologic patient: case report and systematic review. Braz J Infect Dis 23:451–461. https://doi.org/10.1016/j.bjid.2019.10.005

Longcore JE, Simmons DR (2012) The *Polychytriales* ord. nov. contains chitinophilic members of the rhizophlyctoid alliance. Mycologia 104(1):276–294. https://doi.org/10.3852/11-193

Longcore JE, Simmons DR, Letcher PM (2016) *Synchytrium microbalum* sp. nov. is a saprobic species in a lineage of parasites. Fungal Biol 120(9):1156–1164

López-Fernández J, Valero BMD (2020) *Rhizopus oryzae* lipase, a promising industrial enzyme: biochemical characteristics, production and biocatalytic applications. Catal 10:1277. https://doi.org/10.3390/catal10111277

Lücking R (2019) Stop the abuse of time! strict temporal banding is not the future of rank-based classifications in fungi (including lichens) and other organisms. Crit Rev Plant Sci 38(3):199–253. https://doi.org/10.1080/07352689.2019.1650517

Lücking R, Nelsen MP (2018) Ediacarans, protolichens, and lichen-derived *Penicillium*: a critical reassessment of the evolution of lichenization in fungi. Transform Paleobot. https://doi.org/10.1016/B978-0-12-813012-4.00023-1

Lücking R, Huhndorf S, Pfister DH, Plata ER, Lumbsch HT (2009) Fungi evolved right on track. Mycologia 101(6):810–822

Lücking R, Hodkinson BP, Leavitt SD (2017) The 2016 classification of lichenized fungi in the *Ascomycota* and *Basidiomycota*—approaching one thousand genera. Bryologist 119:361–416. https://doi.org/10.1639/0007-2745-119.4.361

Lumbsch HT, Huhndorf SM (2007) Outline of *Ascomycota*—2007. Myconet 13:1–58

Lumbsch HT, Huhndorf SM (2010) Myconet volume 14. Part one. Outline of *Ascomycota*—2009. Part two. Notes on *Ascomycete* Systematics. Nos. 4751–5113. Fieldiana Life Earth Sci 1:1–64. https://doi.org/10.3158/1557.1

Luttrell ES (1955) The ascostromatic ascomycetes. Mycologia 47:511–532. https://doi.org/10.1080/00275514.1955.12024473

Lutz M, Bauer R, Begerow D, Oberwinkler F, Triebel D (2004a) *Tuberculina*: rust relatives attack rusts. Mycologia 96(3):614–626. https://doi.org/10.1080/15572536.2005.11832957

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. https://doi.org/10.1017/S0953756204009359

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. https://doi.org/10.1080/15572536.2005.11832881

Lutzoni F, Kauff F, Cox JC, McLaughlin D, Celio G, Dentinger B, Padamsee M, Hibbett D, James TY, Baloch E, Grube M, Reeb V, Hofstetter V, Schoch C, Arnold AE, Miadlikowska J, Spatafora J, Johnson D, Hambleton S, Crockett M, Shoemaker R, Sung G-H, Lücking R, Lumbsch T, O'Donnell K, Binder M, Diederich P, Ertz D, Gueidan C, Hansen K, Harris RC, Hosaka K, Lim Y-W, Matheny B, Nishida H, Pfister D, Rogers J, Rossman A, Schmitt I, Sipman H, Stone J, Sugiyama J, Yahr R, Vilgalys R (2004) Assembling the fungal tree of life: progress, classification, and evolution of subcellular traits. Am J Bot 91:1446–1480. https://doi.org/10.3732/ajb.91.10.1446

Ma Y, Rajkumar M, Oliveira RS, Zhang C, Freitas H (2019) Potential of plant beneficial bacteria and *arbuscular mycorrhizal* fungi in phytoremediation of metal-contaminated saline soils. J Hazard Mater 379:120813. https://doi.org/10.1016/j.jhazmat.2019.120813

Ma X, Yang M, He Y, Zhai C, Li C (2021) A review on the production, structure, bioactivities and applications of *Tremella* polysaccharides. Int J Immunopathol Pharmacol 35:1–14. https://doi.org/10.1177/20587384211000541

Maatallah F, Mtibaa L, Stambouli H, Baccouchi N, Ghdira H, Souid H, Sami Z, Fehmi M, Jemli B (2022) First case of pulmonary mucormycosis caused by *Rhizomucor miehei*. J Clin Images Med Case Rep 3:1–4

Maekawa N (1987) A new species of the genus *Cerinomyces*. Canad J Bot 65:583–588. https://doi.org/10.1139/b87-074

Maharachchikumbura SS, Hyde KD, Jones EG, McKenzie EH, Huang SK, Abdel-Wahab MA, Daranagama DA, Dayarathne M, D'souza MJ, Goonasekara ID, Hongsanan S (2015) Towards a natural classification and backbone tree for *Sordariomycetes*. Fungal Divers 72:199–301. https://doi.org/10.1007/s13225-015-0331-z

Malar CM, Krüger M, Krüger C, Wang Y, Stajich JE, Keller J, Chen ECH, Yildirir G, Villeneuve-Laroche M, Roux C, Delaux PM, Corradi N (2021) The genome of *Geosiphon pyriformis* reveals ancestral traits linked to the emergence of the *arbuscular mycorrhizal* symbiosis. Curr Biol 31(7):1570-1577.e4. https://doi.org/10.1016/j.cub.2021.01.058

Malicka M, Magurno F, Piotrowska-Seget Z (2022) Phenol and polyaromatic hydrocarbons are stronger drivers tthan host plant species in shaping the *arbuscular mycorrhizal* fungal component of the mycorrhizosphere. Int J Mol Sci 23:12585. https://doi.org/10.3390/ijms232012585

Malone T, Swinton SM, Pudasainee A, Bonito G (2022) Economic assessment of Morel (*Morchella* spp.) foraging in Michigan, USA. Econ Bot 76:1–15. https://doi.org/10.1007/s12231-022-09548-5

Malysheva V, Spirin V, Schoutteten N, De Lange R, Pennanen J, Larsson KH (2020) New and noteworthy species of *Helicogloea* (*Atractiellomycetes*, *Basidiomycota*) from Europe. Ann Bot Fenn 57(1–3):1–7. https://doi.org/10.5735/085.057.0101

Malysheva V, Schoutteten N, Verbeken A, Spirin V (2021) Identity and typification of *Achroomyces effusus* (*Pucciniomycotina*, *Basidiomycota*). Mycol Progress 20:413–417. https://doi.org/10.1007/s11557-021-01671-2

Manamgoda D, Cai L, McKenzie EHC, Crous PW, Madrid H, Chukeatirote E, Shivas RG, Tan YP, Hyde KD (2012) A phylogenetic and taxonomic re-evaluation of the *Bipolaris-Cochliobolus-Curvularia* complex. Fungal Divers 56:131–144. https://doi.org/10.1007/s13225-012-0189-2

Mandal K, Ghosh D, Kar CS (2023) Stem rot of jute (*Corchorus* spp.): new insight on its causal organisms. Plant Pathol 72:322–333. https://doi.org/10.1111/ppa.13656

Manfrão-Netto JHC, Gomes AMV, Parachin NS (2019) Advances in using *Hansenula polymorpha* as chassis for recombinant protein production. Front Bioeng Biotechnol 7:2296–4185. https://doi.org/10.3389/fbioe.2019.00094

Manier JF, Lichtwardt RW (1969) Révision de la Systématique des *Tricomycètes*. Annales Des Sciences Naturelles Botanique 9:519–532

Marek LE (1984) Light affects in vitro development of gametangia and sporangia of *Monoblepharis macrandra* (*Chytridiomycetes*, *Monoblepharidales*). Mycologia 76(3):420–425

Margulies M, Egholm M, Altman WE, Attiya S, Bader JS, Bemben LA, Berka J, Braverman MS, Chen YJ, Chen Z, Dewell SB (2005) Genome sequencing in microfabricated high-density picolitre reactors. Nature 437(7057):376–380

Martin WJ (1964) Effectiveness of fungicides in reducing soft rot in washed, cured sweet potatoes. Plant Dis Report 48:606–607

Martínez-Herrera EO, Arroyo-Camarena S, Tejada-García DL, Porras-López CF, Arenas R (2015) Onychomycosis due to opportunistic molds. An Bras Dermatol 90:334–337. https://doi.org/10.1590/abd1806-4841.20153521

Marvanová L, Bandoni RJ (1987) *Naiadella fluitans* gen. et sp. nov.: a conidial basidiomycete. Mycologia 79(4):578–586

Matheny PB, Gossmann JA, Zalar P, Kumar TA, Hibbett DS (2006) Resolving the phylogenetic position of the *Wallemiomycetes*: an enigmatic major lineage of *Basidiomycota*. Botany 84:1794–1805. https://doi.org/10.1139/b06-128

Maziarz EK, Perfect JR (2016) Cryptococcosis. Infect Dis Clin N Am 30:179–206. https://doi.org/10.1016/j.idc.2015.10.006

McCarty NS, Ledesma-Amaro R (2019) Synthetic biology tools to engineer microbial communities for biotechnology. Trends Biotechnol 37:181–197. https://doi.org/10.1016/j.tibtech.2018.11.002

McCully EK, Robinow CF (1972a) Mitosis in heterobasidiomycetous yeasts. I. *Leucosporidium scottii* (*Candida scottii*). J Cell Sci 10:857–881

McCully EK, Robinow CF (1972b) Mitosis in heterobasidiomycetous yeasts. II. *Rhodosporidium* sp. (*Rodotorula glutinis*) and *Aessosporon salmonicolor* (*Sporobolomyces salmonicolor*). J Cell Sci 11:1–31

McKenzie RA, Connole MD, McGinnis MR, Lepelaar R (1984) Subcutaneous phaeohyphomycosis caused by *Moniliella suaveolens* in two cats. Vet Pathol 21(6):582–586. https://doi.org/10.1177/030098588402100606

McNeil JC, Palazzi DL (2012) *Ustilago* as a cause of fungal peritonitis: case report and review of the literature. J Pediatr Infect Dis Soc 1:337–339. https://doi.org/10.1093/jpids/pis043

McNeil BA, Stuart DT (2018) *Lipomyces starkeyi*: an emerging cell factory for production of lipids, oleochemicals and biotechnology applications. World J Microbiol Biotechnol 34:147. https://doi.org/10.1007/s11274-018-2532-6

McTaggart AR, Shivas RG, Boekhout T, Oberwinkler F, Vánky K, Pennycook SR, Begerow D (2016) *Mycosarcoma* (*Ustilaginaceae*), a resurrected generic name for corn smut (*Ustilago maydis*) and its close relatives with hypertrophied, tubular sori. IMA Fungus 79(2):309–315. https://doi.org/10.5598/imafungus.2016.07.02.10

Medeiros AS, Goto BT, Ganade G (2021) Ecological restoration methods influence the structure of *arbuscular mycorrhizal* fungal communities in degraded drylands. Pedobiol 84:150690. https://doi.org/10.1016/j.pedobi.2020.150690

Medeiros ADM, Junior CJGS, Souza AF, Cavalcanti DL, Rodriguez DM, Silva CAA, Andrade RFS (2022) Production of biosurfactant by *Cunninghamella elegans* UCP 0542 using food industry waste in 3 L flasks and evaluation of orbital agitation effect. Res Soc Dev. https://doi.org/10.33448/rsd-v11i4.27438

Mehrotra VS (1998) *Arbuscular mycorrhizal* associations of plants colonizing coal mine spoil in India. J Agric Sci 130(2):125–133. https://doi.org/10.1017/S0021859697005091

Mehta V, Nayyar C, Gulati N, Singla N, Rai S, Chandar J (2021) A comprehensive review of *Trichosporon* spp.: an invasive and emerging fungus. Cureus 13:e17345. https://doi.org/10.7759/cureus.17345

Mekha N, Takashima M, Boon-long J, Cho O, Sugita T (2014) Three new *basidiomycetous* yeasts, *Pseudozyma alboarmeniaca* sp. nov., *Pseudozyma crassa* sp. nov. and *Pseudozyma siamensis* sp. nov. isolated from Thai patients. Microbiol Immunol 58(1):9–14. https://doi.org/10.1111/1348-0421.12111

Mello CMA, Silva GA, Assis DMA, Pontes JS, de Mello CMA, da Silva GA, de Assis DMA, de Pontes JS, de Almeida Ferreira AC, Leão MPC, Vieira HEE, Maia LC, Oehl F (2013) *Paraglomus pernambucanum* sp. nov. and *Paraglomus bolivianum* com. nov., and biogeographic distribution of *Paraglomus* and *Pacispora*. J Appl Bot Food Qual 86:113–125. https://doi.org/10.5073/JABFQ.2013.086.016

Meng LL, He JD, Zou YN, Wu QS, Kuča K (2020) Mycorrhiza-released glomalin-related soil protein fractions contribute to soil total nitrogen in trifoliate orange. Plant Soil Environ 66:183–189

Menkis A, Urbina H, James TY, Rosling A (2014) *Archaeorhizomyces borealis* sp. nov. and a sequence-based classification of related soil fungal species. Fungal Biol 118:943–955. https://doi.org/10.1016/j.funbio.2014.08.005

Meyer W, Gams W (2003) Delimitation of *Umbelopsis* (*Mucorales*, *Umbelopsidaceae* fam. nov.) based on ITS sequence and RFLP data. Mycol Res 107(3):339–350. https://doi.org/10.1017/S0953756203007226

Miądlikowska J, Kauff F, Hofstetter V, Fraker E, Grube M, Hafellner J, Reeb V, Hodkinson BP, Kukwa M, Lücking R, Hestmark G, Otalora GM, Rauhut A, Büdel B, Scheidegger C, Timdal E, Stenroos S, Brodo I, Perlmutter GB, Ertz D, Diederich P, Lendemer JC, May P, Schoch CL, Arnold AE, Gueidan C, Tripp E, Yahr R, Robertson C, Lutzoni F (2006) New insights into classification and evolution of the *Lecanoromycetes* (*Pezizomycotina*, *Ascomycota*) from phylogenetic analyses of three ribosomal RNA and two protein-coding genes. Mycologia 98:1088–1103

Miądlikowska J, Kauff F, Oliver HF, JC, Molnár K, Fraker E, Gaya E, Hafellner J, Hofstetter V, Gueidan C, Otálora MAG, Hodkinson B, Kukwa M, Lücking R, Björk C, Sipman HJM, Burgaz AR, Thell A, Passo A, Myllys L, Goward T, Fernández-Brime S, Hestmark G, Lendemer J, Lumbsch HT, Schmull M, Schoch CL, Sérusiaux E, Maddison DR, Arnold AE, Lutzoni F, Stenroos S, (2014) A multigene phylogenetic synthesis for the class *Lecanoromycetes* (*Ascomycota*): 1307 fungi representing 1139 infrageneric taxa, 317 genera and 66 families. Mol Phylogenet Evol 79:132–168. https://doi.org/10.1016/j.ympev.2014.04.003

Michailides TJ, Spotts RA (1988) Germination of zygospores of *Mucor piriformis* on the life history of *Mucor piriformis*. Mycologia 80:837–844. https://doi.org/10.2307/3807563

Mikhailov KV, Karpov SA, Letcher PM, Lee PA, Logacheva MD, Penin AA, Nesterenko MA, Pozdnyakov IR, Potapenko EV, Sherbakov DY, Panchin YV, Aleoshin VV (2022) Genomic analysis reveals cryptic diversity in aphelids and sheds light on the emergence of *Fungi*. Curr Biol 32(21):4607–4619.https://doi.org/10.1016/j.cub.2022.08.071

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. https://doi.org/10.1016/j.ympev.2011.05.014

Millanes AM, Diederich P, Wedin M (2016) Cyphobasidium gen. nov., a new lichen-inhabiting lineage in the *Cystobasidiomycetes* (*Pucciniomycotina*, *Basidiomycota*, *Fungi*). Fungal Biol 120(11):1468–1477

Millanes AM, Diederich P, Westberg M, Wedin M (2021) *Crittendenia* gen. nov., a new lichenicolous lineage in the *Agaricostilbomycetes* (*Pucciniomycotina*), and a review of the biology, phylogeny and classification of lichenicolous heterobasidiomycetes. Lichenologist 53(1):103–116

Mills J (1986) *Pneumocystis carinii* and *Toxoplasma gondii* infections in patients with AIDS. Rev Infect Dis 8:1001–1011. https://doi.org/10.1093/clinids/8.6.1001

Minnis AM, Lindner DL (2013) Phylogenetic evaluation of *Geomyces* and allies reveals no close relatives of *Pseudogymnoascus destructans*, comb. nov., in bat hibernacula of eastern North America. Fungal Biol 117(9):638–649

Miranda-González R, Bungartz F, Lücking R, Gaya E, de Oliveira MC, Viñas-Portilla C, da Silva Cáceres ME, de los Angeles Herrera-Campos M (2022) Phylogeny of the *Pyrenula ochraceoflava* group (*Pyrenulaceae*) reveals near-cryptic diversification and the inclusion of the *Mazaediothecium album* aggregate. Bryologist 125:541–557. https://doi.org/10.1639/0007-2745-125.4.541

Mirzaie M, Ladanmoghadam AR, Hakimi L, Danaee E (2020) Water stress modifies essential oil yield and composition, glandular trichomes and stomatal features of lemongrass (*Cymbopogon citratus*) inoculated with *arbuscular mycorrhizal* fungi. J Agric Sci Technol 22(6):1575–1585

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

Mitchell JI, Zuccaro A (2006) Sequences, the Environment and Fungi. Mycologist 20:62–74

Mitra S, Banerjee M (2000) On the occurrence of epiphyllous Deuteromycetous fossil fungi *Palaeocercospora siwalikensis* gen. et sp. nov. and *Palaeocolletotrichum graminioides* gen. et sp. nov. from Neogene sediments of Darjeeling Foothills, Eastern Himalaya. J Mycopathol Res 37(2):7–11

Mix AJ (1949) A monograph of the genus *Taphrina*. Univ Kansas Sci Bull. https://doi.org/10.5962/bhl.part.16125

Money NP (2016) Fungi diversity. In: The Fungi. Miami University, Oxford

Montoliu-Nerin M, Sánchez-García M, Bergin C, Kutschera VE, Johannesson H, Bever JD, Rosling A (2021) In-depth phylogenomic analysis of *arbuscular mycorrhizal* fungi based on a comprehensive set of de novo genome assemblies. Front Fungal Biol 2:716385. https://doi.org/10.3389/ffunb.2021.716385

Moore RT (1980) Taxonomic proposals for the classification of marine yeasts and other yeast-like fungi including the smuts. Bot Mar 23(6):361–373

Moraes RNR, Ribeiro MCT, Nogueira MCL, Soares MMCN, Almeida MTG (2010) First report of *Tritirachium oryzae* infection of human scalp. Mycopathologia 169:257–259. https://doi.org/10.1007/s11046-009-9253-1

Moreira H, Pereira SI, Vega A, Castro PM, Marques AP (2020) Synergistic effects of *arbuscular mycorrhizal* fungi and plant growth-promoting bacteria benefit maize growth under increasing soil salinity. J Environ Manag 257:109982. https://doi.org/10.1016/j.jenvman.2019.109982

Morton JB, Benny GL (1990) Revised classification of *arbuscular mycorrhizal* fungi (*Zygomycetes*): a new order, *Glomales*, two new suborders, *Glomineae* and *Gigasporineae*, and two new families, *Acaulosporaceae* and *Gigasporaceae*, with an emendation of *Glomaceae*. Mycotaxon 37:471–491

Morton JB, Redecker D (2001) Two new families of *Glomales*, *Archaeosporaceae* and *Paraglomaceae*, with two new genera *Archaeospora* and *Paraglomus*, based on concordant molecular and morphological characters. Mycologia 93(1):181–195. https://doi.org/10.1080/00275514.2001.12063147

Mozley-Standridge SE, Letcher PM, Longcore JE, Porter D, Simmons DR (2009) *Cladochytriales*—a new order in *Chytridiomycota*. Mycol Res 113:498–507. https://doi.org/10.1016/j.mycres.2008.12.004

Muggia L, Ametrano CG, Sterflinger K, Tesei D (2020) An overview of genomics, phylogenomics and proteomics approaches in *Ascomycota*. Life 10(12):356

Mukherjee V, Radecka D, Aerts G, Verstrepen KJ, Lievens B, Thevelein JM (2017) Phenotypic landscape of non-conventional yeast species for different stress tolerance traits desirable in bioethanol fermentation. Biotechnol Biofuels 10:216. https://doi.org/10.1186/s13068-017-0899-5

Müller E, Petrini O, Fisher PJ, Samuels GJ, Rossman AY (1987) Taxonomy and anamorphs of the *Herpotrichiellaceae* with notes on generic synonymy. Trans Br Mycol Soc 88:63–74. https://doi.org/10.1016/S0007-1536(87)80186-9

Musyoka DM, Njeru EM, Nyamwange MM, Maingi JM (2020) *Arbuscular mycorrhizal* fungi and *Bradyrhizobium* co-inoculation enhances nitrogen fixation and growth of green grams (*Vigna radiata* L.) under water stress. J Plant Nutr 43:1036–1047. https://doi.org/10.1080/01904167.2020.1711940

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 provide insights into the origins of lignocellulosic decay capabilities. Mol Biol Evol 33(4):959–970. https://doi.org/10.1093/molbev/msv337

Nakase T (2000) Expanding world of ballistosporous yeasts: Distribution in the phyllosphere, systematics and phylogeny. J Gen Appl Microbiol 46:189–216. https://doi.org/10.2323/jgam.46.189

Nakashima K, Tomida J, Hirai T, Kawamura Y, Inoue M (2019) Paraconiothins A-J: sesquiterpenoids from the endophytic fungus *Paraconiothyrium brasiliense* ECN258. J Nat Prod 82:3347–3356. https://doi.org/10.1021/acs.jnatprod.9b00638

Naranjo-Ortiz MA, Gabaldón T (2019) Fungal evolution: diversity, taxonomy and phylogeny of the fungi. Biol Rev 94(6):2101–2137. https://doi.org/10.1111/brv.12550

Nardi JB, Bee CM, Miller LA, Nguyen NH, Suh SO, Blackwell M (2006) Communities of microbes that inhabit the changing hindgut landscape of a subsocial beetle. Arthropod Struct Dev 35:57–68. https://doi.org/10.1016/j.asd.2005.06.003

Naseri A, Fata A, Najafzadeh MJ (2013) First case of *Tritirachium oryzae* as agent of onychomycosis and its susceptibility to antifungal drugs. Mycopathologia 176:119. https://doi.org/10.1007/s11046-013-9653-0

Nassonova ES, Bondarenko NI, Paskerova GG, Kováčiková M, Frolova EV, Smirnov AV et al (2016) Evolutionary relationships of *Metchnikovella dogieli* Paskerova et al., 2016 (*Microsporidia*: *Metchnikovellidae*) revealed by multigene phylogenetic analysis. Parasitol Res 120(2):525–234

Naz T, Nosheen S, Li S, Nazir Y, Mustafa K, Liu Q, Garre V, Song Y (2020) Comparative analysis of β-carotene production by *Mucor circinelloides* strains CBS 277.49 and WJ11 under light and dark conditions. Metab 10:38. https://doi.org/10.3390/metabo10010038

Nguyen HD, Nickerson NL, Seifert KA (2013) *Basidioascus* and *Geminibasidium*: a new lineage of heat-resistant and xerotolerant *basidiomycetes*. Mycologia 105(5):1231–1250. https://doi.org/10.3852/12-351

Nguyen LT, Schmidt HA, von Haeseler A, Minh BQ (2015) IQ-TREE: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. Mol Biol Evol 32(1):268–274. https://doi.org/10.1093/molbev/msu300

Nguyen TTT, Voigt K, Santiago ALCMA, Kirk PM, Lee HB (2021) Discovery of novel *Backusella* (*Backusellaceae*, *Mucorales*) isolated from invertebrates and toads in Cheongyang. Korea J Fungi 7:513. https://doi.org/10.3390/jof7070513

Nie Y, Yu DS, Wang CF, Liu XY, Huang B (2020) A taxonomic revision of the genus *Conidiobolus* (*Ancylistaceae*, *Entomophthorales*): Four clades including three new genera. MycoKeys 66:55–81. https://doi.org/10.3897/mycokeys.66.46575

Niego AGT, Lambert C, Mortimer P, Thongklang N, Rapior S, Grosse M, Schrey H, Charria-Girón E, Walker A, Hyde KD, Stadler M (2023) The contribution of fungi to the global economy. Fungal Divers 121:95–137. https://doi.org/10.1007/s13225-023-00520-9

Nielsen J, Thomas P (1996) Loose Smut. In: Wilcoxson RD, Saari EE (ed) Bunt and smut diseases of wheat concepts and methods of disease management. CIMMYT, Mexico, pp 33–47

Nilsson RH, Larsson K-H, Taylor AFS, Bengtsson-Palme J, Jeppesen TS, Schigel D, Kennedy P, Picard K, Glöckner FO, Tedersoo L, Saar I, Kõljalg U, Abarenkov K (2018) The UNITE database for molecular identification of fungi: handling dark taxa and parallel taxonomic classifications. Nucleic Acids Res 47:D259–D264

Nishida H, Katsuhiko A, Ando Y, Hirata A, Sugiyama (1995) *Mixia osmundae*: transfer from the *Ascomycota* to the *Basidiomycota* based on evidence from molecules and morphology. Canad J Bot 73:S660–S666. https://doi.org/10.1139/b95-308

Niskanen T, Lücking R, Dahlberg A, Gaya E, Suz LM, Mikryukov V, Liimatainen K, Druzhinina I, Westrip JR, Mueller GM, Martins-Cunha K, Kirk P, Tedersoo L, Antonelli A (2023) Pushing the frontiers of biodiversity research: unveiling the global diversity, distribution, and conservation of fungi. Annu Rev Environ Resour 48:149–176. https://doi.org/10.1146/annurev-environ-112621-090937

Norman JE, Egger KN (1999) Molecular phylogenetic analysis of *Peziza* and related genera. Mycologia 91:820–829. https://doi.org/10.1080/00275514.1999.12061087

Nout MJR, Kiers JL (2005) Tempe fermentation, innovation and functionality: update into the third millennium. J Appl Microbiol 98:789–805. https://doi.org/10.1111/j.1365-2672.2004.02471.x

Nutaratat P, Boontham W, Khunnamwong P (2022) A novel yeast genus and two novel species isolated from pineapple leaves in Thailand: S*avitreella phatthalungensis* gen. nov., sp. nov. and *Goffeauzyma siamensis* sp. nov. J Fungi 8(2):118

Oberwinkler F (1994) Genera in a monophyletic group: the *Dacrymycetales*. Mycologia Helvetica 6:35–72

Oberwinkler F (2014) *Dacrymycetes*. In: McLaughlin DJ, Spatafora JW (eds) Systematics and evolution, Part A 2nd edn, Berlin, pp 357–372

Oberwinkler F (2017) Yeasts in *Pucciniomycotina*. Mycol Prog 16:831–856. https://doi.org/10.1007/s11557-017-1327-8

Oberwinkler F, Bandoni RJ (1982a) *Atractogloea*: a new genus in the *Hoehnelomycetaceae* (*Heterobasidiomycetes*). Mycologia 74:634–639. https://doi.org/10.1080/00275514.1982.12021560

Oberwinkler F, Bandoni RJ (1982b) A taxonomic survey of the gasteroid, auricularioid *Heterobasidiomycetes*. Canad J Bot 60:1726–1750. https://doi.org/10.1139/b82-221

Oberwinkler F, Bauer R (1989) The systematics of gastroid, auricularioid *Heterobasidiomycetes*. Sydowia 41:224–256

Oberwinkler F, Bauer R (1990a) *Cryptomycocolax*: a new mycoparasitic *heterobasidiomycete*. Mycologia 82:671–692. https://doi.org/10.1080/00275514.1990.12025948

Oberwinkler F, Bauer R, Bandoni RJ (1990) *Heterogastridiales*: a new order of *Basidiomycetes*. Mycologia 82(1):48–58

Oberwinkler F, Kirschner R, Arenal F, Villarreal M, Rubio V, Begerow D, Bauer R (2006a) Two new pycnidial members of the *Atractiellales*: *Basidiopycnis hyalina* and *Proceropycnis pinicola*. Mycologia 98:637–649. https://doi.org/10.1080/15572536.2006.11832667

Oehl F, Sieverding E (2004) *Pacispora*, a new vesicular arbuscular mycorrhizal fungal genus in the *Glomeromycetes*. J Appl Bot 78:72–82

Oehl F, Silva GA, Goto BT, Maia LC, Sieverding E (2008) *Glomeromycota*: two new classes and a new order. Mycotaxon 116:365–379. https://doi.org/10.5248/116.365

Oehl F, Sieverding E, Palenzuela J, Ineichen K, da Silva GA (2011a) Advances in *Glomeromycota* taxonomy and classification. IMA Fungus 2(2):191–199

Oehl F, Silva GA, Goto BT, Sieverding E (2011b) *Glomeromycota*: three new genera and glomoid species reorganized. Mycotaxon 116:75–120. https://doi.org/10.5248/116.75

Oehl F, Santos VM, Palenzuela J (2016) *Paraglomus turpe*, a new *arbuscular mycorrhizal* fungal species from Central European agricultural soils. Nova Hedwig 103(3):491–499. https://doi.org/10.1127/nova_hedwigia/2016/0367

Ojo AO, de Smidt O (2023) Microbial composition, bioactive compounds, potential benefits and risks associated with kombucha: a concise review. Ferment 9(5):472. https://doi.org/10.3390/fermentation9050472

Ökmen B, Schwammbach D, Bakkeren G, Neumann U, Doehlemann G (2021) The *Ustilago hordei*-barley interaction is a versatile system for characterization of fungal effectors. J Fungi 7(2):86. https://doi.org/10.3390/jof7020086

Okolo OM, Van Diepeningen AD, Toma B, Nnadi NE, Ayanbimpe MG, Onyedibe IK, Sabitu MZ, Banwat BE, Groenewald M, Scordino F, Egah ZD, Criseo G, Romeo O (2015) First report of neonatal sepsis due to *Moesziomyces* bullatus in a preterm low-birth-weight infant. JMM Case Rep. https://doi.org/10.1099/jmmcr.0.000011

Olariaga I, Buyck B, Esteve-Raventós F, Hofstetterd V, ManJóna JL, Morenoa G, Salcedo I (2015) Assessing the taxonomic identity of white and orange specimens of *Cantharellus*: occasional colour variants or independent species? Cryptogam Mycolog 36:287–301. https://doi.org/10.7872/crym/v36.iss3.2015.287

Oliach D, Vidale E, Brenko A, Marois O, Andrighetto N, Stara K, de Aragón JM, Colinas C, Bonet JA (2021) Truffle market evolution: an application of the Delphi method. Forests 12:1174. https://doi.org/10.3390/f12091174

Olive LS (1980) *Caulochytrium protostelioides* sp. nov., a new chytrid with aerial sporangia. Am J Bot 67(4):568–574

Olive LS (1983) A new variety of *Caulochytrium protostelioides*. Mycologia 75(5):923–926

Opulente DA, Langdon QK, Buh KV, Haase MAB, Sylvester K, Moriarty RV, Jarzyna M, Considine SL, Schneider RM, Hittinger CT (2019) Pathogenic budding yeasts isolated outside of clinical settings. FEMS Yeast Res 19:32

Ortiz SC, Pennington K, Thomson DD, Bertuzzi M (2022) Novel insights into *Aspergillus fumigatus* pathogenesis and host response from state-of-the-art imaging of host-pathogen interactions during Infection. J Fungi 8:264

Osório-Aragon IY, Toussaint-Claire S, Guzmán-Bucio S, Barbosa-Ramírez BM, Vázquez-Aceituno VA, Xicohtencatl-Cortes J, Hernández-Castro R (2023) Primary cutaneous mucormycosis due to *Rhizopus arrhizus* in an immunosuppressed patient with paroxysmal nocturnal haemoglobinuria. Trop Med Int Health 28(7):580–584. https://doi.org/10.1111/tmi.13898

Otani Y (1982) Cup fungi in Nepal 1. In: Otany Y (ed) Reports on the cryptogamic study in Nepal. National Science Museum Tokyo, Tokyo, pp 75–91

Palmieri D, Barone G, Cigliano RA, Curtis FD, Lima G, Castoria R, Ianiri G (2021) Complete genome sequence of the biocontrol yeast *Papiliotrema terrestris* strain LS28. G3 Genes Genomes Genetics 11:332. https://doi.org/10.1093/g3journal/jkab332

Pan WH, Liao WQ, Hagen F, Theelen B, Shi WM, Meis JF, Boekhout T (2012) Meningitis caused by *Filobasidium uniguttulatum*: case report and overview of the literature. Mycoses 55:105–109. https://doi.org/10.1111/j.1439-0507.2011.02054.x

Park MJ, Shin HD (2011) *Cladophialophora pucciniophila*, a new *hyphomycete* parasitizing a rust fungus. Mycotaxon 116:449–456. https://doi.org/10.5248/116.449

Patel RN (2001) Enzymatic synthesis of chiral intermediates for Omapatrilat, an antihypertensive drug. Biomol Eng 17:167–182. https://doi.org/10.1016/S1389-0344(01)00068-5

Paul NC, Kim WK, Woo SK, Park MS, Yu SH (2007) Fungal endophytes in roots of *Aralia* species and their antifungal activity. Plant Pathol J 23(4):287–294. https://doi.org/10.5423/PPJ.2007.23.4.287

Pawłowska J, Okrasińska A, Kisło K, Aleksandrzak-Piekarczyk T, Szatraj K, Dolatabadi S, Muszewska A (2019) Carbon assimilation profiles of mucoralean fungi how their metabolic versatility. Sci Rep 9:11864. https://doi.org/10.1038/s41598-019-48296-w

Peng X, Wei Z, Wang L, Cheng J (2023) Invasive splenic mucormycosis due to *Rhizopus microsporus* during chemotherapy for acute monocytic leukemia: a case report and literature review. Front Oncol 13:1237807. https://doi.org/10.3389/fonc.2023.1237807

Pérez-Ortega S, Garrido-Benavent I, Grube M, Olmo R, de los Ríos A (2016) Hidden diversity of marine borderline lichens and a new order of fungi: *Collemopsidiales* (*Dothideomyceta*). Fungal Divers 80:285–300

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 Evol Microbiol **71**: 004655 https://doi.org/10.1099/ijsem.0.004655

Perry BA, Hansen K, Pfister DH (2007) A phylogenetic overview of the family *Pyronemataceae* (*Ascomycota*, *Pezizales*). Mycol Res 111:549–571. https://doi.org/10.1016/j.mycres.2007.03.014

Petersen HE (1910) An account of Danish freshwater *Phycomycetes*, with biological and systematical remarks. Ann Mycol 8:494–560

Petersen PM (1970) Danish fireplace fungi. An ecological investigation on fungi on burns. Dansk Botanisk Arkiv 27:1–97

Pfister DH (1997) Castor, Pollux and life histories of fungi. Mycologia 89:1–23

Pfister DH, Healy R (2021) *Pezizomycetes*. In: Zaragoza O (ed) Encyclopedia of mycology, vol 1. Elsevier, Oxford, pp 295–309

Philippe H, Brinkmann H, Lavrov DV, Littlewood DT, Manuel M, Worheide G, Baurain D (2011) Resolving difficult phylogenetic questions: why more sequences are not enough. PLoS Biol 9(3):e1000602. https://doi.org/10.1371/journal.pbio.1000602

Phillips AJL, Alves A, Abdollahzadeh J, Slippers B, Wingfield MJ, Groenewald JZ, Crous PW (2013) The *Botryosphaeriaceae*: genera and species known from culture. Stud Mycol 76:51–167. https://doi.org/10.3114/sim0021

Piątek M, Lutz M, Sousa FMP, Santos ARO, Félix CR, Landell MF, Gomes FCO, Rosa CA (2017) *Pattersoniomyces tillandsiae* gen. et comb. nov.: linking sexual and asexual morphs of the only known smut fungus associated with *Bromeliaceae*. Org Divers Evol 17:531–543. https://doi.org/10.1007/s13127-017-0340-8

Piepenbring M (2001) Smut fungi (*Ustilaginomycetes* and *Microbotryales*, *Basidiomycota*) in Panama. Rev Biol Trop 49(2):411–428

Pinheiro BG, Hahn RC, Camargo ZP, Rodrigues AM (2020) Molecular tools for detection and identification of *Paracoccidioides* species: current status and future perspectives. J Fungi 6:293. https://doi.org/10.3390/jof6040293

Pinto-Figueroa EA, Seddon E, Yashiro E, Buri A, Niculita-Hirzel H, van der Meer JR, Guisan A (2019) *Archaeorhizomycetes* spatial distribution in soils along wide elevational and environmental gradients reveal co-abundance patterns with other fungal saprobes and potential weathering capacities. Front Microbiol 10:656. https://doi.org/10.3389/fmicb.2019.00656

Pipiková J, Horváthová Á, Schusterová H, Vadkertiová R (2023) *Moniliella zaluziensis* sp. nov., a black yeast related to fruit trees of the *Rosaceae* family. Int J Syst Evol Microbiol 73(2):005719. https://doi.org/10.1099/ijsem.0.005719

Platt JL, Spatafora JW (2000) Evolutionary relationships of nonsexual lichenized fungi: molecular phylogenetic hypotheses for the genera *Siphula* and *Thamnolia* from SSU and LSU rDNA. Mycologia 92(3):475–487. https://doi.org/10.1080/00275514.2000.12061183

Polo-Marcial MH, Lara-Pérez LA, Goto BT, Margarito-Vista X, Andrade-Torres A (2021) *Glomeromycota* in Mexico: a country with very high richness. Sydowia 74:33–63

Porter TM, Schadt CW, Rizvi L, Martin AP, Schmidt SK, Scott-Denton L, Vilgalys R, Moncalvo JM (2008) Widespread occurrence and phylogenetic placement of a soil clone group adds a prominent new branch to the fungal tree of life. Mol Phylogenet Evol 46:635–644. https://doi.org/10.1016/j.ympev.2007.10.002

Porter TM, Martin W, James TY, Longcore JE, Gleason FK, Adler PH, Letcher PM, Vilgalys R (2011) Molecular phylogeny of the *Blastocladiomycota* (*Fungi*) based on nuclear ribosomal DNA. Fungal Biol 115:381–392. https://doi.org/10.1016/j.funbio.2011.02.004

Powell MJ (2017) *Blastocladiomycota*. In: Archibald J, Simpson A, Slamovits C (eds) Handbook of the protists. Springer, Cham

Powell MJ, Letcher PM (2014) *Chytridiomycota*, *Monoblepharidomycota*, and *Neocallimastigomycota*. In: Esser K (ed) The Mycota VII Systematics and Evolution PartA. Springer, Berlin e Heidelberg, pp 141–176

Powell MJ, Letcher PM, Longcore JE, Blackwell WH (2018) *Zopfochytrium* is a new genus in the *Chytridiales* with distinct zoospore ultrastructure. Fungal Biol 122:1041–1049. https://doi.org/10.1016/j.funbio.2018.08.005

Pozdnyakov IR, Potapenko EV, Nassonova ES, Babenko VV, Boldyreva DI, Tcvetkova VS, Karpov SA (2023) To the origin of fungi: analysis of MFS transporters of first assembled *Aphelidium* genome highlights dissimilarity of osmotrophic abilities between *Aphelida* and *Fungi*. J Fungi 9:1021. https://doi.org/10.3390/jof9101021

Prieto M, Wedin M (2013) Dating the diversification of the major lineages of *Ascomycota* (Fungi). PLoS ONE 8(6):e65576

Prieto M, Baloch E, Tehler A, Wedin M (2013) Mazaedium evolution in the *Ascomycota* (*Fungi*) and the classification of mazaediate groups of formerly unclear relationship. Cladistics 29:296–308. https://doi.org/10.1111/j.1096-0031.2012.00429.x

Prieto M, Schultz M, Olariaga I, Wedin M (2019) *Lichinodium* is a new lichenized lineage in the *Leotiomycetes*. Fungal Divers 94(1):23–39. https://doi.org/10.1007/s13225-018-0417-5

Prieto M, Etayo J, Olariaga I (2021) A new lineage of mazaediate fungi in the *Eurotiomycetes*: *Cryptocaliciomycetidae* subclass. nov., based on the new species *Cryptocalicium blascoi* and the revision of the ascoma evolution. Mycol Prog 20:889–904. https://doi.org/10.1007/s11557-021-01710-y

Prokhorov VP, Bodyagin VV (2007) The ecology of aero-aquatic *hyphomycetes*. Moscow Univ Biol Sci Bull 62:15–20. https://doi.org/10.3103/S009639250701004X

Pruksaphon K, Nosanchuk JD, Ratanabanangkoon K, Youngchim S (2022) *Talaromyces marneffei* infection: virulence, intracellular lifestyle and host defense mechanisms. J Fungi 8:200. https://doi.org/10.3390/jof8020200

Pykälä J, Kantelinen A, Myllys L (2020) Taxonomy of *Verrucaria* species characterised by large spores, perithecia leaving pits in the rock and a pale thin thallus in Finland. MycoKeys 72:43–92. https://doi.org/10.3897/mycokeys.72.56223

Qadri M, Rajput R, Abdin MZ, Vishwakarma RA, Riyaz-Ul-Hassan S (2014) Diversity, molecular phylogeny, and bioactive potential of fungal endophytes associated with the Himalayan blue pine (*Pinus wallichiana*). Microb Ecol 67:877–887. https://doi.org/10.1007/s00248-014-0379-4

Qazi MA, Wang Q, Dai Z (2022) Sophorolipids bioproduction in the yeast *Starmerella bombicola*: current trends and perspectives. Bioresour Technol 346:126593. https://doi.org/10.1016/j.biortech.2021.126593

Oberwinkler F (2012) Evolutionary trends in basidiomycota. Stapefia 96:45–104

Oberwinkler F, Bandoni RJ (1982c) *Atractogloea*: a new genus in the *Hoehnelomycetaceae* (*Heterobasidiomycetes*). Mycologia 74(4):634–639

Oberwinkler F, Bauer R (1990b) *Cryptomycocolax*: a new mycoparasitic heterobasidiomycete. Mycologia 82(6):671–692

Oberwinkler F, Kirschner R, Arenal F, Villarreal M, Rubio V, Begerow D, Bauer R (2006b) Two new pycnidial members of the *Atractiellales*: *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

Qiao M, Li W, Huang Y, Xu JP (2018) *Classicula sinensis*, a new species of *basidiomycetous* aquatic *hyphomycetes* from Southwest China. MycoKeys 40:1–12. https://doi.org/10.3897/mycokeys.40.23828

Quandt CA, Haelewaters D (2021) Phylogenetic Advances in *Leotiomycetes*, an understudied clade of taxonomically and ecologically diverse fungi. In: Zaragoza Ó, Casadevall A (eds) Encyclopedia of mycology, vol 1. Elsevier, Oxford, pp 284–294

Quang le S, Gascuel O, Lartillot N (2008) Empirical profile mixture models for phylogenetic reconstruction. Bioinformatics 24(20):2317–2323. https://doi.org/10.1093/bioinformatics/btn445

Queiroz MB, Jobim K, Vista XM, Leroy JAS, Gomes SRBS, Goto BT (2020) Occurrence of *Glomeromycota* species in aquatic habitats: a global overview. Mycotaxon 135:469–469. https://doi.org/10.5248/135.469

Queiroz MB, Leroy JAS, Gomes SRBS, Fiuza PO, Goto BT (2022) *Arbuscular mycorrhizal* fungi (*Glomeromycota*) species inhabiting sediments of lentic and lotic Brazilian ecosystems: addition of new global records for aquatic condition. Nova Hedwig 115:227–251. https://doi.org/10.1127/nova_hedwigia/2022/0701

Quijada L, Johnston PR, Cooper JA, Pfister DH (2018) Overview of *Phacidiales*, including *Aotearoamyces* gen. nov. on Nothofagus. IMA Fungus 9:371–382. https://doi.org/10.5598/imafungus.2018.09.02.08

Quijada L, Tanney JB, Popov E, Johnston PR, Pfister DH (2020) Cones, needles and wood: *Micraspis* (*Micraspidaceae*, *Micraspidales* fam. et ord. nov.) speciation segregates by host plant tissues. Fungal Syst Evol 5(1):99–112

Quijada L, Matočec N, Kušan I, Tanney JB, Johnston PR, Mešić A, Pfister DH (2022) Apothecial ancestry, evolution, and re-evolution in *Thelebolales* (*Leotiomycetes*, Fungi). Biology 11:583. https://doi.org/10.3390/biology11040583

Quintieri L, Fancello F, Caputo L, Sorrentino A, Zara S, Lippolis V, Cervellieri S, Fanelli F, Corvino A, Pace B, Cefola M (2022) Effect of gaseous citral on table grapes contaminated by *Rhizopus oryzae* ITEM 18876. Foods 11:2478. https://doi.org/10.3390/foods11162478

Page RD (2016) DNA barcoding and taxonomy: dark taxa and dark texts. Philos Trans R Soc Lond B 371(1702):20150334. https://doi.org/10.1098/rstb.2015.0334

Perreau M, Haelewaters D, Tafforeau P (2021) A parasitic coevolution since the Miocene revealed by phase-contrast synchrotron X-ray microtomography and the study of natural history collections. Sci Rep 11(1):2672

Ragupathy S, Mohankumar V, Mahadevan A (1990) Occurrence of vesicular-arbuscular mycorrhizae in tropical hydrophytes. Aquat Bot 36(3):287–291. https://doi.org/10.1016/0304-3770(90)90043-K

Ramanujam CGK (1982) Recent advances in the study of fossil fungi. In: Bharadwaj DC (ed) Recent advances in cryptogamic botany 2. Palaeobotanical Society, Lucknow, pp 287–301

Ramanujam CGK, Ramachar P (1980) Recognizable spores of rust fungi (*Uridinales*) from Neyveli lignite, Tamil Nadu. Rec Geol Surv India 113(5):80–85

Ramanujam CGK, Srisailam K (1980) Fossil fungal spores from the Neogene Beds around Cannanore in Kerala state. Botanique 9:119–138

Rambold G, Triebel D (1992) The inter-lecanoralean associations. Bibl Lichenol 48:1–201

Rattan GS, Aujla SS, Randhawa HS (1995) Morphology of the teliospores of some smut fungi—an electron microscopy. Cereal Res Commun 23(4):445–451

Raudabaugh DB, Brandon Matheny P, Hughes KW, Iturriag T, Sargent M, Miller AN (2020) Where are they hiding? Testing the body snatchers hypothesis in pyrophilous fungi. Fungal Ecol 43:100870. https://doi.org/10.1016/j.funeco.2019.100870

Ray RC, Ravi V (2005) Post harvest spoilage of sweet potato in tropics and control measures. Crit Rev Food Sci Nutr 45:623–644. https://doi.org/10.1080/10408390500455516

Réblová M, Seifert KA (2012) *Cirrosporium novae-zelandiae*, an enigmatic *coelomycete* with meristem arthroconidia, with ancestors in the *Eurotiomycetes*. Mycologia 104:1315–1324. https://doi.org/10.3852/12-040

Réblová M, Untereiner WA, Réblová K (2013) Novel evolutionary lineages revealed in the *Chaetothyriales* (fungi) based on multigene phylogenetic analyses and comparison of its secondary structure. PLoS ONE 8:e63547. https://doi.org/10.1371/journal.pone.0063547

Réblová M, Miller AN, Rossman AY, Seifert KA, Crous PW, Hawksworth DL, Abdel-Wahab MA, Cannon PF, Daranagama DA, De Beer ZW, Huang SK, Hyde KD, Jayawardena R, Jaklitsch W, Jones EBG, Ju YM, Judith C, Maharachchikumbura SSN, Pang KL, Petrini LE, Raja HA, Romero AI, Shearer C, Senanayake IC, Voglmayr H, Weir BS, Wijayawarden NN (2016) Recommendations for competing sexual-asexually typified generic names in *Sordariomycetes* (except *Diaporthales*, *Hypocreales*, and *Magnaporthales*). IMA Fungus 7:131–153. https://doi.org/10.5598/imafungus.2016.07.01.08

Reboux G, Piarroux R, Mauny F, Madroszyk A, Millon L, Bardonnet K, Dalphin JC (2001) Role of molds in farmer's lung disease in eastern France. Am J Respir Crit Care Med 163:1534–1539. https://doi.org/10.1164/ajrccm.163.7.2006077

Reddy MS, Kramer CA (1975) Taxonomic revision of the *Protomycetales*. Mycotaxon 3:1–50

Redecker D, Kodner R, Graham LE (2000) Glomalean fungi from the ordovician. Science 289:1920–1921. https://doi.org/10.1126/science.289.5486.1920

Reeb V, Lutzoni F, Roux C (2004) Contribution of RPB2 to multilocus phylogenetic studies of the *euascomycetes* (*Pezizomycotina*, Fungi) with special emphasis on the lichen-forming *Acarosporaceae* and evolution of polyspory. Mol Phylogenetics Evol 32:1036–1060. https://doi.org/10.1016/j.ympev.2004.04.012

Reichle RE, Lichtwardt RW (1972) Fine structure of the trichomycete, *Harpella melusinae*, from black-fly guts. Arch Mikrobiol 81:103–125

Reinsch PF (1877) Beobachtungen über einige neue Saprolegnieae, über die Parasiten in Desmidienzellen und über die Stachelkugeln in Achlyaschläuchen. Pringsheim's Jahrbucher fur Wissenschaftliche Botanik 11:283–311

Reis CER, Bento HBS, Carvalho AKF, Rajendran A, Hu B, Castro HF (2019) Critical applications of *Mucor circinelloides* within a biorefinery context. Crit Rev Biotechnol 39:555–570. https://doi.org/10.1080/07388551.2019.1592104

Ren H, Gao Y, Feng E-x, He S-q, Huang Q (2023) First report of *Mucor inaequisporus* (*Mucorales*, *Mucoromycota*) causing postharvest rot of strawberry fruit in Kunming. China Plant Dis 107(7):2241. https://doi.org/10.1094/PDIS-09-22-2262-PDN

Ri T, Suyama M, Takashima Y, Seto K, Degawa Y (2022) A new genus *Unguispora* in *Kickxellales* shows an intermediate lifestyle between saprobic and gut-inhabiting fungi. Mycologia 114(6):934–946. https://doi.org/10.1080/00275514.2022.2111052

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. https://doi.org/10.1371/journal.pone.0147107

Rikkinen J, Meinke SKL, Grabenhorst H, Gröhn C, Kobbert M, Wunderlich J, Schmidt AR (2018) *Calicioid lichens* and fungi in amber—tracing extant lineages back to the Paleogene. Geobios 51(5):469–479. https://doi.org/10.1016/j.geobios.2018.08.009

Roberts P (1996) *Heterobasidiomycetes* from Majorca & Cabrera (Balearic Islands). Mycotaxon 60:111–123

Roberts P (1997) New heterobasidiomycetes from Great Britain. Mycotaxon 63:195–216

Rodrigues MG, Fonseca A (2003) Molecular systematics of the dimorphic *ascomycete* genus *Taphrina*. Int J Syst Evol Microbiol 53(2):607–616. https://doi.org/10.1099/ijs.0.02437-0

Rodrigues AM, Hagen F, Puccia R, Hahn RC, Camargo ZP (2023) *Paracoccidioides* and *Paracoccidioidomycosis* in the 21st century. Mycopathologia 188:129–133. https://doi.org/10.1007/s11046-022-00704-y

Rosa CA, Jindamorakot S, Limtong S, Nakase T, Lachance MA, Fidalgo-JiménezA DHM, Pagnocca FC, Inácio J, Morais PB (2009) Synonymy of the yeast genera *Moniliella* and *Trichosporonoides* and proposal of *Moniliella fonsecae* sp. nov. and five new species combinations. Int J Syst Evol Microbiol 59:425–429. https://doi.org/10.1099/ijs.0.65117-0

Rosling A, Cox F, Cruz-Martinez K, Ihrmark K, Grelet G-A, Lindahl BD, Menkis A, James TY (2011) *Archaeorhizomycetes*: unearthing an ancient class of ubiquitous soil fungi. Science 333:876–879. https://doi.org/10.1126/science.1206958

Rosling A, Timling I, Taylor DL (2013) Archaeorhizomycetes: patterns of distribution and abundance in soil. In: Horwitz BA, Mukherjee PK, Mukherhee M, Kubicek CP (eds) Genomics of soil- and plant. Associated Fungi. pp 333–349

Rossi W, Kotrba M, Triebel D (2005) A new species of *Stigmatomyces* from Baltic amber, the first fossil record of *Laboulbeniomycetes*. Mycol Res 109(3):271–274. https://doi.org/10.1017/S0953756204001819

Rossman AY, Aime MC, Farr DF, Castlebury LA, Peterson KR, Leahy R (2004) The *coelomycetous* genera *Chaetomella* and *Pilidium* represent a newly discovered lineage of inoperculate *discomycetes*. Mycol Prog 3:275–290. https://doi.org/10.1007/s11557-006-0098-4

Rossman AY, Schoch CL, Farr DF, Nishijima K, Keith L, Goenaga R (2010) *Dolabra nepheliae* on rambutan and lychee represents a novel lineage of phytopathogenic *Eurotiomycetes*. Mycoscience 51:300–309. https://doi.org/10.1007/s10267-010-0042-y

Rossman AY, Adams GC, Cannon PF, Castlebury LA, Crous PW, Gryzenhout M, Jaklitsch WM, Mejia LC, Stoykov D, Udayanga D, Voglmayr H, Walker DM (2015a) Recommendations of generic names in *Diaporthales* competing for protection or use. IMA Fungus 6:145–54

Rossman AY, Crous PW, Hyde KD, Hawksworth DL, Aptroot A, Bezerra JL, Bhat JD, Boehm E, Braun U, Boonmee S, Camporesi E, Chomnunti P, Dai DQ, D'Souza MJ, Dissanayake A, Jones EBG, Groenewald JZ, Hernández-Restrepo M, Hongsanan S, Jaklitsch WM, Jayawardena R, Jing LW, Kirk PM, Lawrey JD, Mapook A, McKenzie EHC, Monkai J, Phillips AJL, Phookamsak R, Raja HA, Seifert KA, Senanayake I, Slippers B, Suetrong S, Taylor JE, Thambugala KM, Tian Q, Tibpromma S, Wanasinghe DN, Wijayawardene NN, Wikee S, Woudenberg JHC, Wu HX, Yan JY, Yang T, Zhang Y (2015b) Recommended names for pleomorphic genera in *Dothideomycetes*. IMA Fungus 6:507–523. https://doi.org/10.5598/imafungus.2015.06.02.14

Rossman AY, Allen WC, Braun U, Castlebury LA, Chaverri P, Crous PW, Hawksworth DL, Hyde KD, Johnston P, Lombard L, Romberg M, Samson RA, Seifert KA, Stone JK, Udayanga D, White JF (2016) Overlooked competing asexual and sexually typified generic names of *Ascomycota* with recommendations for their use or protection. IMA Fungus 7:289–308. https://doi.org/10.5598/imafungus.2016.07.02.09

Roure B, Rodriguez-Ezpeleta N, Philippe H (2007) SCaFoS: a tool for selection, concatenation and fusion of sequences for phylogenomics. BMC Evol Biol 7(Suppl 1):S2. https://doi.org/10.1186/1471-2148-7-S1-S2

Roussel S, Reboux G, Dalphin JC, Bardonnet K, Millon L, Piarroux R (2005) Microbiological evolution of hay and relapse in patients with farmer's lung. Occup Environ Med 61(1):3e

Rubner A (1996) Revision of predacious hyphomycetes in the Dactylella-Monacrosporium complex. Stud Mycol 39:1–134

Ruggiero MA, Gordon DP, Orrell TM, Bailly N, Bourgoin T, Brusca RC, Cavalier-Smith T, Guiry MD, Kirk PM (2015) A higher level classification of all living organisms. PLoS ONE 10(4):e0119248. https://doi.org/10.1371/journal.pone.0119248

Ryu H, Hong S, Choi HW, Son KA (2023) First report of *Choanephora* rot on lettuce (*Lactuca sativa*) caused by *Choanephora cucurbitarum* in Korea. Plant Dis 107:1217. https://doi.org/10.1094/PDIS-01-22-0197-PDN

Saccardo PA (1904) De Diagnostica et nomenclatura mycologica, Admonita quaedam. Annales Mycologici 2:195–198 [English translation by Clements FE (1904) J Mycol10: 109–112]

Sahni B, Rao HS (1943) A silicified flora from the Intertrappean cherts round Sausar in the Deccan. Proc Nat Acad Sci India 13(1):36–75

Sahodaran NK, Arun AK, Ray J (2019) Native *arbuscular mycorrhizal* fungal isolates (*Funneliformis mosseae* and *Glomus microcarpum*) improve plant height and nutritional status of banana plants. Exp Agric 55(6):924–933. https://doi.org/10.1017/S0014479719000036

Sahraei SE, Sanchez-Garcia M, Montoliu-Nerin M, Manyara D, Bergin C, Rosendahl S, Rosling A (2022) Whole genome analyses based on single, field collected spores of the *arbuscular mycorrhizal* fungus *Funneliformis geosporum*. Mycorrhiza 32(5–6):361–371. https://doi.org/10.1007/s00572-022-01091-4

Salazar-López NJ, Barco-Mendoza GA, Zuñiga-Martínez BS, Domínguez-Avila JA, Robles-Sánchez RM, Ochoa MAV, González-Aguilar GA (2022) Single-cell protein production as a strategy to reincorporate food waste and agro by-products back into the processing chain. Bioeng 9:623. https://doi.org/10.3390/bioengineering9110623

Salt GA (1974) Etiology and morphology of *Geniculodendron pyriforme* gen. et sp. nov., a pathogen of conifer seeds. Trans Br Mycol Soc 63:339–351. https://doi.org/10.1016/S0007-1536(74)80179-8

Samarakoon MC, Hyde KD, Promputtha I, Hongsanan S, Ariyawansa HA, Maharachchikumbura SSN, Daranagama DA, Stadler M, Mapook A (2016) Evolution of *Xylariomycetidae* (*Ascomycota*: *Sordariomycetes*). Mycosphere 7(11):1746–1761. https://doi.org/10.5943/mycosphere/7/11/9

Samarakoon MC, Hyde KD, Hongsanan S, McKenzie EHC, Ariyawansa HA, Promputtha I, Zeng X-Y, Tian Q, Liu J-K (2019) Divergence time calibrations for ancient lineages of *Ascomycota* classification based on a modern review of estimations. Fungal Diversity 96:285–346

Samarakoon MC, Hyde KD, Maharachchikumbura SS, Stadler M, Gareth Jones EB, Promputtha I, Suwannarach N, Camporesi E, Bulgakov TS, Liu J (2022) Taxonomy, phylogeny, molecular dating and ancestral state reconstruction of *Xylariomycetidae* (*Sordariomycetes*). Fungal Divers 112(1):1–88. https://doi.org/10.1007/s13225-021-00495-5

Sampaio JP (2004) Diversity, phylogeny and classification of *basidiomycetous* yeasts. In: Agerer R, Piepenbring M, Blanz P (eds) Frontiers in basidiomycote mycology. IHV-Verlag, Eching, pp 49–80

Samson RA, Visagie CM, Houbraken J, Hong SB, Hubka V, Klaassen CHW, Perrone G, Seifert KA, Susca A, Tanney JB, Varga J, Kocsubé S, Szigeti G, Yaguchi T, Frisvad JC (2014) Phylogeny, identification and nomenclature of the genus *Aspergillus*. Stud Mycol 78:141–173. https://doi.org/10.1016/j.simyco.2014.07.004

Sanchez EC, Jaramillo IR, Castro JYS, Peréz NV, Fregoso LV (2018) Cuatro nuevos registros de hongos micorrizógenos arbusculares (*Glomeromycota*) asociados con *Agave karwinskii* y *A. angustifolia* (*Agavaceae*) de Oaxaca, México. Acta Botánica Mexicana. https://doi.org/10.21829/abm125.2018.1356

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 117:32528–32534. https://doi.org/10.1073/pnas.192253911

Sandargo B, Chepkirui C, Cheng T, Chaverra-Muñoz L, Thongbai B, Stadler M, Hüttel S (2019) Biological and chemical diversity go hand in hand: *Basidiomycota* as source of new pharmaceuticals and agrochemicals. Biotechnol Adv 37(6):107344

Sangeeta C, Ghasolia RP, Lalita L (2018) Studies on physiological parameters of *Choanephora cucurbitarum*, the incitant of wet rot of cucumber. J Pharmacogn Phytochem 7(3):3227–3229

Santana NA, Ferreira PAA, Tarouco CP, Schardong IS, Antoniolli ZI, Nicoloso FT, Jacques RJS (2019) Earthworms and mycorrhization increase copper phytoextraction by *Canavalia ensiformis* in sandy soil. Ecotoxicol Environ Saf 182:109383. https://doi.org/10.1016/j.ecoenv.2019.109383

Santander C, Aroca R, Cartes P, Vidal G, Cornejo P (2021) Aquaporins and cation transporters are differentially regulated by two *arbuscular mycorrhizal* fungi strains in lettuce cultivars growing under salinity conditions. Plant Physiol Biochem 158:396–409. https://doi.org/10.1016/j.plaphy.2020.11.025

Sarkar S, Prasad V (2003) *Koshalia,* an *Incertae sedis* fossil from the Subathu Formation (Late Ypresian) Himachal Pradesh, India. Palaeobotanist 52:113–116

Savchenko A, Zamora JC, Shirouzu T, Spirin V, Malysheva V, Kõljalg U, Miettinen O (2021) Revision of *Cerinomyces* (*Dacrymycetes*, *Basidiomycota*) with notes on morphologically and historically related taxa. Stud Mycol 99(1):100117. https://doi.org/10.1016/j.simyco.2021.100117

Saxena RK (2012) Validation of names of fossil fungi from Tertiary sediments of India. Novon 22:223–226

Saxena RK, Khare S (1992) Fungal remains from the Neyveli Formation of Tiruchirapalli District, Tamil Nadu, India. Geophytology 21:37–43

Saxena RK, Misra NK (1990) Palynological investigation of the Ratnagiri Beds of Sindhu Durg District, Maharashtra. Palaeobotanist 38:263–276

Saxena RK, Tripathi SKM (2011) Indian Fossil Fungi. Palaeobotanist 60:1–208

Saxena RK, Wijayawardene NN, Dai DQ, Hyde KD, Kirk PM (2021) Diversity in fossil fungal spores. Mycosphere 12(1):670–874. https://doi.org/10.5943/mycosphere/12/1/8

Schadt CW, Martin AP, Lipson DA, Schmidt SK (2003) Seasonal dynamics of previously unknown fungal lineages in tundra soils. Science 301:1359–1361. https://doi.org/10.1126/science.1086940

Schaffner JH (1909) The classification of plants. IV Ohio Naturalist 9(4):446–455

Schell WA, Lee AG, Aime MC (2011) A new lineage in *Pucciniomycotina*: class *Tritirachiomycetes*, order *Tritirachiales*, family *Tritirachiaceae*. Mycologia 103:1331–1340. https://doi.org/10.3852/10-333

Scheuer C, Bauer R, Lutz M, Stabentheiner E, Mel'nik V, Grube M (2008) *Bartheletia paradoxa* is a living fossil on Ginkgo leaf litter with a unique septal structure in the *Basidiomycota*. Mycol Res 112:1265–1279. https://doi.org/10.1016/j.mycres.2008.06.008

Schmidt I, Schewe H, Gassel S, Jin C, Buckingham J, Hümbelin M, Sandmann G, Schrader J (2011) Biotechnological production of astaxanthin with *Phaffia rhodozyma*/*Xanthophyllomyces dendrorhous*. Appl Microbiol Biotechnol 89:555–571. https://doi.org/10.1007/s00253-010-297

Schneider GX, Gomes RR, Bombassaro A, Zamarchi K, Voidaleski MF, Costa FF, Leão ACR, Lima BJFS, Soley BS, Colombo IR, Cândido GZ, Najafzadeh MJ, Sun JF, de Azevedo CMPS, Marques SG, de Hoog GS, Vicente VA (2019) New molecular markers distinguishing *Fonsecaea* agents of chromoblastomycosis. Mycopathologia 184:493–504. https://doi.org/10.1007/s11046-019-00359-2

Schoch CL, Shoemaker RA, Seifert KA, Hambleton S, Spatafora JW, Crous PW (2006) A multigene phylogeny of the *Dothideomycetes* using four nuclear loci. Mycologia 98:1041–1052. https://doi.org/10.3852/mycologia.98.6.1041

Schoch CL, Crous PW, Groenewald JZ, Boehm EWA, Burgess TI, de Gruyter J, de Hoog GS, Dixon LJ, Grube M, Gueidan C, Harada Y, Hatakeyama S, Hirayama K, Hosoya T, Huhndorf SM, Hyde KD, Jones EBG, Kohlmeyer J, Kruys Å, Li YM, Lücking R, Lumbsch HT, Marvanová L, Mbatchou JS, McVay AH, Miller AN, Mugambi GK, Muggia L, Nelsen MP, Nelson P, Owensby CA, Phillips AJL, Phongpaichit S, Pointing SB, Pujade-Renaud V, Raja HA, Rivas Plata E, Robbertse B, Ruibal C, Sakayaroj J, Sano T, Selbmann L, Shearer CA, Shirouzu T, Slippers B, Suetrong S, Tanaka K, Volkmann-Kohlmeyer B, Wingfield MJ, Wood AR, Woudenberg JHC, Yonezawa H, Zhang Y, Spatafora JW (2009a) A class-wide phylogenetic assessment of *Dothideomycetes*. Stud Mycol 64:1–15. https://doi.org/10.3114/sim.2009.64.01

Schoch CL, Sung GH, López-Giráldez F, Townsend JP, Miadlikowska J, Hofstetter V, Robbertse B, Matheny PB, Kauff F, Wang Z, Gueidan C, Andrie RM, Trippe K, Ciufetti LM, Wynns A, Fraker E, Hodkinson BP, Bonito G, Groenewald JZ, Arzanlou M, de Hoog GS, Crous PW, Hewitt D, Pfister DH, Peterson K, Gryzenhout M, Wingfield MJ, Aptroot A, Suh SQ, Blackwell M, Hillis DM, Griffith GW, Castlebury LA, Rossman AY, Lumbsch HT, Lücking R, Büdel B, Rauhut A, Diederich P, Ertz D, Geiser DM, Hosaka K, Inderbitzin P, Kohlmeyer J,Volkmann-Kohlmeyer B, Mostert L, O'Donnell K, Sipman H, Rogers JD, Shoemaker RA, Sugiyama J, Summerbell RC, Untereiner W, Johnston PR, Stenroos S, Zuccaro A, Dyer PS, Crittenden PD, Cole MS, Hansen K, Trappe JM, Yahr R, Lutzoni F, Spatafora JW (2009b) The *Ascomycota* tree of life: a phylum-wide phylogeny clarifies the origin and evolution of fundamental reproductive and ecological traits. Syst Biol 58:224–239. https://doi.org/10.1093/sysbio/syp020

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 39(3):311–323. https://doi.org/10.7872/crym/v39.iss3.2018.311

Schoutteten N, Poer A, 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(1):41–94. https://doi.org/10.3114/sim.2022.106.02

Schoutteten N, Begerow D, Verbeken A (2024). Mycoparasitism in *Basidiomycota*. In: Biodiversity and Evolution of Fungal Parasites and Pathogens (Haelewaters, D, ed). Elsevier, Germany (In press). Preprint available on Authorea. https://doi.org/10.22541/au.171386938.80462578/v1

Schröder T, Kehr R, Hüttermann A (2002) First report of the seed-pathogen *Geniculodendron pyriforme*, the imperfect state of the *ascomycete Caloscypha fulgens*, on imported conifer seeds in Germany. For Pathol 32:225–230. https://doi.org/10.1046/j.1439-0329.2002.00288.x

Schüßler A (2012) 5 The *Geosiphon-Nostoc* endosymbiosis and its role as a model for arbuscular mycorrhiza research. In: Hock B (ed) The mycota—fungal associations, vol 9, 2nd edn. Springer, Heidelberg

Schüßler A, Walker C (2010) The *Glomeromycota*. A species list with new families and new genera. Gloucester, The Royal Botanic Garden Edinburgh, The Royal Botanic Garden Kew, Botanische Staatssammlung Munich, Oregon State University

Schüßler A, Wolf E (2005) *Geosiphon pyriformis*—aglomeromycotan soil fungus forming endosymbiosis with cyanobacteria. In: Declerck S, Fortin JA, Strullu D-G (eds) In vitro culture of mycorrhizas, 1st edn. Springer, Berlin, Heidelberg, pp 271–289

Schüßler A, Schwarzott D, Walker C (2001) A new fungal phylum, the *Glomeromycota*: evolution and phylogeny. Mycol Res 105(12):1413–1421. https://doi.org/10.1017/S0953756201005196

Schuh RT (2003) The Linnaean system and its 250-year persistence. Bot Rev 69(1):59–78

Schumacher T (1990) The genus *Scutellinia*. *Pyronemataceae*. Opera Botanica 101:1–107

Schumm F, Aptroot A (2023) Images of *Lichinaceae*. Books on Demand, Norderstedt, p 320

Schuster SC (2008) Next-generation sequencing transforms today's biology. Nat Methods 5(1):16–18

Schweikert M, Schnepf E (1996) *Pseudaphelidium drebesii*, genet specnov (*incerta sedis*), a Parasite of the Marine Centric Diatom *Thalassiosira punctigera*. Arch Protistenk 147(1):11–17. https://doi.org/10.1016/S0003-9365(96)80004-2

Schweikert M, Schnepf E (1997) Electron microscopical observations on *Pseudaphelidium drebesii* Schweikert and Schnepf, a parasite of the centric diatom *Thalassiosira punctigera*. Protoplasma 199:113–123. https://doi.org/10.1007/BF01294500

Seifert KA (1983) Decay of wood by the *Dacrymycetales*. Mycologia 75:1011–1018. https://doi.org/10.2307/3792657

Seifert KA (2009) Progress towards DNA barcoding of fungi. Mol Ecol Resour 9(S1):83–89

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

Sekimoto S, Rochon DA, Long JE, Dee JM, Berbee ML (2011) A multigene phylogeny of *Olpidium* and its implications for early fungal evolution. BMC Evol Biol 11:1–10. https://doi.org/10.1186/1471-2148-11-331

Selkirk DR (1975) Tertiary fossil fungi from Kiandra, New South Wales. Proc Linn Soc New South Wales 100:70–94

Sepkowitz KA (1993) *Pneumocystis carinii* pneumonia in patients without AIDS. Clin Infect Dis 17(2):416–422. https://doi.org/10.1093/clinids/17.supplement_2.s416

Sepkowitz KA, Brown AE, Telzak EE, Gottlieb S, Armstrong D (1992) *Pneumocystis carinii* pneumonia among patients without AIDS at a cancer hospital. JAMA 267:832–837. https://doi.org/10.1001/jama.1992.03480060078034

Sepúlveda VE, Márquez R, Turissini DA, Goldman WE, Matute DR (2017) Genome sequences reveal cryptic speciation in the human pathogen *Histoplasma capsulatum*. Mbio. https://doi.org/10.1128/mBio.01339-17

Séry DJM, Kouadjo ZGC, Voko BRR, Zézé A (2016)Selecting native *arbuscular mycorrhizal* fungi to promote cassava growth and increase yield under field conditions. Front Microbiol 7:1–13. https://doi.org/10.3389/fmicb.2016.02063

Seto K, Degawa Y (2015) *Cyclopsomyces plurioperculatus*: a new genus and species of *Lobulomycetales* (*Chytridiomycota*, *Chytridiomycetes*) from Japan. Mycologia 107(3):633–640

Seto K, Degawa Y (2017) *Pendulichytrium sphaericum* gen. et sp. nov. (*Chytridiales*, *Chytriomycetaceae*), a new chytrid parasitic on the diatom, *Aulacoseira granulata*. Mycoscience 59(1):59–66. https://doi.org/10.1016/j.myc.2017.08.004

Seto K, Degawa Y (2018) *Pendulichytrium sphaericum* gen. et sp. nov. (*Chytridiales*, *Chytriomycetaceae*), a new chytrid parasitic on the diatom, *Aulacoseira granulata*. Mycoscience 59(1):59–66. https://doi.org/10.1016/j.myc.2017.08.004

Seto K, Kagami M, Degawa Y (2017) Phylogenetic position of parasitic chytrids on diatoms: characterization of a novel clade in *Chytridiomycota*. J Eukary Microbiol 64(3):383–393. https://doi.org/10.1111/jeu.12373

Seto K, Matsuzawa T, Kuno H, Kagami M (2020) Morphology, ultrastructure, and molecular phylogeny of *Aphelidium collabens* sp. nov. (*Aphelida*), a parasitoid of a green alga *Coccomyxa* sp. Protist 171(3):125728. https://doi.org/10.1016/j.protis.2020.125728

Seto K, Nakada T, Tanabe Y, Yoshida M, Kagami M (2022) *Aphelidium parallelum* sp. nov., a new aphelid parasitic on selenastracean green algae. Mycologia 114(3):544–555. https://doi.org/10.1080/00275514.2022.2039487

Sevgili A, Erkmen O (2019) Improved lycopene production from different substrates by mated fermentation of *Blakeslea trispora*. Foods 8(4):120. https://doi.org/10.3390/foods8040120

Shahidi F, Arachchi JKV, Jeon YJ (1999) Food applications of chitin and chitosan. Trends Food Sci Technol 10:37–51. https://doi.org/10.1016/S0924-2244(99)00017-5

Sharma M, Chakrabarti A (2023) Candidiasis and other emerging yeasts. Curr Fungal Infect Rep 17:15–24. https://doi.org/10.1007/s12281-023-00455-3

Shen XX, Zhou X, Kominek J, Kurtzman CP, Hittinger CT, Rokas A (2016) Reconstructing the backbone of the *saccharomycotina* yeast phylogeny using genome-scale data. G3 (6):3927–3939. https://doi.org/10.1534/g3.116.034744

Shen XX, Opulente DA, Kominek J, Zhou XF, Steenwyk JL, Buh KV, Haase MAB, Wisecaver JH, Wang MS, Doering DT, Boudouris JT, Schneider RM, Langdon QK, Ohkuma M, Endoh R, Takashima M, Manabe RI, Čadež N, Libkind D, Rosa CA, Virgilio JD, Hulfachor AB, Groenewald M, Kurtzman CP, Hittinger CT, Rokas A (2018) Tempo and mode of genome evolution in the budding yeast subphylum. Cell 175:1533–1545. https://doi.org/10.1016/j.cell.2018.10.023

Shen XX, Steenwyk JL, LaBella AL, Opulente DA, Zhou X, Kominek J, Li Y, Groenewald M, Hittinger CT, Rokas A (2020) Genome-scale phylogeny and contrasting modes of genome evolution in the fungal phylum *Ascomycota*. Sci Adv 6:eabd0079. https://doi.org/10.1126/sciadv.abd0079

Shen H, Cai X, Liu J, Yan G, Ye Y, Dong R, Wu J, Li L, Shen Q, Ma Y, Ou Q, Shen M, Chen W, Lu G (2023) Case report: The clinical utility of metagenomic next-generation sequencing in mucormycosis diagnosis caused by fatal *Lichtheimia ramosa* infection in pediatric neuroblastoma. Front Pediatr 11:1130775. https://doi.org/10.3389/fped.2023.1130775

Shendure J, Ji H (2008) Next-generation DNA sequencing. Nat Biotech 26(10):1135–1145

Shendure J, Porreca GJ, Reppas NB, Lin X, McCutcheon JP, Rosenbaum AM, Wang MD, Zhang K, Mitra RD, Church GM (2005) Accurate multiplex polony sequencing of an evolved bacterial genome. Science 309(5741):1728–1732

Shimodaira H (2002) An approximately unbiased test of phylogenetic tree selection. Syst Biol 51(3):492–508. https://doi.org/10.1080/10635150290069913

Shirouzu T, Hirose D, Oberwinkler F, Shimomura N, Maekawa N, Tokumasu S (2013) Combined molecular and morphological data for improving phylogenetic hypotheses in *Dacrymycetes*. Mycologia 105:1110–1125. https://doi.org/10.3852/12-147

Shirouzu T, Uno K, Hosaka K, Hosoya T (2016) Early-diverging wood-decaying fungi detected using three complementary sampling methods. Mol Phylogenet Evol 98:11–20. https://doi.org/10.1016/j.ympev.2016.01.015

Shirouzu T, Hosaka K, Nam KO, Weir BS, Johnston PR, Hosoya T (2017) Phylogenetic relationships of eight new *Dacrymycetes* collected from New Zealand. Persoonia 38(1):156–169. https://doi.org/10.3767/003158517X695280

Shivas RG, Vánky K, Cunnington JH (2006) The smut fungi (*Ustilaginomycetes*) on *Triodia*, including *Ustilago lituana* sp. nov.

from Australia. Australas Plant Pathol 35:363–365. https://doi.org/10.1071/AP06021

Shokralla S, Spall JL, Gibson JF, Hajibabaei M (2012) Next-generation sequencing technologies for environmental DNA research. Mol Ecol 21(8):1794–1805. https://doi.org/10.1111/j.1365-294X.2012.05538.x

Shukla S, Bahuguna A, Park HK, Kim JK, Kim M (2020) Effect of *Rhizopus nigricans* (*Rhizopus stolonifera*)-based novel starter culture on quality and safety attributes of doenjang, a traditional Korean soybean fermented food product. Sci Rep 10:1081. https://doi.org/10.1038/s41598-019-57382-y

Sierota Z (1998) *Rhizina undulata* on stem and roots of 84-year-old Scots pine trees. Acta Mycol 33:69–76. https://doi.org/10.5586/am.1998.006

Sietsma JH, Wessels JG (1990) The occurrence of glucosaminoglycan in the wall of *Schizosaccharomyces pombe*. Microbiology 136(11):2261–2265

Sieverding E (1990) Ecology of VAM fungi in tropical agrosystems. Agric Ecosyst Environ 29:369–390.https://doi.org/10.1016/0167-8809(90)90303-U

Sieverding E, da Silva GA, Berndt R, Oehl F (2015) *Rhizoglomus*, a new genus of the *Glomeraceae*. Mycotaxon 129(2):373–386. https://doi.org/10.5248/129.373

Silva AFS, Souza AF, Pinheiro IO, Takaki GMC (2022a) Green synthesis of chitosan by *Cunninghamella elegans* UCP 1306 using sustainable substrates mediated morphological changes. Res Soc Dev. https://doi.org/10.33448/rsd-v11i7.29387

Silva KJG, Fernandes JAL, Magurno F, Leandro LBA, Goto BT, Theodoro RC (2022b) Phylogenetic review of *Acaulospora* (*Diversisporales, Glomeromycota*) and the homoplasic nature of its ornamentations. J Fungi 8:892

Silva-Hanlin DMW, Hanlin RT (1999) Small subunit ribosomal RNA gene phylogeny of several *loculoascomycetes* and its taxonomic implications. Mycol Res 103:153–160. https://doi.org/10.1017/S0953756298006972

Simmons DR, James TY, Meyer AF, Longcore JE (2009) *Lobulomycetales*, a new order in the *Chytridiomycota*. Mycol Res 113:450–460. https://doi.org/10.1016/j.mycres.2008.11.019

Simmons DR, Letcher PM, Powell MJ, Longcore JE (2012) *Alogomyces tanneri* gen. et sp. nov., a chytrid in *Lobulomycetales* from horse manure. Mycologia 104(1):157–163. https://doi.org/10.3852/11-043

Singh G, Pankaj U, Chand S, Verma RK (2019) Arbuscular mycorrhizal fungi-assisted phytoextraction of toxic metals by *Zea mays* L. from Tannery Sludge. Soil Sediment Contam. https://doi.org/10.1080/15320383.2019.1657381

Singh AK, Zhu XA, Chen CF, Wu JE, Yang B, Zakari S, Jiang XJ, Singh N, Liu WJ (2020) The role of glomalin in mitigation of multiple soil degradation problems. Crit Rev Environ Sci Technol. https://doi.org/10.1080/10643389.2020.1862561

Singh S, Kanaujia R, Kuma MB, Irrinki RNNS, Satish SN, Choudhary H, Kaur H, Rudramurthy SM (2023) *Saksenaea vasiformis* infection: extensive abdominal wall necrotizing fasciitis with systematic review and analysis of 65 cases. Mycoses 66(8):697–704. https://doi.org/10.1111/myc.13592

Six DL (2013) The bark beetle holobiont: why microbes matter. J Chem Ecol 39:989–1002. https://doi.org/10.1007/s10886-013-0318-8

Smith ME, Gryganskyi A, Bonito G, Nouhrae E, Moreno-Arroyo B, Benny G (2013) Phylogenetic analysis of the genus *Modicella* reveals an independent evolutionary origin of sporocarp-forming fungi in the *Mortierellales*. Fungal Genet Biol 61:61–68. https://doi.org/10.1016/j.fgb.2013.10.001

Smith DS, Rocheleau H, Chapados JT, Abbott C, Ribero S, Redhead SA, Lévesque CA, De Boer SH (2014) Phylogeny of the genus *Synchytrium* and the development of TaqMan PCR assay for sensitive detection of *Synchytrium endobioticum* in soil. Phytopathol 104:422–432. https://doi.org/10.1094/PHYTO-05-13-0144-R

Solieri L (2021) The revenge of *Zygosaccharomyces* yeasts in food biotechnology and applied microbiology. World J Microbiol Biotechnol 37:96. https://doi.org/10.1007/s11274-021-03066-7

Song Y, Laureijssen-van de Sande WWJ, Moreno LF, van den Ende BG, Li RY, de Hoog S (2017) Comparative ecology of capsular *Exophiala* species causing disseminated infection in humans. Front Microbiol 8:2514. https://doi.org/10.3389/fmicb.2017.02514

Song Z, Rogers A, Cho BA, Jing K, Zhang D (2022) Kinetic modelling of γ-linolenic acid production by *Cunninghamella echinulata*. Comput Aided Chem Eng 51:109–114. https://doi.org/10.1016/B978-0-323-95879-0.50019-9

Souza ALA, Santiago ALCMA, Brito ACQ, Mello JF, Neto JVS, Souza-Motta CM, Machado AR (2023) New reports of *Gilbertella persicaria* causing post-harvest rot in different fruits in Brazil. J Plant Dis Prot. https://doi.org/10.1007/s41348-023-00816-7

Sparrow FK (1933) The *monoblepharidales*. Ann Bot 47(187):517–542

Sparrow FK (1960) Aquatic *Phycomycetes*. University of Michigan Press, Michigan

SparrowFK (1962) *Urophlyctis* and *Physoderma*. Trans Mycol Soc Jpn 3:16–18

Spatafora JW, Mitchell TG, Vilgalys R (1995) Analysis of genes coding for small-subunit rRNA sequences in studying phylogenetics of dematiaceous fungal pathogens. J Clin Microbiol 33:1322–1326. https://doi.org/10.1128/JCM.33.5.1322-1326.1995

Spatafora JW, Sung G-H, Johnson D, Hesse C, O'Rourke B, Serdani M, Spotts R, Lutzoni F, Hofstetter V, Miadlikowska J, Reeb V, Gueidan C, Fraker E, Lumbsch T, Lücking R, Schmitt I, Hosaka K, Aptroot A, Roux C, Miller AN, Geiser DM, Hafellner J, Hestmark G, Arnold AE (2006) A five-gene phylogeny of *Pezizomycotina*. Mycologia 98:1018–1028. https://doi.org/10.3852/mycologia.98.6.1018

Spatafora JW, Chang Y, Lazarus BGL, K, Smith ME, Berbee ML, Bonito G, Corradi N, Grigoriev IV, Gryganskyi A, James TY, O'Donnell K, Roberson RW, Taylor TN, Uehling J, Vilgalys R, White MM, Stajich JE (2016) A phylum-level phylogenetic classification of *zygomycete* fungi based on genome-scale data. Mycologia 108(5):1028–1046. https://doi.org/10.3852/16-042

Spatafora JW, Aime MC, Grigoriev IV, Martin F, Stajich JE, Blackwell M (2017) The fungal tree of life: from molecular systematics to genome-scale phylogenies. Fungal Kingdom. https://doi.org/10.1128/microbiolspec.FUNK-0053-2016

Spirin V, Nordén J, Svantesson S, Larsson KH (2016) New records of intrahymenial heterobasidiomycetes (*Basidiomycota*) in north Europe. Nord J Bot 34(4):475–477

Spirin V, Malysheva V, Trichies G, Savchenko A, Põldmaa K, Nordén J, Miettinen O, Larsson KH (2018) A preliminary overview of the corticioid *Atractiellomycetes* (*Pucciniomycotina*, *Basidiomycetes*). Fungal Syst Evol 2:311–340

Spooner BM (1987) Helotiales of Australasia: *Geoglossaceae, Orbiliaceae, Sclerotiniaceae, Hyaloscyphaceae*. Bibl Mycol 116:1–711

Sprague V (1977) Classification and phylogeny of the *Microsporidia*. Comp Patho volume 2 Systematics of the Microsporidia 1–30

Spribille T, Tuovinen V, Resl P, Vanderpool D, Wolinski H, Aime MC, Schneider K, Stabentheiner E, Toome-Heller M, Thor G, Mayrhofer H, Johannesson H, McCutcheon JP (2016) *Basidiomycete* yeasts in the cortex of *ascomycete* macrolichens. Science 353(6298):488–492. https://doi.org/10.1126/science.aaf8287

Stahmann KP, Revuelta J, Seulberger H (2000) Three biotechnical processes using *Ashbya gossypii, Candida famata*, or *Bacillus subtilis* compete with chemical riboflavin production. Appl Microbiol Biotechnol 53:509–516. https://doi.org/10.1007/s002530051649

Steensels J, Daenen L, Malcorps P, Derdelinckx G, Verachtert H, Verstrepen KJ (2015) *Brettanomyces* yeasts—from spoilage organisms to valuable contributors to industrial fermentations. Int J Food Microbiol 206:24–38. https://doi.org/10.1016/j.ijfoodmicro.2015.04.005

Stentiford GD, Ramilo A, Abollo E, Kerr R, Bateman KS, Feist SW, Bass D, Villalba A (2017) *Hyperspora aquatica* n. gen, n. sp. (*Microsporidia*), hyperparasitic in *Marteilia cochil*lia (*Paramyxida*), is closely related to crustacean-infecting microspordian taxa. Parasitol 144(2):186–99

Strassert JFH, Monaghan MT (2022a) Phylogenomic insights into the early diversification of fungi. Curr Biol 32(16):3628–3635. https://doi.org/10.1016/j.cub.2022.06.057

Strassert JFH, Monaghan MT (2022b) Phylogenomics unravels the early diversification of fungi. Biorxiv. https://doi.org/10.1101/2021.12.12.472261

Stringer JR (2002) Pneumocystis. Int J Med Microbiol 292:391–404. https://doi.org/10.1078/1438-4221-00222

Stringer SL, Hudson K, Blase MA, Walzer PD, Cushion MT, Stringer JR (1989) Sequence from ribosomal RNA of Pneumocystis carinii compared to those of four fungi suggests an *ascomycetous* affinity. J Protozool 36:14S-16S. https://doi.org/10.1111/j.1550-7408.1989.tb02670.x

Stürmer SL, Bever JD, Morton JB (2018) Biogeography of *arbuscular mycorrhizal* fungi (*Glomeromycota*): a phylogenetic perspective on species distribution patterns. Mycorrhiza 28:587–603. https://doi.org/10.1007/s00572-018-0864-6

Subramanian CV (1974) Two new families of chytrids. Curr Sci 43:722–723

Sugita T, Takashima M, Poonwan N, Mekha N, Malaithao K, Thungmuthasawat B, Prasarn S, Pk L, Kudo T (2003) The first isolation of ustilaginomycetous anamorphic yeasts, *Pseudozyma* species, from patients' blood and a description of two new species: *P. parantarctica and P. thailandica*. Microbiol Immunol 47:183–190. https://doi.org/10.1111/j.1348-0421.2003.tb03385.x

Sugiyama J, Hosaka K, Suh SO (2006) Early diverging *Ascomycota*: phylogenetic divergence and related evolutionary enigmas. Mycologia 98:996–1005. https://doi.org/10.3852/mycologia.98.6.996

Sugiyama J, Nishida H, Hosoya T, Kakishima M (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 SO, Kurtzman CP, Blackwell M (2001) The status of Endomyces scopularum—a filamentous fungus and two yeasts. Mycologia 93:317–322

Suh SO, Marshall CJ, McHugh JV, Blackwell M (2003) Wood ingestion by passalid beetles in the presence of xylose-fermenting gut yeasts. Mol Ecol 12:3137–3145. https://doi.org/10.1046/j.1365-294x.2003.01973.x

Suh SO, McHugh JV, Pollock DD, Blackwell M (2005) The beetle gut: a hyperdiverse source of novel yeasts. Mycol Res 109:261–265. https://doi.org/10.1017/S0953756205002388

Suh SO, Nguyen NH, Blackwell M (2006) A yeast clade near *Candida kruisii* uncovered: nine novel *Candida* species associated with basidioma-feeding beetles. Mycol Res 110:1379–1394. https://doi.org/10.1016/j.mycres.2006.09.009

Sum WC, Ebada SS, Matasyoh JC, Stadler M (2023) Recent progress in the evaluation of secondary metabolites from *Basidiomycota*. Curr Res Biotechnol 6:100155

Sun BD, Zhou YG, Chen AJ, Houbraken J (2019a) Phylogeny and a new species of the genus *Arachnomyces* (*Arachnomycetaceae*). Phytotaxa 394:89

Sun X, Chen W, Ivanov S, MacLea AM, Wight H, Ramaraj T, Mudge J, Harrison MJ, Fei Z (2019b) Genome and evolution of the *arbuscular mycorrhizal* fungus *Diversispora epigaea* (*Glomus versiforme*) and its bacterial endosymbionts. New Phytol 221:1556–1573. https://doi.org/10.1111/nph.15472

Sun T, Wang R, Sun D, Li S, Xu H, Qiu YB, Lei P, Sun L, Xu XQ, Zhu YF (2020) High-efficiency production of *Tremella aurantialba* polysaccharide through basidiospore fermentation. Bioresour Technol 318:124268. https://doi.org/10.1016/j.biortech.2020.124268

Sun JE, Zhang Q, Luo WM, Yang YQ, An HM, Wang Y (2022) Four new *Phragmidium* (*Phragmidiaceae, Pucciniomycetes*) species from *Rosaceae* plants in Guizhou Province of China. MycoKeys 93:193–213. https://doi.org/10.3897/mycokeys.93.90861

Surendirakumar K, Pandey RR, Muthukumar T, Sathiyaseelan A, Loushambam S, Seth A (2022) Characterization and biological activities of melanin pigment from root endophytic fungus, *Phoma* sp. RDSE17. Arch Microbiol 204:171. https://doi.org/10.1007/s00203-022-02788-y

Svrček M (1954) Revisio critica J. Velenovskýi specierum generis *Orbilia*. Acta Entomol Mus Natl Pragae. Ser Bot 10(1):1–23

Sweany RR, Picha DH, Clark CA (2019) Hot-water baths, biologicals and re-curing effects on *Rhizopus* soft rot during sweet potato packing. Plant Pathol 69:284–293. https://doi.org/10.1111/ppa.13126

Szantho LL, Lartillot N, Szollosi GJ, Schrempf D (2023) Compositionally constrained sites drive long-branch attraction. Syst Biol 72(4):767–780. https://doi.org/10.1093/sysbio/syad013

Takashima M, Sugita T (2022) Taxonomy of pathogenic yeasts *Candida*, *Cryptococcus*, *Malassezia*, and *Trichosporon*. Med Mycol J 63:119–132. https://doi.org/10.3314/mmj.22.004

Takashima M, Hamamoto M, Nakase T (2000) Taxonomic significance of fucose in the class *Urediniomycetes*: distribution of fucose in cell wall and phylogeny of urediniomycetous yeasts. Syst Appl Microbiol 23(1):63–70

Takashima Y, Degawa Y, Nishizawa T, Ohta H, Narisawa K (2020) Aposymbiosis of a *Burkholderiaceae*-related endobacterium impacts on sexual reproduction of its fungal host. Microbes Environ 35(2):19167. https://doi.org/10.1264/jsme2.ME19167

Takushi T, Yamashiro M, Kawano S, Matsumura M (2020) First report of fruit rot caused by *Gilbertella persicaria* on Barbados cherry (*Malpighia glabra* L.) in Japan. Jpn J Phytopathol 86:102–107. https://doi.org/10.3186/jjphytopath.86.102

Tanabe Y, O'Donnell K, Saikawa M, Sugiyama J (2000) Molecular phylogeny of parasitic *Zygomycota* (*Dimargaritales*, *Zoopagales*) based on nuclear small subunit ribosomal DNA sequences. Mol Phyl Evol 16(2):253–262

Taylor JW, Berbee ML (2006) Dating divergences in the Fungal Tree of Life: review and new analyses. Mycologia 98(6):838–849

Taylor TN, Remy W, Hass H, Kerp H (1995) Fossil *arbuscular mycorrhizae* from the early Devonian. Mycol 87:560–573. https://doi.org/10.2307/3760776

Taylor TN, Hass H, Kerp H, Krings M, Hanlin RT (2005) Perithecial ascomycetes from the 400 million year old Rhynie chert: an example of ancestral polymorphism. Mycologia 97(1):269–285

Tcvetkova VS, Zorina NA, Mamkaeva MA, Karpov SA (2019) Molecular phylogeny of *Aphelidium arduennense* sp. nov.-new representative of *Aphelida* (*Opisthosporidia*). Protistol 13(4):192–198

Tcvetkova VS, Pozdnyakov IR, Seliuk AO, Zorina NA, Karpov SA (2023) Vegetative cell fusion and a new stage in the life cycle of the *Aphelida* (*Opisthosporidia*). J Eukaryot Microbiol 70:e012977. https://doi.org/10.1111/jeu.12977

Tedersoo L, Hansen K, Perry BA, Kjøller R (2006) Molecular and morphological diversity of pezizalean ectomycorrhiza. New Phytol 170:581–596. https://doi.org/10.1111/j.1469-8137.2006.01678.x

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, Ruiz LV, Vasco-Palacios AM, Thu PQ, Suija A, Smith ME, Sharp C, Saluveer E, Saitta A, Rosas M, Riit T, Ratkowsky D, Pritsch K, Põldmaa K, Piepenbring M, Phosri C, Peterson M, Parts K, Pärtel K, Otsing E, Nouhra E, Njouonkou AL, Nilsson RH, Morgado LN, Mayor J, May TW, Majuakim L, Lodge DJ, Lee SS, Larsson KH, Kohout P, Hosaka K, Hiiesalu I, Henkel TW, Harend H, Guo LD, Greslebin A, Grelet G, Geml J, Gates G, Dunstan W, Dunk C, Drenkhan R, Dearnaley J, De Kesel A, Dang T, Chen X, Buegger F, Brearley FQ, Bonito G, Anslan S, Abell S, Abarenkov K (2014) Global diversity and geography of soil fungi. Science 346:1256688. https://doi.org/10.1126/science.1256688

Tedersoo L, Sánchez-Ramírez S, Kõljalg U, Bahram M, Döring M, Schigel D, May T, Ryberg M, Abarenkov K (2018) High-level classification of the *Fungi* and a tool for evolutionary ecological analyses. Fungal Divers 90:135–159. https://doi.org/10.1007/s13225-018-0401-0

Tehler A (1988) A cladistic outline of the *Eumycota*. Cladistics 4:227–277. https://doi.org/10.1111/j.1096-0031.1988.tb00474.x

Tehler A, Irestedt M, Wedin M, Ertz D (2010) The old world *Roccella* species outside Europe and Macaronesia: taxonomy, evolution and phylogeny. Syst Biodivers 8:223–246. https://doi.org/10.1080/14772001003789554

Telagathoti A, Probst M, Peintner U (2021) Habitat, snow-cover and soil pH, affect the distribution and diversity of *Mortierella* species and their associations to bacteria. Front Microbiol 12:1817. https://doi.org/10.3389/fmicb.2021.669784

Teo LH, Tay YK (2006) *Ustilago* species infection in humans. BJD 155:1096–1097. https://doi.org/10.1111/j.1365-2133.2006.07515.x

Thambugala D, Menzies JG, Knox RE, Campbell HL, McCartney CA (2020) Genetic analysis of loose smut (*Ustilago tritici*) resistance in Sonop spring wheat. BMC Plant Biol 20:314. https://doi.org/10.1186/s12870-020-02525-x

Thanh VN, Hien DD (2019) *Moniliella floricola* sp. nov., a species of black yeast isolated from flowers. Int J Syst Evol Microbiol 69(1):87–92

Thanh VN, Hai DA, Hien DD, Takashima M, Lachance MA (2012) *Moniliella carnis* sp. nov. and *Moniliella dehoogii* sp. nov., two novel species of black yeasts isolated from meat processing environments. Int J Syst Evol Microbiol 62:3088–3094. https://doi.org/10.1099/ijs.0.044255-0

Thanh VN, Hien DD, Thom TT (2013) *Moniliella byzovii* sp. nov., a chlamydospore-forming black yeast isolated from flowers. Int J Syst Evol Microbiol 63:1192–1196. https://doi.org/10.1099/ijs.0.049767-0

Thanh VN, Hien DD, Yaguchi T, Sampaio JP, Lachance MA (2018) *Moniliella sojae* sp. nov., a species of black yeasts isolated from Vietnamese soy paste (tuong), and reassignment of *Moniliella suaveolens* strains to *Moniliella pyrgileucina* sp. nov., *Moniliella casei* sp. nov. and *Moniliella macrospora* emend. comb. nov. Int J Syst Evol Microbiol 68(5):1806–1814. https://doi.org/10.1099/ijsem.0.002690

Thaxter R (1922) A revision of the *Endogoneae*. In: Proceedings of the American Academy of Arts and Sciences, vol. 57, no. 12, pp. 291–350. American Academy of Arts & Sciences

Thiyagaraja V, Lücking R, Ertz D, Wanasinghe DN, Karunarathna SC, Camporesi E, Hyde KD (2020) Evolution of non-lichenized, saprotrophic species of *Arthonia* (*Ascomycota*, *Arthoniales*) and resurrection of *Naevia*, with notes on *Mycoporum*. Fungal Divers 102:205–224. https://doi.org/10.1007/s13225-020-00451-9

Thomidis T, Prodromou I, Zambounis A (2019) First report of *Mucor piriformis* causing postharvest fruit rot of kiwifruit in Greece. Plant Dis 103(4):770. https://doi.org/10.1094/PDIS-08-18-1473-PDN

Thongbai B, Rapior S, Hyde KD, Wittstein K, Stadler M (2015) *Hericium erinaceus*, an amazing medicinal mushroom. Mycol Prog 14:1–23

Tian J, Wang H, Vilgalys R, Ho M, Flanagan N, Richardson CJ (2021) Response of fungal communities to fire in a subtropical peatland. Plant Soil 466:525–543. https://doi.org/10.1007/s11104-021-05070-0

Tikhonenkov DV, Mikhailov KV, Hehenberger E, Karpov SA, Prokina KI, Esaulov AS, Belyakova OI, Mazei YA, Mylnikov AP, Aleoshin VV, Keeling PJ (2020) New lineage of microbial predators adds complexity to reconstructing the evolutionary origin of animals. Curr Biol 30(22):4500–4509. https://doi.org/10.1016/j.cub.2020.08.061

Timofeev S, Tokarev Y, Dolgikh V (2020) Energy metabolism and its evolution in Microsporidia and allied taxa. Parasitol Res 119(5):1433–1441. https://doi.org/10.1007/s00436-020-06657-9

Tretter ED, Johnson EM, Wang Y, Kandel P, White MM (2013) Examining new phylogenetic markers to uncover the evolutionary history of early-diverging fungi: comparing MCM7, TSR1 and rRNA genes for single-and multi-gene analyses of the *Kickxellomycotina*. Persoonia 30(1):106–125

Toome M, Aime MC (2014) *Pycnopulvinus aurantiacus* gen. et sp. nov., a new sporocarp-forming member of Pucciniomycotina. MycoKeys 8:43–50. https://doi.org/10.3897/mycokeys.8.7676

Toome M, Roberson RW, Aime MC (2013) *Meredithblackwellia eburnea* gen. et sp. nov., *Kriegeriaceae* fam. nov. and *Kriegeriales* ord. nov. toward resolving higher-level classification in *Microbotryomycetes*. Mycologia 105(2):486–495

Torruella G, Grau-Bove X, Moreira D, Karpov SA, Burns JA, Sebe-Pedros A, Volcker E, López-García P (2018) Global transcriptome analysis of the aphelid *Paraphelidium tribonemae* supports the phagotrophic origin of fungi. Commun Biol 1:231. https://doi.org/10.1038/s42003-018-0235-z

Trierveiler-Pereira L, Baltazar JM, Loguercio-Leite C (2008) *Xylobotryum portentosum* (Mont.) Pat. (*Ascomycota*): a second record from Brazil after a hundred years. Nova Hedwig 87:169–174. https://doi.org/10.1127/0029-5035/2008/0087-0169

Tripathi SKM (2009) Fungi from palaeoenvironments: their role in environmental interpretations. In: Misra JK, Deshmukh S (eds) Fungi from different environments. Science Publishers Enfield, pp 1–27

Tsang CC, Tang JYM, Lau SKP, Woo PCY (2018) Taxonomy and evolution of *Aspergillus*, *Penicillium* and *Talaromyces* in the omics era—past, present and future. Comput Struct Biotechnol J 16:197–210. https://doi.org/10.1016/j.csbj.2018.05.003

Umai D, Kayalvizhi R, Kumar V, Jacob S (2022) Xylitol: bioproduction and applications-a review. Front Sustain 3:826190. https://doi.org/10.3389/frsus.2022.826190

Untereiner WA, Gueidan C, Orr MJ, Diederich P (2011) The phylogenetic position of the lichenicolous *ascomycete Capronia peltigerae*. Fungal Divers 49:225–233. https://doi.org/10.1007/s13225-011-0097-x

Uppalapati SR, Young CA, Marek SM, Mysore KS (2010) *Phymatotrichum* (cotton) root rot caused by *Phymatotrichopsis omnivora*: retrospects and prospects. Mol Plant Pathol 11:325–334

Urbina H, Breed MF, Zhao W, Gurrala KL, Andersson SG, Ågren J, Baldauf S, Rosling A (2018) Specificity in *Arabidopsis thaliana* recruitment of root fungal communities from soil and rhizosphere. Fungal Biol 122(4):231–240. https://doi.org/10.1016/j.funbio.2017.12.013

Valdez AF, Miranda DZ, Guimarães AJ, Nimrichter L, Nosanchuk JD (2022) Pathogenicity & virulence of *Histoplasma capsulatum*—a multifaceted organism adapted to intracellular environments. Virulence 13:1900–1919. https://doi.org/10.1080/21505594.2022.2137987

Valenzuela-Lopez N, Cano-Lira JF, Guarro J, Sutton DA, Wiederhold N, Crous PW, Stchigel AM (2018) Coelomycetous *Dothideomycetes* with emphasis on the families *Cucurbitariaceae* and *Didymellaceae*. Stud Mycol 90:1–69. https://doi.org/10.1016/j.simyco.2017.11.003

Valle LG (2006) *Asellariales* (*Trichomycetes*) from the Iberian Peninsula. Fungal Divers 21:167–179

Vallejos-Torres G, Arévalo L, Cáceres B, Solis R (2023) Influence of arbuscular mycorrhizal fungi on biological control of coffee leaf rust (*Hemileia vastatrix* BERK. & BROOME). Bioagro 35(1):21–32

Van den Wyngaert S, Seto K, Rojas-Jimenez K, Kagami M, Grossart HP (2017) A new parasitic chytrid, *Staurastromyces oculus* (*Rhizophydiales*, *Staurastromycetaceae* fam. nov.), infecting the freshwater desmid *Staurastrum* sp. Protist 168:392–407. https://doi.org/10.1016/j.protis.2017.05.001

Van Vooren N (2021) Nomenclatural novelties in pezizales. Ascomycete. Org 13(2):83–84

Vanam HP, Rao PN, Mohanram K, Yegneswaran PP, Rudramurthy SPM (2018) Distal lateral subungual onychomycosis owing to *Tritirachium oryzae*: a bystander or invader? Mycopathologia 183:459–463. https://doi.org/10.1007/s11046-017-0226-5

Vandepol N, Liber J, Desirò A, Na H, Kennedy M, Barry K, Grigoriev IV, Miller AN, Donnell KO, Stajich JE, Bonito G (2020) Resolving the Mortierellaceae phylogeny through synthesis of multi-gene phylogenetics and phylogenomics. Fungal Divers 104:267–289. https://doi.org/10.1007/s13225-020-00455-5

Vánky K, Shivas RG, McTaggart AR, Vánky C, Arce WA (2009) Additions to the smut fungi (*Ustilaginomycetes*) of Bolivia. Mycol Balcan 6:99–105

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 BL, Buchanan P, Buyck B, Bense Y, 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. https://doi.org/10.1038/s41559-019-0834-1

Vávra J, Lukeš J (2013) *Microsporidia* and 'the art of living together.' Advances Parasitol 82:253–319. https://doi.org/10.1016/B978-0-12-407706-5.00004-6

Velenovský J (1934) Monographia discomycetum Bohemiae. Vol. 1, 2. – Pragae.

Vélez CG, Letcher PM, Schultz S, Powell MJ, Churchill PF (2011) Molecular phylogenetic and zoospore ultrastructural analyses of *Chytridium olla* establish the limits of a monophyletic *Chytridiales*. Mycologia 103:118–130. https://doi.org/10.3852/10-001

Vélez CG, Letcher PM, Schultz S, Mataloni G, Lefevre E, Powell MJ (2013) Three new genera from aquatic habitats in Argentina. Mycologia 105:1251–1265

Ventura-Aguilar RI Díaz-G, Bautista-Baños S, Mendoza-Acevedo S, Munguía-Cervantes JE, Correa-Pacheco ZN, Bosquez-Molina E (2021) Monitoring the infection process of *Rhizopus stolonifer* on strawberry fruit during storage using films based on chitosan/polyvinyl alcohol/polyvinylpyrrolidone and plant extracts. Int J Biol Macromol 182:583–594. https://doi.org/10.1016/j.ijbiomac.2021.03.187

Větrovský T, Morais D, Kohout P, Lepinay C, Algora C, Hollá SA, Bahnmann BD, Bílohnědá K, Brabcová V, D'Alò F, Human ZR, Jomura M, Kolařík M, Kvasničková J, Lladó S, López-Mondéjar R, Martinović T, Mašínová T, Meszárošová L, Michalčíková L, Michalová T, Mundra S, Navrátilová D, Odriozola I, Piché-Choquette S, Štursová M, Švec K, Tláskal V, Urbanová M, Vlk L, Voříšková J, Žifčáková L, Baldrian P (2020) Global Fungi, a global database of fungal occurrences from high-throughput-sequencing metabarcoding studies. Sci Data 7:228

Vicente J, Calderón F, Santos A, Marquina D, Benito S (2021) High potential of *Pichia kluyveri* and other *Pichia* species in wine technology. Int J Mol Sci 22(3):1196. https://doi.org/10.3390/ijms22031196

Vieira PDS, Souza Motta CM, Lima D, Torres JB, Quecine MC, Azevedo JL, de Oliveira NT (2011) Endophytic fungi associated with transgenic and non-transgenic cotton. Mycology 2:91–97. https://doi.org/10.1080/21501203.2011.584390

Vieira JCB, Câmara MPS, Bezerra JDP, Motta CMS, Machado AR (2018) First report of *Gilbertella persicaria* causing soft rot in eggplant fruit in Brazil. Plant Dis 120(6):1172. https://doi.org/10.1094/PDIS-09-17-1379-PDN

Vijayakumar VE, Venkataraman K (2023) Asystematic review of the potential of *Pichia pastoris* (*Komagataella phaffii*) as an alternative host for biologics production. Mol Biotechnol. https://doi.org/10.1007/s12033-023-00803-1

Vijaykrishna D, Jeewon R, Hyde KD (2006) Molecular taxonomy, origins and evolution of freshwater ascomycetes. Fungal Diversity 23:351–390

Vilela R, de Hoog S, Bensch K, Bagagli E, Mendoza L (2023) A taxonomic review of the genus *Paracoccidioides*, with focus on the uncultivable species. PLoS Negl Trop Dis 17:e0011220. https://doi.org/10.1371/journal.pntd.0011220

Villanueva P, Vásquez G, Gil-Durán C, Oliva V, Díaz A, Henríquez M, Álvarez E, Laich F, Chávez R, Vaca I (2021) Description of the first four species of the genus *Pseudogymnoascus* from Antarctica. Front Microbiol 12:713189

Voglmayr H, Fournier J, Jaklitsch WM (2019) Two new classes of *Ascomycota*: *Xylobotryomycetes* and *Candelariomycetes*. Persoonia 42:36–49. https://doi.org/10.3767/persoonia.2019.42.02

Voigt K, James TY, Kirk PM, de A. Santiago ALCM, Waldman B, Griffith GW, Fu MJ, Radek R, Strassert JFH, Wurzbacher C, Jerônimo GH, Simmons DR, Seto K, Gentekaki E, Hurdeal VG, Hyde KD, Nguyen TTT, Lee HB (2021) Early-diverging fungal phyla: taxonomy, species concept, ecology, distribution, anthropogenic impact, and novel phylogenetic proposals. Fungal Divers 109:59–98. https://doi.org/10.1007/s13225-021-00480-y

Volfold B, Varga M, Szekeres A, Kotogán A, Nagy G, Vágvölgy C, Papp T, Takó M (2021) β-Galactosidase-producing isolates in *Mucoromycota*: screening, enzyme production, and applications for functional oligosaccharide synthesis. J Fungi 7:229. https://doi.org/10.3390/jof7030229

Von Arx JA (1982) On *Mucoraceae* s. str. and other families of the *Mucorales*. Sydowia 35:10–26

Voos JR, Olive LS (1968) A new chytrid with aerial sporangia. Mycologia 60(3):730–733. https://doi.org/10.1080/00275514.1968.12018631

Wagner L, Stielow B, Hoffmann K, Petkovits T, Papp T, Vágvölgyi C, de Hoog GS, Verkley G, Voigt K (2013) A comprehensive molecular phylogeny of the *Mortierellales* (*Mortierellomycotina*) based on nuclear ribosomal DNA. Persoonia 30:77–93. https://doi.org/10.3767/003158513X666268

Wagner L, Stielow JB, de Hoog GS, Bensch K, Schwartze VU, Voigt K, Alastruey-Izquierdo A, Kurzai O, Walther G (2020) A new species concept for the clinically relevant *Mucor circinelloides* complex. Persoonia 44:67–97. https://doi.org/10.3767/persoonia.2020.44.03

Walker C, Vestberg M, Demircik F, Stockinger H, Saito M, Sawaki H, Nishmura I, Schüßler A (2007) Molecular phylogeny and new taxa in the *Archaeosporales* (*Glomeromycota*): *Ambispora* *fennica* gen. sp. nov., *Ambisporaceae* fam. nov., and emendation of *Archaeospora* and *Archaeosporaceae*. Mycol Res 111(2):137–153. https://doi.org/10.1016/j.mycres.2006.11.008

Walker C, Harper CJ, Brundrett M, Krings M (2021) The Early Devonian fungus *Mycokidstonia sphaerialoides* from the Rhynie chert is a member of the *Ambisporaceae* (*Glomeromycota*, *Archaeosporales*), not an Ascomycete. Rev of Palaeobot and Palynol 287:104384. https://doi.org/10.1016/j.revpalbo.2021.104384

Walther G, Wagner L, Kurzai O (2019) Updates on the taxonomy of *Mucorales* with an emphasis on clinically important taxa. J Fungi 5(4):106. https://doi.org/10.3390/jof5040106

Wang Z, Johnston PR, Takamatsu S, Spatafora JW, Hibbett DS (2006) Toward a phylogenetic classification of the *Leotiomycetes* based on rDNA data. Mycologia 98(6):1065–1075. https://doi.org/10.1080/15572536.2006.11832634

Wang H, Guo S, Huang M, Thorsten LH, Wei J (2010) *Ascomycota* has a faster evolutionary rate and higher species diversity than *Basidiomycota*. Sci China Life Sci 53:1163–1169

Wang Y-N, Liu X-Y, Zheng R-Y (2013) Four new species records of *Umbelopsis* (*Mucoromycotina*) from China. J Mycol 2013:970216. https://doi.org/10.1155/2013/970216

Wang Q, Theelen B, Groenewald M, Bai F, Boekhout T (2014) *Moniliellomycetes* and *Malasseziomycetes*, two new classes in *Ustilaginomycotina*. Persoonia 33:41–47. https://doi.org/10.3767/003158514X682313

Wang QM, Begerow D, Groenewald M, Liu XZ, Theelen B, Bai FY, Boekhout T (2015a) Multigene phylogeny and taxonomic revision of yeasts and related fungi in the *Ustilaginomycotina*. Studies Mycol 81:55–83. https://doi.org/10.1016/j.simyco.2015.10.004

Wang QM, Yurkov AM, Göker M, Lumbsch HT, Leavitt SD, Groenewald M, Theelen B, Liu XZ, Boekhout T, Bai FY (2015b) Phylogenetic classification of yeasts and related taxa within *Pucciniomycotina*. Stud Mycol 81:149–189. https://doi.org/10.1016/j.simyco.2015.12.002

Wang K, Sipilä TP, Overmyer K (2016a) The isolation and characterization of resident yeasts from the phylloplane of *Arabidopsis thaliana*. Sci Rep 6(1):39403. https://doi.org/10.1038/srep39403

Wang TW, de Kesel A, Haelewaters D, Pfister DH (2016b) Farlow Herbarium cockroach hosts new record of *Laboulbeniales* for North America. Rhodora 118(973):26–31. https://doi.org/10.3119/15-20

Wang HC, Minh BQ, Susko E, Roger AJ (2018) Modeling site heterogeneity with posterior mean site frequency profiles accelerates accurate phylogenomic estimation. Syst Biol 67(2):216–235. https://doi.org/10.1093/sysbio/syx068

Wang T, Sun CX, Zhun PK (2022) First report of *Mucor irregularis* causing postharvest fruit rot on *Garcinia mangostana* in China. Plant Dis 106:766. https://doi.org/10.1094/pdis-07-21-1431-pdn

Wang F, Han R, Chen S (2023a) An overlooked and underrated endemic mycosis—talaromycosis and the pathogenic fungus *Talaromyces marneffei*. Clin Microbiol Rev 36:e0005122. https://doi.org/10.1128/cmr.00051-22

Wang L, Qu Y, Tang L, Li Y, Liu L, Liu Y (2023b) Case report: a case of pulmonary mucormycosis caused by *Rhizopus azygosporus* infection complicated by type 2 diabetes mellitus. Front Med 10:1240436. https://doi.org/10.3389/fmed.2023.1240436

Wang Y, Chang Y, Ortañez J, Peña JF, Carter-House D, Reynolds NK, Smith ME, Benny G, Mondo SJ, Salamov A, Lipzen A, Pangilinan J, Guo J, LaButti K, Andreopolous W, Tritt A, Keymanesh K, Yan M, Barry K, Grigoriev IV, Spatafora JW, Stajich JE (2023c) Divergent evolution of early terrestrial fungi reveals the evolution of Mucormycosis pathogenicity factors. Genome Biol Evol. https://doi.org/10.1093/gbe/evad046

Warming E (1884) Haandbog i Den Systematiske Botanik 2:1–434

Wei YL, Yuan HS, Dai YC (2007) First report of *Henningsomyces* (*Basidiomycetes*) in China. J Fungal Res 5(04):187–189

Weiß M, Bauer R, Begerow D (2004) Spotlights on *Heterobasidiomycetes*. In: Agerer R, Piepenbring M, Blanz P (eds) Frontiers in basidiomycote mycology. IHW, Germany, pp 7–48

Weiß M, Bauer R, Sampaio JP, Oberwinkler F (2014) *Tremellomycetes* and related groups. In: McLaughlin DJ, Spatafora JW (eds) The mycota VII. Systematics and evolution. Part A. Springer, Germany, pp 331–355. https://doi.org/10.1007/978-3-642-55318-9_12

Weir A, Blackwell M (2001) Molecular data support the *Laboulbeniales* as a separate class of *Ascomycota*. *Laboulbeniomycetes* Mycol Res 105(10):1182–1190. https://doi.org/10.1017/S0953756201004919

Wells K (1994) Jelly fungi then and now! Mycologia 86:18–48. https://doi.org/10.1080/00275514.1994.12026372

Wendt L, Sir EB, Kuhnert E, Heitkämper S, Lambert C, Hladki AI, Romero AI, Luangsa-ard JJ, Srikitikulchai P, Peršoh D, Stadler M (2018) Resurrection and emendation of the *Hypoxylaceae*, recognised from a multigene phylogeny of the *Xylariales*. Mycol Prog 17:115–154. https://doi.org/10.1007/s11557-017-1311-3

Whelan S, Irisarri I, Burki F (2018) PREQUAL: detecting non-homologous characters in sets of unaligned homologous sequences. Bioinformatics 34(22):3929–3930. https://doi.org/10.1093/bioinformatics/bty448

White TJ, Bruns T, Lee S, Taylor J (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA, Gelfand DH, Sninsky JJ, White TJ (eds) PCR protocols. Academic Press, San Diego, pp 315–322

White MM, James TY, O'Donnell K, Cafaro MJ, Tanabe Y, Sugiyama J (2006) Phylogeny of the *Zygomycota* based on nuclear ribosomal sequence data. Mycologia 98(6):872–884. https://doi.org/10.3852/mycologia.98.6.872

Whittaker RH (1959) On the broad classification of organisms. Q Rev Biol 34:210–226

Wijayawardene DNN, McKenzie EHC, Hyde KD (2012) Towards incorporating anamorphic fungi in a natural classification–checklist and notes for 2011. Mycosphere 3:157–228. https://doi.org/10.5943/mycosphere/3/2/5

Wijayawardene NN, Crous PW, Kirk PM, Hawksworth DL, Boonmee S, Braun U, Dai DQ, Dsouza MJ, Diederich P, Dissanayake A, Doilom M, Hongsanan S, Jones EBG, Groenewald JZ, Jayawardena R, Lawrey JD, Liu JK, Lücking R, Madrid H, Manamgoda DS, Muggia L, Nelsen MP, Phookamsak R, Suetrong S, Tanaka K, Thambugala KM, Wanasinghe DN, Wikee S, Zhang Y, Aptroot A, Ariyawansa HA, Bahkali AH, Bhat DJ, Gueidan C, Chomnunti P, de Hoog GS, Knudsen K, Li WJ, McKenzie EHC, Miller AN, Phillips AJL, Piątek M, Raja HA, Shivas RS, Slippers B, Taylor JE, Tian Q, Wang Y, Woudenberg JHC, Cai L, Jaklitsch WM, Hyde KD (2014) Naming and outline of *Dothideomycetes*–2014 including proposals for the protection or suppression of generic names. Fungal Divers 69:1–55. https://doi.org/10.1007/s13225-014-0309-2

Wijayawardene NN, Hyde KD, Rajeshkumar KC, Hawksworth DL, Madrid H, Kirk PM, Braun U, Singh RV, Crous PW, Kukwa M, Lücking R, Kurtzman CP, Yurkov A, Haelewaters D, Aptroot A, Lumbsch HT, Timdal E, Ertz D, Etayo J, Phillips AJL, Groenewald JZ, Papizadeh M, Selbmann L, Dayarathne MC, Weerakoon G, Jones EBG, Suetrong S, Tian Q, Castañeda-Ruiz RF, Bahkali AH, Pang K-L, Tanaka K, Dai DQ, Sakayaroj J, Hujslová M, Lombard L, Shenoy BD, Suija A, Maharachchikumbura SSN, Thambugala KM, Wanasinghe DN, Sharma BO, Gaikwad S, Pandit G, Zucconi L, Onofri S, Egidi E, Raja HA, Kodsueb R, Cáceres MES, Pérez-Ortega S, Fiuza PO, Monteiro JS, Vasilyeva LN, Shivas RG, Prieto M, Wedin M, Olariaga I, Lateef AA, Agrawal Y, Fazeli SAS, Amoozegar MA, Zhao GZ, Pfliegler WP, Sharma G, Oset M, Abdel-Wahab MA, Takamatsu S, Bensch K, de Silva NI, De Kese A, Karunarathna A, Boonmee S, Pfister DH, Lu YZ, Luo ZL, Boonyuen N, Daranagama DA, Senanayake IC, Jayasiri SC, Samarakoon MC, Zeng XY, Doilom M, Quijada L, Rampadarath S, Heredia G, Dissanayake AJ, Jayawardana RS, Perera RH, Tang LZ, Phukhamsakda C, Hernández Restrepo M, Ma X, Tibpromma S, Gusmao LFP, Weerahewa D, Karunarathna SC (2017a) Notes for Genera *Ascomycota*. Fungal Divers 86:1–594. https://doi.org/10.1007/s13225-017-0386-0

Wijayawardene NN, Hyde KD, Tibpromma S, Wanasinghe DN, Thambugala KM, Tian Q, Wang Y, Fu L (2017b) Towards incorporating asexual fungi in a natural classification: checklist and notes 2012–2016. Mycosphere 8(9):1457–1555. https://doi.org/10.5943/mycosphere/8/9/10

Wijayawardene NN, Hyde KD, Lumbsch T, Liu JK, Maharachchikumbura SSN, Ekanayaka AH, Tian Q, Phookamsak R (2018a) Outline of *Ascomycota*: 2017. Fungal Divers 88(1):167–263. https://doi.org/10.1007/s13225-018-0394-8

Wijayawardene NN, Pawlowska J, Letcher PM, Kirk PM, Humber RA, Schüßler A, Wrzosek M, Muszewska A, Okrasińska IL, Gęsiorska A, Mungai P, Lateef AA, Rajeshkumar KC, Singh RV, Radek R, Walther G, Wagner L, Walker C, Wijesundara DSA, Papizadeh M, Dolatabadi S, Shenoy BD, Tokarev YS, Lumyong S, Hyde KD (2018b) Notes for genera: basal clades of Fungi (including *Aphelidiomycota*, *Basidiobolomycota*, *Blastocladiomycota*, *Calcarisporiellomycota*, *Caulochytriomycota*, *Chytridiomycota*, *Entomophthoromycota*, *Glomeromycota*, *Kickxellomycota*, *Monoblepharomycota*, *Mortierellomycota*, *Mucoromycota*, *Neocallimastigomycota*, *Olpidiomycota*, *Rozellomycota* and *Zoopagomycota*). Fungal Divers 92:43–129. https://doi.org/10.1007/s13225-018-0409-5

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, Pfiegler WP, Horváth E, Bensch K, Kirk PM, Kolaříková K, Raja HA, Radek R, Papp V, Dima V, 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 (2020a) Outline of *Fungi* and fungus-like taxa. Mycosphere 11:1060–1456. https://doi.org/10.5943/mycosphere/11/1/8

Wijayawardene NN, Hyde KD, Dai DQ, Tang LZ, Aptroot A, Castañeda-Ruiz RF, Druzhinina IS, Cai F, Ekanayaka AH, Erdoğdu M, Fiuza PO, Gentekaki E, Goto BT, Haelewaters D, Hongsanan S, Jeewon R, Kirk PM, Jayalal U, Karunarathna SC, Wanasinghe DN, Lumbsch HT, Madrid H, Maharachchikumbura SSN, Monteiro JS, Shivaprakash N, Pfliegler WP, Phillips AJL, Saxena RK, Stadler M, Tian Q, Tokarev YS, Tsurykau A, Ertz D, Lee HB, Etayo J, Vizzini A, Jones EGB, Lin CG, Li WJ, Dai YC, Fan XL, McKenzie EHC, Shivas RG, Hustad V, Leontyev DV, de Hoog GS, Niskanen T, Boekhout T, Gaya E, Thines M (2020b) A dynamic portal for a community-driven, continuously updated classification of *Fungi* and fungus-like organisms: outlineoffungi.org. Mycosphere 11(1), 1514–1526. https://doi.org/10.5943/mycosphere/11/1/11

Wijayawardene NN, Bahram M, Sánchez-Castro I, Dai DQ, Ariyawansa KG, Jayalal U, Suwannarach N, Tedersoo L (2021a) Current insight into culture-dependent and culture-independent methods in discovering Ascomycetous Taxa. J Fungi 7(9):703. https://doi.org/10.3390/jof7090703

Wijayawardene NN, Hyde KD, Anand G, Dissanayake LS, Tang LZ, Dai DQ (2021b) Towards incorporating asexually reproducing fungi in the natural classification and notes for pleomorphic genera. Mycosphere 12:238–405. https://doi.org/10.5943/mycosphere/12/1/4

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 13:53–453. https://doi.org/10.5943/mycosphere/13/1/2

Wijayawardene NN, Phillips AJ, Pereira DS, Dai DQ, Aptroot A, Monteiro JS, Druzhinina IS, Cai F, Fan X, Selbmann L, Coleine C (2022b) Forecasting the number of species of asexually reproducing fungi (*Ascomycota* and *Basidiomycota*). Fungal Divers 114(1):463–490. https://doi.org/10.1007/s13225-022-00500-5

Williamson WC (1878) On the organization of fossil plants of the Coal Measures. Part IX. Philos Trans R Soc Lond 169:319–364

Williamson WC (1880) On the organization of the fossil plants of the Coal-Measures – Part X. Including an examination of the supposed radiolarians of the Carboniferous rocks. Philos Trans R Soc Lond 171:493–539

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. https://doi.org/10.1007/s11557-023-01879-4

Wright JE (1970) *Agaricostilbum*, a new genus of Deuteromycetes on palm spathes from Argentina. Mycologia 62:679–682

Wołczańska A, Szysz MP (2018) *Mycosarcoma maydis* (*Ustilago maydis*)- benefits and harmful effects of the phytopathogenic fungus for humans. Biomed J Sci & Tech Res 4(1):3746–3748. https://doi.org/10.26717/BJSTR.2018.04.001005

Woronin MS (1878) Plasmodiophora Brassicae. Urheber der Kohlpflanzenhernie Jahrbücher Für Wissenschaftliche Botanik 11:548–574

Worrall J, Anagnost S, Zabel RA (1997) Comparison of wood decay among diverse lignicolous fungi. Mycologia 89:199–219. https://doi.org/10.2307/3761073

Wu HH, Zou YN, Rahman MM, Ni QD, Wu QS (2017) Mycorrhizas alter sucrose and proline metabolism in trifoliate orange exposed to drought stress. Scientific Rep 7:1–10. https://doi.org/10.1038/srep42389

Xie MM, Zhang YC, Liu LP, Zou YN, Wu QS, Kuča K (2019) Mycorrhiza regulates signal substance levels and pathogen defense gene expression to resist Citrus Canker. Not Bot Horti Agrobo 47:1161–1167. https://doi.org/10.15835/nbha47411561

Xie Y, Guan Z, Zhang X, Zhang J, Yang Z, Regenstein JM, Zhou P (2023) Evaluation of sufu fermented using *Mucor racemosus* M2: Biochemical, textural, structural and microbiological properties. Foods 12:1706. https://doi.org/10.3390/foods12081706

Yamada Y, Banno I (1987) *Hasegawaea* gen. nov., an ascosporogenous yeast genus for the organisms whose asexual reproduction is by fission and whose ascospores have smooth surfaces without papillae and which are characterized by the absence of coenzyme Q and by the presence of linoleic acid in cellular fatty acid composition. J Gen App Microbiol 33(3):295–298

Yamada Y, Arimoto M, Kondo K (1973) Coenzyme Q system in the classification of the ascosporogenous yeast genus *Schizosaccharomyces* and yeast-like genus *Endomyces*. J Gen App Microbiol 19(5):353–358

Yamamoto K, Degawa Y, Hirose D, Fukuda M, Yamada A (2015) Morphology and phylogeny of four *Endogone* species and *Sphaerocreas pubescens* collected in Japan. Mycol Prog 14:86. https://doi.org/10.1007/s11557-015-1111-6

Yamamoto K, Degawa Y, Takashima Y, Fukuda M, Yamada A (2017) *Endogone corticioides* sp. nov. from subalpine conifer forests in Japan and China, and its multi-locus phylogeny. Mycoscience 58:23–29. https://doi.org/10.1016/j.myc.2016.08.001

Yamazaki A, Lorliam W, Kawasaki H, Uchino M, Suzuki KI (2020) Fourteen novel lipomycetaceous yeast species isolated from soil in Japan and transfer of *Dipodascopsis anomala* to the genus *Babjevia* based on ascospore production phenotype. Int J Syst Evol Microbiol 70:1372–1397. https://doi.org/10.1099/ijsem.0.003924

Yan W, Gao H, Qian X, Jiang Y, Zhou J, Dong W, Xin F, Zhang W, Jiang M (2021) Biotechnological applications of the non-conventional yeast Meyerozyma guilliermondii. Biotechnol Adv 46:107674. https://doi.org/10.1016/j.biotechadv.2020.107674

Yan YH, Wang MT, Chen N, Wang X, Fu CH, Li YM, Gan XR, Lv P, Zhang Y (2022) Isolation, structures, bioactivities, application and future prospective for polysaccharides from *Tremella aurantialba*: a review. Front Immunol 13:1091210. https://doi.org/10.3389/fimmu.2022.1091210

Yang E, Xu L, Yang Y, Zhang X, Xiang M, Wang C, An Z, Liu X (2012) Origin and evolution of carnivorism in the *Ascomycota* (fungi). Proc Natl Acad Sci 109(27):10960–10965

Yao D, Xu L, Wu M, Wang X, Wang K, Li Z, Zhang D (2021) Microbial community succession and metabolite changes during fermentation of BS sufu, the fermented black soybean curd by *Rhizopus microsporus*, *Rhizopus oryzae*, and *Actinomucor elegans*. Front Microbiol 12:665826. https://doi.org/10.3389/fmicb.2021.665826

Yilmaz N, Visagie CM, Houbraken J, Frisvad JC, Samson RA (2014) Polyphasic taxonomy of the genus *Talaromyces*. Stud Mycol 78:175–341. https://doi.org/10.1016/j.simyco.2014.08.001

Yonow T, Ramirez-Villegas J, Abadie C, Darnell RE, Ota N, Kriticos DJ (2019) Black Sigatoka in bananas: ecoclimatic suitability and disease pressure assessments. PLoS ONE 14:e0220601. https://doi.org/10.1371/journal.pone.0220601

Yu MQ, Ko WH (1997) Factors affecting germination and mode of germination of zygospores of *Choanephora cucurbitarum*. J Phytopathol 145:357–361

Yu ZF, Mo MH, Zhang Y, Zhang KQ (2014) Taxonomy of nematode-trapping fungi from *Orbiliaceae*, *Ascomycota*. In: Zhang KQ, Hyde KD (eds) Nematode-trapping fungi. Fungal divers research series 23. Springer, Dordrecht, pp 41–210

Yuan H, Dong L, Zhang Z, He Y, Ma X (2022) Production, structure, and bioactivity of polysaccharide isolated from *Tremella fuciformis*. Food Sci Hum Wellness 11:1010–1017. https://doi.org/10.1016/j.fshw.2022.03.030

Yurlova NA, de Hoog GS, Fedorova LG (2008) The influence of ortho- and para-diphenoloxidase substrates on pigment formation in black yeast-like fungi. Stud Mycol 61:39–49. https://doi.org/10.3114/sim.2008.61.03

Zajc J, Gunde-Cimerman N (2018) The genus *Wallemia*-from contamination of food to health threat. Microorganisms 6:46. https://doi.org/10.3390/microorganisms6020046

Zalar P, Sybren de Hoog G, Schroers HJ, Frank JM, Gunde-Cimerman N (2005) Taxonomy and phylogeny of the xerophilic genus *Wallemia* (*Wallemiomycetes* and *Wallemiales*, cl. et ord. nov.). Antonie Van Leeuwenhoek 87:311–328

Zamora JC, Ekman S (2020) Phylogeny and character evolution in the *Dacrymycetes*, and systematics of *Unilacrymaceae* and *Dacryonaemataceae* fam. nov. Persoonia 44(1):161–205. https://doi.org/10.3767/persoonia.2020.44.07

Zeng M, Gentekaki E, Zeng XY, Tian Q, Zhao Q, Hyde KD (2022) Evolutionary relationships and allied species of *Pyronemataceae*, with segregation of the novel family *Pyropyxidaceae*. Mycosphere 13:207–280. https://doi.org/10.5943/mycosphere/si/1f/7

Zhang N, Luo J, Rossman AY, Aoki T, Chuma I, Crous PW, Dean R, de Vries RP, Donofrio N, Hyde KD, Lebrun MH, Talbot NJ, Tharreau D, Tosa Y, Valent B, Wang ZH, Xu JR (2016) Generic Names in *Magnaporthales* 7:155–159. https://doi.org/10.5598/imafungus.2016.07.01.09

Zhang YC, Xie MM, Feng HD, Zhou M, Zhang ZZ, Liu CY, Wu QS (2018a) Common mycelium networks with *Paraglomus occultum* induce better plant growth and signal substance changes between trifoliate orange seedlings. Acta Sci Pol Hortorum Cultus 17:95–104

Zhang Z-F, Zhao P, Cai L (2018b) Origin of cave fungi. Front Microbiol 9:1407. https://doi.org/10.3389/fmicb.2018.01407

Zhang Y, Hu J, Bai J, Qin H, Wang J, Wang J, Lin X (2019) Intercropping with sunflower and inoculation with *arbuscular mycorrhizal* fungi promotes growth of garlic chive in metal-contaminated soil at a WEEE-recycling site. Ecotoxicol Environ Saf 167:376–384. https://doi.org/10.1016/j.ecoenv.2018.10.046

Zhang J, Kou J, Ozbudak E, Zhong T, Pan T, Bai J, Cano LM, Ritenour MA (2020) First report of *Gilbertella persicaria* causing postharvest soft rot of strawberry fruit in Florida. Plant Dis 104(10):2736. https://doi.org/10.1094/PDIS-10-19-2081-PDN

Zhang JR, Ge YY, Liu PH, Wu DT, Liu HY, Li HB, Corke H, Gan RY (2022a) Biotechnological strategies of riboflavin biosynthesis in microbes. Engineering 12:115–127. https://doi.org/10.1016/j.eng.2021.03.018

Zhang Q, Liu X, Liu Y, Wang H, Zhao R, Lv X, Wei X, Zhou K (2022b) Nasal and cutaneous mucormycosis in two patients with lymphoma after chemotherapy and target therapy: early detection by metagenomic next-generation sequencing. Front Cell Infect Microbiol 12:960766. https://doi.org/10.3389/fcimb.2022.960766

Zhang S, Wang L, Han Q, Sun A, Liu X, Xue L (2022c) Lung cancer coexisting with *Papiliotrema flavescens* infection diagnosed by next-generation sequencing: a case report. BMC Infect Dis 22:684. https://doi.org/10.1186/s12879-022-07591-0

Zhang T, Zhu X, Vizzini A, Li B, Cao Z, Guo W, Qi S, Wei X, Zhao R (2022d) New insights into lichenization in *Agaricomycetes* based on an unusual new basidiolichen species of *Omphalina s. str.* J Fungi. https://doi.org/10.3390/jof8101033

Zhang YN, Wang JZ, Swingle B, Niu BY, Xu J, Ma X, Wei WL, Gao M (2023) First report of *Rhizopus arrhizus* (syn. *R. oryzae*) causing garlic bulb soft rot in Hebei province, China. Plant Dis 107(3):949. https://doi.org/10.1094/pdis-05-22-1024-pdn

Zhao ML, Huang JS, Mo MH, Zhang KQ (2005) A potential virulence-factor involved in fungal pathogenicity: serine-like proteaseactivity of nematophagous fungus *Clonostachys rosea*. Fungal Divers 19:217–234

Zhao RL, Li GJ, Sánchez-Ramírez S, Stata M, Yang ZL, Wu G, Dai YC, He SH, Cui BK, Zhou JL, Wu F, He MQ, Moncalvo JM, Hyde KD (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/s13225-017-0381-5

Zhao H, Dai YC, Liu XY (2022) Outline and divergence time of subkingdom *mucoromyceta*: two new phyla, five new orders, six new families and seventy-three new species. bioRxiv. https://doi.org/10.1101/2022.07.05.498902

Zhao H, Nie Y, ZongTK WK, Lv ML, Cui YJ, Tohtirjap A, Chen JJ, Zhao CL, Wu F, Cui BK, Yuan Y, Dai YC, Liu XY (2023) Species diversity, updated classification and divergence times of the phylum *Mucoromycota*. Fungal Divers 123:49–157. https://doi.org/10.1007/s13225-023-00525-4

Zullo BA, Ciafardini G (2022) Role of yeasts in the qualitative structuring of extra virgin olive oil. J Appl Microbiol 132:4033–4041. https://doi.org/10.1111/jam.15478

Zycha H, Siepmann R, Linnemann G (1969) *Mucorales*. Eine Beschreibung aller Gattungen und Arten dieser Pilzgruppe. Cramer, Lehre

Springer Nature or its licensor (e.g. a society or other partner) holds exclusive rights to this article under a publishing agreement with the author(s) or other rightsholder(s); author self-archiving of the accepted manuscript version of this article is solely governed by the terms of such publishing agreement and applicable

Authors and Affiliations

Nalin N. Wijayawardene[1,2,3] · Kevin D. Hyde[4,5,6,7] · Kirill V. Mikhailov[8,9] · Gábor Péter[10] · André Aptroot[11] · Carmen L. A. Pires-Zottarelli[12] · Bruno T. Goto[13] · Yuri S. Tokarev[14] · Danny Haelewaters[15,16,17] · Samantha C. Karunarathna[1] · Paul M. Kirk[18] · André L. C. M. de A. Santiago[19] · Ramesh K. Saxena[20] · Nathan Schoutteten[21,90] · Madhara K. Wimalasena[3,22] · Vladimir V. Aleoshin[8,9] · Abdullah M. S. Al-Hatmi[23] · Kahandawa G. S. U. Ariyawansa[24] · Amanda R. Assunção[13] · Thushara C. Bamunuarachchige[3] · Hans-Otto Baral[25] · D. Jayarama Bhat[26,27] · Janusz Błaszkowski[28] · Teun Boekhout[29] · Nattawut Boonyuen[30] · Michael Brysch-Herzberg[31] · Bin Cao[32] · Jonathan Cazabonne[33,34] · Xue-Mei Chen[1] · Claudia Coleine[35] · Dong-Qin Dai[1] · Heide-Marie Daniel[36] · Suzana B. G. da Silva[19] · Francisco Adriano de Souza[37] · Somayeh Dolatabadi[38] · Manish K. Dubey[39] · Arun K. Dutta[40] · Aseni Ediriweera[2,41] · Eleonora Egidi[42,43] · Mostafa S. Elshahed[44] · Xinlei Fan[45,46] · Juliana R. B. Felix[13] · Mahesh C. A. Galappaththi[47] · Marizeth Groenewald[48] · Li-Su Han[1] · Bo Huang[49] · Vedprakash G. Hurdeal[50] · Anastasia N. Ignatieva[14] · Gustavo H. Jerônimo[12] · Ana L. de Jesus[12] · Serhii Kondratyuk[51,52] · Jaturong Kumla[53,54] · Martin Kukwa[55] · Qirui Li[56,57] · Juliana L. R. Lima[13] · Xiao-Yong Liu[58] · Wenhua Lu[1,53] · H. Thorsten Lumbsch[59] · Hugo Madrid[60] · Franco Magurno[61] · Guy Marson[62] · Eric H. C. McKenzie[63] · Audrius Menkis[64] · Armin Mešić[65] · Elaine C. R. Nascimento[13] · Elena S. Nassonova[66] · Yong Nie[67] · Naasson V. L. Oliveira[13] · Emilia A. Ossowska[55] · Julia Pawłowska[68] · Ursula Peintner[69] · Igor R. Pozdnyakov[70] · Bhagya M. Premarathne[71] · A. K. Hasith Priyashantha[72,73] · C. Alisha Quandt[16] · Mariana B. Queiroz[13] · Kunhiraman C. Rajeshkumar[74] · Mubashar Raza[75] · Niranjan Roy[40] · Milan C. Samarakoon[76] · Alessandra A. Santos[13] · Lidiane A. Santos[77] · Felix Schumm[78] · Laura Selbmann[35,79] · Faruk Selçuk[80] · D. Rabern Simmons[81] · Anastasia V. Simakova[82] · Maudy Th. Smith[48] · Onden Paraparath Sruthi[74] · Nakarin Suwannarach[53,54] · Kazuaki Tanaka[83] · Saowaluck Tibpromma[1] · Elias O. Tomás[13] · Merve Ulukapı[80] · Nicolas Van Vooren[84] · Dhanushka N. Wanasinghe[85] · Evi Weber[24] · Qianzhen Wu[56,57] · Er Fu Yang[1,73] · Ryuichi Yoshioka[83,91] · Noha H. Youssef[44] · Annemarie Zandijk[48] · Gui-Qing Zhang[1] · Jin-Yong Zhang[86] · Heng Zhao[87] · RuiLin Zhao[32] · Oleg A. Zverkov[9] · Marco Thines[88,89] · Sergey A. Karpov[70]

✉ Nalin N. Wijayawardene
nalinwijayawardene@yahoo.com

✉ Dong-Qin Dai
cicidaidongqin@gmail.com

✉ Sergey A. Karpov
sakarpov4@gmail.com

[1] Center for Yunnan Plateau Biological Resources Protection and Utilization, College of Biological Resource and Food Engineering, Qujing Normal University, Qujing 655011, Yunnan, People's Republic of China

[2] Tropical Microbiology Research Foundation, 96/N/10, Meemanagoda Road, Pannipitiya 10230, Sri Lanka

[3] Department of Bioprocess Technology, Faculty of Technology, Rajarata University, Mihintale, Sri Lanka

[4] Center of Excellence in Fungal Research, Mae Fah Luang University, Chiang Rai 57100, Thailand

[5] School of Science, Mae Fah Luang University, ChiangRai 57100, Thailand

[6] Innovative Institutefor Plant Health, Zhongkai University of Agriculture and Engineering, Guangzhou 510225, People's Republic of China

[7] CAS Key Laboratory for Plant Biodiversity and Biogeography of East Asia (KLPB), Kunming Institute of Botany, Chinese Academy of Science, Kunming, Yunnan, China

[8] Belozersky Institute of Physicochemical Biology, Lomonosov Moscow State University, Leninskye Gory, 1, Build. 40, Moscow 119991, Russian Federation

[9] Kharkevich Institute for Information Transmission Problems, Russian Academy of Sciences, Moscow 127051, Russian Federation

[10] National Collection of Agricultural and Industrial Microorganisms, Institute of Food Science and Technology, Hungarian University of Agriculture and Life Sciences, Somlói út 14-16, 1118 Budapest, Hungary

[11] Instituto de Biociências, Universidade Federal de Mato Grosso do Sul, Avenida Costa e Silva, s/n Bairro Universitário, Campo Grande, MS CEP 79070-900, Brazil

[12] Instituto de Pesquisas Ambientais, Secretaria do Meio Ambiente, Infraestrutura e Logística, Av. Miguel Stéfano 3687, São Paulo, SP CEP 04301-902, Brazil

[13] Departamento de Botânica e Zoologia, Universidade Federal do Rio Grande do Norte, Campus Universitário, Natal, RN 59078–900, Brazil

[14] All-Russian Institute of Plant Protection, Sh. Podbelskogo 3, Pushkin, St. Petersburg 196608, Russia

[15] Research Group Mycology, Department of Biology, Ghent University, 9000 Ghent, Belgium

[16] Faculty of Science, University of South Bohemia, 370 05 České Budějovice, Czech Republic

[17] Department of Ecology and Evolutionary Biology, University of Colorado Boulder, Boulder, CO 80309, USA

[18] Biodiversity Informatics and Spatial Analysis, Jodrell Laboratory, Royal Botanic Gardens, Kew, Surrey TW9 3AB, UK

[19] Departamento de Micologia, Centro de Biociências, Universidade Federal de Pernambuco, Av. Prof. Nelson Chaves, s/n, Recife, Pernambuco 50670-420, Brazil

[20] Birbal Sahni Institute of Palaeosciences, 53 University Road, Lucknow 226007, India

[21] Research Group Mycology, Department of Biology, Ghent University, K.L. Ledeganckstraat 35, 9000 Ghent, Belgium

[22] Faculty of Graduate Studies, Sabaragamuwa University of Sri Lanka, Belihuloya 70140, Sri Lanka

[23] Natural & Medical Sciences Research Center, University of Nizwa, Nizwa 616, Oman

[24] Department of Plant Sciences, Faculty of Science, University of Colombo, Colombo 00300, Sri Lanka

[25] Blaihofstraße 42, 72074 Tübingen, Germany

[26] Biology Division, Vishnugupta Vishwavidyapeetam, Ashoke, Gokarna 581326, India

[27] Formerly Department of Botany, Goa University, Goa 403206, India

[28] Department of Environmental Management, West Pomeranian University of Technology in Szczecin, Słowackiego 17, 71434 Szczecin, Poland

[29] The Yeasts Foundation, 1015JR Amsterdam, The Netherlands

[30] National Center for Genetic Engineering and Biotechnology (BIOTEC), National Science and Technology Development Agency (NSTDA), 111 Thailand Science Park, Phahonyothin Road, Khlong Nueng, Khlong Luang 12120, Pathum Thani, Thailand

[31] Laboratory for Wine Microbiology, Department International Business, Heilbronn University of Applied Sciences, Heilbronn, Germany

[32] State Key Laboratory of Mycology, Institute of Microbiology, Chinese Academy of Sciences, Beijing 100101, China

[33] Forest Research Institute, Université du Québec en Abitibi-Témiscamingue, 445, Boul. de l'Université, Rouyn-Noranda, QC J9X 5E4, Canada

[34] Centre for Forest Research, Université du Québec à Montréal, Montréal, QC H3C 3P8, Canada

[35] Department of Ecological and Biological Sciences, University of Tuscia, 01100 Viterbo, Italy

[36] BCCM/MUCL, Earth and Life Institute, Mycology Laboratory, Université catholique de Louvain, 1348 Louvain-la-Neuve, Belgium

[37] Núcleo de Biologia Aplicada, Embrapa Milho e Sorgo, Empresa Brasileira de Pesquisa Agropecuária, Sete Lagoas, Minas Gerais 35702-098, Brazil

[38] Department of Biology, Hakim Sabzevari University, Sabzevar, Iran

[39] Department of Biotechnology, University Centre for Research and Development, Chandigarh University, Mohali 140413, Punjab, India

[40] Molecular & Applied Mycology Laboratory, Department of Botany, Gauhati University, Gopinath Bordoloi Nagar, Jalukbari, Guwahati, Assam 781014, India

[41] B-Hood Myco-Tropic Innovations, 1/9, 1st Lane, Issadeen Town, Matara, Sri Lanka

[42] Hawkesbury Institute for the Environment, Western SydneyUniversity, Penrith, Australia

[43] Global Centre for Land-Based Innovation, Western Sydney University, Penrith, Australia

[44] Department of Microbiology and Molecular Genetics, Oklahoma State University, Stillwater, OK, USA

[45] State Key Laboratory of Efficient Production of Forest Resources, Beijing Forestry University, Beijing 100083, People's Republic of China

[46] Key Laboratory for Silviculture and Conservation of the Ministry of Education, Beijing Forestry University, Beijing 100083, People's Republic of China

[47] Harry Butler Institute, Murdoch University, Murdoch, WA 6150, Australia

[48] Westerdijk Fungal Biodiversity Institute, Uppsalalaan 8, 3584CT Utrecht, The Netherlands

[49] Anhui Provincial Key Laboratory for Microbial Pest Control, Anhui Agricultural University, Hefei 230036, People's Republic of China

[50] Department of Botany, University of British Columbia, Vancouver, British Columbia V6T 1Z4, Canada

[51] M. H. Kholodny Institute of Botany, Tereshchenkivska Str. 2, Kyiv 01004, Ukraine

[52] Molecular Cell Biology Unit, Lund University, Solvegatan
35, 22362 Lund, Sweden

[53] Center of Excellence in Microbial Diversity and Sustainable
Utilization, Faculty of Science, Chiang Mai University,
Chiang Mai 50200, Thailand

[54] Office of Research Administration, Chiang Mai University,
Chiang Mai 50200, Thailand

[55] Department of Plant Taxonomy and Nature Conservation,
Faculty of Biology, University of Gdańsk, Wita Stwosza 59,
80-308 Gdańsk, Poland

[56] State Key Laboratory of Functions and Applications
of Medicinal Plants, Guizhou Medical University, Guiyang,
Guizhou, China

[57] The High Efficacy Application of Natural Medicinal
Resources Engineering Center of Guizhou Province (The
Key Laboratory of Optimal Utilization of Natural Medicine
Resources), School of Pharmaceutical Sciences, Guizhou
Medical University, University Town, Guian New District,
Guiyang, Guizhou, People's Republic of China

[58] College of Life Sciences, Shandong Normal University,
Jinan 250014, People's Republic of China

[59] Collections, Conservation & Research Division, The Field
Museum, 1400 S. DuSable Lake Shore Drive, Chicago,
IL 60605, USA

[60] Departamento de Tecnología Médica, Facultad de Ciencias
de la Salud, Universidad de Tarapacá, Sede Iquique, Av. Luis
Emilio Recabarren, 2477 Iquique, Chile

[61] Institute of Biology, Biotechnology and Environmental
Protection, Faculty of Natural Sciences, University of Silesia
in Katowice, Jagiellońska 28, 40-032 Katowice, Poland

[62] National Museum of Natural History Luxembourg, 25 rue
Münster, 2160 Grund, Luxembourg

[63] Manaaki Whenua–Landcare Research, Private Mail Bag
92170, Auckland, New Zealand

[64] Department of Forest Mycology and Plant Pathology,
Uppsala BioCenter, Swedish University of Agricultural
Sciences, Box 7026, 75007 Uppsala, Sweden

[65] Laboratory for Biological Diversity, Ruđer Bošković
Institute, Bijenička cesta 54, 10000 Zagreb, Croatia

[66] Laboratory of Cytology of Unicellular Organisms, Institute
of Cytology RAS, Tikhoretsky ave. 4, St. Petersburg 194064,
Russia

[67] School of Civil Engineering and Architecture, Anhui
University of Technology, Ma'anshan 243002,
People's Republic of China

[68] Institute of Evolutionary Biology, Faculty of Biology,
Biological and Chemical Research Center, University
of Warsaw, Zwirki i Wigury 101, 02-089 Warsaw, Poland

[69] Department of Microbiology, University Innsbruck,
Technikerstrasse 25, 6020 Innsbruck, Austria

[70] Zoological Institute, Russian Academy of Sciences,
Universitetskaya emb. 1, St Petersburg 198904,
Russian Federation

[71] National Institute of Fundamental Studies, Hantana Road,
Kandy, Sri Lanka

[72] The Sustainable Development of Biological Resources
Laboratory, Faculty of Science, Chiang Mai University,
Chiang Mai 50200, Thailand

[73] Department of Biology, Faculty of Science, Chiang Mai
University, Chiang Mai 50200, Thailand

[74] National Fungal Culture Collection of India (NFCCI),
Biodiversity and Palaeobiology (Fungi) Gr., MACS Agharkar
Research Institute, G. G. Agarkar Road, Pune 411 004,
Maharashtra, India

[75] Key Laboratory of Integrated Pest Management on Crops
in Northwestern Oasis, Ministry of Agriculture and Rural
Affairs, Institute of Plant Protection, Xinjiang Academy
of Agricultural Sciences, Urumqi 830091, Xinjiang,
People's Republic of China

[76] Department of Entomology and Plant Pathology, Faculty
of Agriculture, Chiang Mai University, Chiang Mai 50200,
Thailand

[77] Programa de Pós-Graduação em Biologia de Fungos,
Departamento de Micologia, Universidade Federal
dePernambuco, CampusUniversitário, Recife,
PE CEP 50670-901, Brazil

[78] Mozartstrasse 9, 73117 Wangen, Germany

[79] Mycological Section, Italian Antarctic National Museum
(MNA), Genoa, Italy

[80] Department of Molecular biology and Genetics, Faculty
of Sciences and Arts, Kırşehir Ahi Evran University,
40169 Kırşehir, Turkey

[81] Department of Botany and Plant Pathology, Purdue
University, West Lafayette, IN 47907, USA

[82] Tomsk State University, pr. Lenina 36, Tomsk 634050,
Russia

[83] Faculty of Agriculture and Life Science, Hirosaki University,
3 Bunkyo-cho, Hirosaki, Aomori 036-8561, Japan

[84] Ascomycete.org, 13 chemin du Bois Ponard,
69160 Tassin-la-Demi-Lune, France

[85] Honghe Center for Mountain Futures, Kunming
Institute of Botany, Chinese Academy of Sciences,
Honghe County 654400, Yunnan, People's Republic of China

[86] Laboratory of Aquatic Parasitology and Microbial Resources,
School of Marine Science and Engineering, Qingdao
Agricultural University, Qingdao, Shandong 266109,
People's Republic of China

[87] Institute of Microbiology, School of Ecology and Nature
Conservation, Beijing Forestry University, Beijing 100083,
People's Republic of China

[88] Department for Biological Sciences, Institute
of Ecology, Evolution and Diversity, Goethe University,
Max-vonLaueStr. 13, 60486 Frankfurt am Main, Germany

[89] Senckenberg Biodiversity and Climate Research Centre,
Senckenberganlage 25, 60325 Frankfurt am Main, Germany

[90] Organismic Botany and Mycology, Institute of Plant Science
and Microbiology, University of Hamburg, Ohnhorststraße
18, 22609 Hamburg, Germany

[91] The United Graduate School of Agricultural Sciences, Iwate
University, 18-8 Ueda 3 chome, Morioka, Iwate 020-8550,
Japan