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ARTICLE

Families of non-*Dikarya* fungi

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Abstract

The magnitude and understanding of the Kingdom *Fungi* are expanding with the application of DNA-based molecular approaches. Non-*Dikarya* fungi (sometimes referred to as 'basal fungi', 'early divergent fungi' or 'lower fungi'), a large group of fungi that are included in 16 different phyla, comprise approximately 5000 species to date. This paper compiles all existing information on the families of the non-*Dikarya* fungal phyla. Two phylogenomic analyses are provided separately to show the relationships of the phyla of non-*Dikarya* and families of *Mucoromycota*, respectively. A phylogenetic tree based on partial 45S or partial 28S sequences is provided to show the placements of families in *Glomeromycota*. We provide the descriptions of each family and its type genus, including an illustration of the type species or a well-established other genus in the family. All the genera included in the family are listed with their type species. *Bulbosporaceae* fam. nov. is introduced to accommodate *Bulbospora* in *Gigasporales* (*Glomeromycetes*, *Glomeromycota*). *Densosporales* Tedersoo, *Densosporaceae* Desirò et al., and *Jimgerdemanniaceae* Tedersoo are validated. Taxa in *Rozellomycota* (including *Microsporidia*) and *Aphelidiomycota* are currently accepted as groups of fungi. Still, most species names require further revision following the International Code of Nomenclature for algae, fungi, and plants. *Caudosporina* Y.S. Tokarev & I.V. Issi nom. nov. and *Mesnilivella* Frolova & Nassonova nom. nov. are provided to accommodate *Caudospora* J. Weiser (nom. illegit.) and *Mesnilia* Frolova et al. 2023 (nom. illegit.), respectively. Taxa introduced based on eDNA (by Tedersoo et al. 2024) are listed separately, as currently these taxa are treated as invalid. Fossil non-*Dikarya* taxa are also provided separately.

Keywords – Aphelids – 'basal fungi' – Microsporidia – *Rozellomycota* – subkingdoms

INTRODUCTION

The magnitude of the Kingdom *Fungi* and the 'mega classification' of the kingdom are two important topics among mycologists. A recent estimation predicted 2–3 million species in the kingdom (Niskanen et al. 2023). Currently, only ca. 205,000 species are accepted in Species Fungorum (2025). However, most of these belong to *Ascomycota* and *Basidiomycota* in *Dikarya*. According to Species Fungorum, 2025 (accessed on 15 April 2025), approximately 5000 species have been accepted under 16 phyla of basal taxa, which share 0.02% of total species (Fig. 1, species number based on Species Fungorum 2025). Among the non-*Dikarya* fungi, a comparatively large number of species have been reported from *Chytridiomycota*, *Mucoromycota*, *Glomeromycota* and *Rozellomycota*.

The classification of *Fungi* has been changing with the advancements of molecular techniques. For instance, Tedersoo et al. (2018) used *rpb1* and *rpb2* loci, Voigt et al. (2021) used LSU and SSU, Wijayawardene et al. (2020a) used LSU, SSU, *rpb1* and *rpb2*, and Li et al. (2021), as well as Strassert & Monaghan (2022) used genomes and transcriptomes for phylogenetic tree inferences. Recently, Wijayawardene et al. (2024a) used a phylogenomic analysis and accepted 19 phyla in the Kingdom *Fungi viz.*, *Aphelidiomycota*, *Ascomycota*, *Basidiomycota*, *Basidiobolomycota*, *Blastocladiomycota*, *Calcarisporiellomycota*, *Chytridiomycota* (=*Caulochytriomycota*), *Entomophthoromycota*, *Entorrhizomycota*, *Glomeromycota*, *Kickxellomycota*, *Monoblepharomycota*, *Mortierellomycota*, *Mucoromycota*, *Neocallimastigomycota*, *Olpidiomycota*, *Rozellomycota*, *Sanchytriomycota* and *Zoopagomycota*.

James & Rokas (2025) argued that the terms 'early divergent fungi, lower fungi and basal fungi' are not appropriate and suggested using formal taxonomic names. In this compilation, we do not argue against or support this suggestion. However, for the convenience of readers, we use 'non-*Dikarya* fungi' as an umbrella term to refer to *Aphelidiomycota*, *Basidiobolomycota*, *Blastocladiomycota*, *Calcarisporiellomycota*, *Chytridiomycota* (= *Caulochytriomycota*), *Entomophthoromycota*, *Glomeromycota*, *Kickxellomycota*, *Monoblepharomycota*, *Mortierellomycota*, *Mucoromycota*, *Neocallimastigomycota*, *Olpidiomycota*, *Rozellomycota*, *Sanchytriomycota* and *Zoopagomycota*.

Phyla	Number of species
Aphelidiomycota	19
Basidiobolomycota	11
Blastocladiomycota	214
Calcarisporiellomycota	2
Chytridiomycota	1036
Entomophthoromycota	334
Glomeromycota	363
Kickxellomycota	243
Monoblepharomycota	40
Mortierellomycota	149
Mucoromycota	1033
Neocallimastigomycota	47
Olpidiomycota	57
Rozellomycota	965
Sanchytriomycota	2
Zoopagomycota	223

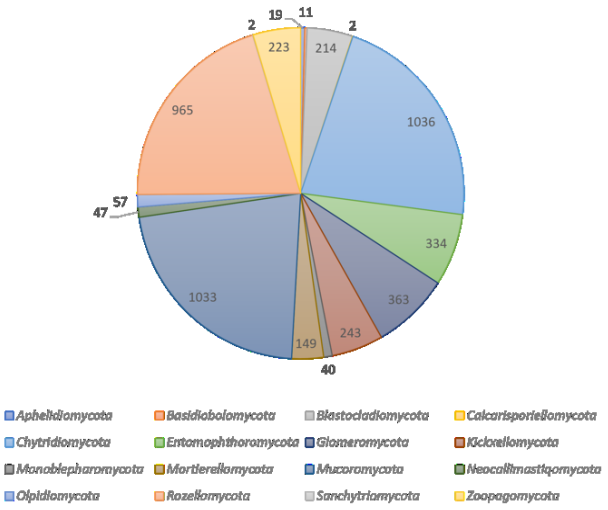


Figure 1 – Number of species in the phyla of non-*Dikarya* fungi

Classification of the non-*Dikarya* fungi

Wijayawardene et al. (2024) accepted 16 phyla that comprise non-*Dikarya* fungi, i.e., except three phyla in subkingdom *Dikarya* (*viz.*, *Ascomycota*, *Basidiomycota* and *Entorrhizomycota*). These 16 phyla were accommodated in eight sub-kingdoms, namely *Aphelidiomyceta*, *Basidiobolomyceta*, *Blastocladiomyceta*, *Chytridiomyceta*, *Mucoromyceta*, *Olpidiomyceta*, *Rozellomyceta* and *Zoopagomyceta* (Tedersoo et al. 2018; Wijayawardene et al. 2024; Fig. 1).

Phylum *Caulochytriomycota* Doweld has been rejected as its lineages are nested within the phylum *Chytridiomycota* (Galindo et al. 2021, Strassert & Monaghan 2022, Wijayawardene et al. 2024). Table 1 summarises the classes, orders, and families of the phyla of non-*Dikarya* fungi.

Table 1 The classes, orders, and families of the phyla of non-*Dikarya* fungi. The number of genera accepted in each family is provided in brackets.

Phyla	Classes	Orders	Families
Aphelidiomycota	*Aphelidiomycetes*	*Aphelidiales*	*Aphelidiaceae* (5)
Basidiobolomycota	*Basidiobolomycetes*	*Basidiobolales*	*Basidiobolaceae* (2)
Blastocladiomycota	*Blastocladiomycetes*	*Blastocladiales*	*Blastocladiaceae* (3)
			Catenariaceae (2)
			Paraphysodermataceae (1)
			Sorochytriaceae (1)
		Callimastigales	*Callimastigaceae* (1)
		Catenomycetales	*Catenomycetaceae* (1)
			Coelomomycetaceae (2)
	Physodermatomycetes	*Physodermatales*	*Physodermataceae* (1)
Calcarisporiellomycota	*Calcarisporiellomycetes*	*Calcarisporiellales*	*Calcarisporiellaceae*
Chytridiomycota	*Caulochytriomycetes*	*Caulochytriales*	*Caulochytriaceae*
	Chytridiomycetes	*Chytridiales*	*Asterophlyctaceae* (2)
			Chytridiaceae (6)
			Chytriomycetaceae (15)
			Pseudorhizidiaceae (2)
			Scherffeliomycetaceae (1)
		Nephridiophagales	*Nephridiophagaceae* (6)
		Polyphagales	*Polyphagaceae* (2)
		Saccopodiales	*Saccopodiaceae* (1)
		Zygophlyctidales	*Zygophlyctidaceae* (1)
		families incertae sedis	*Amoebochytriaceae* (1)
			Sparrowiaceae (1)
			Sphaeromonadaceae (1)
			Tetrachytriaceae (2)
			Thalassochytriaceae (1)
	Cladochytriomycetes	*Cladochytriales*	*Cladochytriaceae* (1)
			Endochytriaceae (1)
			Nowakowskiellaceae (1)
			Septochytriaceae (7)
	Lobulomycetes	*Lobulomycetales*	*Lobulomycetaceae* (7)
	Mesochytriomycetes	*Gromochytriales*	*Gromochytriaceae* (2)
		Mesochytriales	*Mesochytriaceae* (1)
	Polychytriomycetes	*Polychytriales*	*Polychytriaceae* (5)
	Rhizophlyctidomycetes	*Rhizophlyctidales*	*Arizonaphlyctidaceae* (1)
			Borealophlyctidaceae (1)
			Rhizophlyctidaceae (1)
			Sonoraphlyctidaceae (1)
	Rhizophydiomycetes	*Rhizophydiales*	*Alphamycetaceae* (3)
			Angulomycetaceae (1)
			Aquamycetaceae (1)

Table 1 Continued

Phyla	Classes	Orders	Families
			Batrachochytriaceae (1)
			Collimycetaceae (1)
			Coralloidiomycetaceae (1)
			Dinomycetaceae (2)
			Ericiomycetaceae (1)
			Globomycetaceae (2)
			Gorgonomycetaceae (1)
			Halomycetaceae (4)
			Kappamycetaceae (1)
			Operculomycetaceae (1)
			Pateramycetaceae (1)
			Protrudomycetaceae (1)
			Rhizophydiaceae (1)
			Staurastromycetaceae (1)
			Terramycetaceae (2)
			Uebelmesseromycetaceae (1)
	Spizellomycetes	*Spizellomycetales*	*Powellomycetaceae* (4)
			Spizellomycetaceae (8)
	Synchytriomycetes	*Synchytriales*	*Synchytriaceae* (6)
Chytridiomycota family *incertae sedis*			*Quaeritorhizaceae* (1)
Entomophthoromycota	*Entomophthoromycetes*	*Entomophthorales*	*Ancylistaceae* (2)
			Batkoaceae (1)
			Capillidiaceae (1)
			Completoriaceae (1)
			Conidiobolaceae (3)
			Entomophthoraceae (10)
			Meristacraceae (2)
			Neoconidiobolaceae (1)
	Neozygitomycetes	*Neozygitales*	*Neozygitaceae* (3)
Glomeromycota	*Archaeosporomycetes*	*Archaeosporales*	*Ambisporaceae* (1)
			Archaeosporaceae (2)
			Geosiphonaceae (1)
			Polonosporaceae (1)
	Glomeromycetes	*Diversisporales*	*Acaulosporaceae* (1)
			Diversisporaceae (5)
			Pacisporaceae (1)
			Sacculosporaceae (1)
		Entrophosporales	*Entrophosporaceae* (1)
		Gigasporales	*Bulbosporaceae* (1)
			Dentiscutataceae (2)
			Gigasporaceae (1)
			Intraornatosporaceae (2)
			Racocetraceae (2)
			Scutellosporaceae (2)
		Glomerales	*Glomeraceae* (3)
			Dominikiaceae (5)

Table 1 Continued

Phyla	Classes	Orders	Families
			Kamienskiaceae (3)
			Sclerocystaceae (6)
			Septoglomeraceae (5)
	Paraglomeromycetes	*Paraglomerales*	*Paraglomeraceae* (2)
			Pervetustaceae (1)
Kickxellomycota	*Asellariomycetes*	*Asellariales*	*Asellariaceae* (1)
	Barbatosporomycetes	*Barbatosporales*	*Barbatosporaceae* (1)
	Dimargaritomycetes	*Dimargaritales*	*Dimargaritaceae* (3)
	Harpellomycetes	*Harpellales*	*Harpellaceae* (6)
			Legeriomycetaceae (36)
	Kickxellomycetes	*Kickxellales*	*Kickxellaceae* (10)
		Orphellales	*Orphellaceae* (1)
	Ramicandelaberomycetes	*Ramicandelaberales*	*Ramicandelaberaceae* (1)
Monoblepharomycota	*Hyaloraphidiomycetes*	*Hyaloraphidiales*	*Hyaloraphidiaceae* (1)
	Monoblepharidomycetes	*Monoblepharidales*	*Gonapodyaceae* (2)
			Harpochytriaceae (1)
			Monoblepharidaceae (1)
			Oedogoniomycetaceae (1)
			Telasphaerulaceae (1)
Mortierellomycota	*Mortierellomycetes*	*Mortierellales*	*Mortierellaceae* (14)
Mucoromycota	*Endogonomycetes*	*Bifiguratales*	*Bifigurataceae* (1)
		Densosporales	*Densosporaceae* (1)
		Endogonales	*Densosporaceae* (1)
			Endogonaceae (5)
			Jimgerdemanniaceae (1)
			Vinositunicaceae (1)
	Mucoromycetes	*Mucorales*	*Backusellaceae* (1)
			Circinellaceae (5)
			Cunninghamellaceae (6)
			Lentamycetaceae (1)
			Lichtheimiaceae (2)
			Mucoraceae (24)
			Mycocladaceae (1)
			Phycomycetaceae (2)
			Pilobolaceae (2)
			Protomycocladaceae (1)
			Radiomycetaceae (1)
			Rhizomucoraceae (1)
			Rhizopodaceae (1)
			Saksenaeaceae (2)
			Syncephalastraceae (2)
			Syzygitaceae (2)
			Thermomucoraceae (1)
	Umbelopsidomycetes	*Umbelopsidales*	*Pygmaeomycetaceae* (1)
			Umbelopsidaceae (1)
Neocallimastigomycota	*Neocallimastigomycetes*	*Neocallimastigales*	*Anaeromycetaceae* (4)
			Caecomycetaceae (2)

Table 1 Continued

Phyla	Classes	Orders	Families
			Neocallimastigaceae (6)
			Piromycetaceae (1)
Olpidiomycota	*Olpidiomycetes*	*Olpidiales*	*Olpidiaceae* (4)
Rozellomycota	*Rozellidea*	*Rozellida*	*Rozellidae* (1)
	Chytridiopsea	*Chytridiopsida*	*Buxtehudiidae* (2)
			Chytridiopsidae (5)
			Hesseidae (1)
			Burkeidae (1)
	Rudimicrosporea	*Metchnikovellida*	*Amphiacanthidae* (1)
			Metchnikovellidae (4)
	Microsporidea	*Amblyosporida*	*Amblyosporidae* (17)
			Caudosporidae (10)
			Gurleyidae (13)
		Neopereziida	*Berwaldiidae* (2)
			Neopereziidae (5)
			Tubulinosematidae (3)
		Ovavesiculida	*Ovavesiculidae* (3)
		Glugeida	*Facilisporidae* (1)
			Glugeidae (9)
			Myosporidae (1)
			Pereziidae (4)
			Pleistophoridae (7)
			Spragueidae (8)
			Thelohaniidae (15)
			Unikaryonidae (4)
		Nosematida	*Encephalitozoonidae* (2)
			Enterocytozoonidae (6)
			Heterovesiculidae (1)
			Mrazekiidae (9)
			Nosematidae (2)
			Ordosporidae (1)
Microsporidia families *incertae sedis*			*Abelsporidae* (1)
			Areosporiidae (1)
			Burenellidae (3)
			Cougourdellidae (1)
			Cylindrosporidae (1)
			Duboscqiidae (5)
			Golbergiidae (3)
			Microfilidae (1)
			Neonosemoidiidae (1)
			Pleistosporidiidae (1)
			Pseudopleistophoridae (2)
			Striatosporidae (2)
			Telomyxidae (1)
			Toxoglugeidae (1)
			Tuzetiidae (4)

Table 1 Continued

Phyla	Classes	Orders	Families
	Rozellomycota orders *incertae sedis*	*Paramicrosporidiales*	*Paramicrosporidiaceae* (1)
		Morellosporales	*Morellosporaceae* (1)
			Mitosporidiaceae (1)
		Nucleophagales	*Nucleophagaceae* (1)
Sanchytriomycota	*Sanchytriomycetes*	*Sanchytriales*	*Sanchytriaceae* (2)
Zoopagomycota	*Zoopagomycetes*	*Zoopagales*	*Cochlonemataceae* (6)
			Helicocephalidaceae (4)
			Piptocephalidaceae (3)
			Sigmoideomycetaceae (4)
			Zoopagaceae (7)

Taxa registered under the Zoological Nomenclature

Chapter F of the International Code of Nomenclature for Algae, Fungi, and Plants (ICNafp) or Shenzhen Code currently governs the registration of newly introduced fungal taxa. It is essential to register novel taxa (including fossil fungi and lichen-forming fungi) in a repository such as Fungal Names, Index Fungorum, and MycoBank before publishing and including citation of the identifier in the protologue (Redhead & Norvell 2013). The taxa described in *Aphelidiomycota* and *Rozellomycota* (including *Microsporidia*), which were traditionally regarded as protists, have, however, been governed by the Code of Zoological Nomenclature (see Article 1.1.1, ICZN). Nevertheless, Karpov et al. (2013) showed that '*Amoeboaphelidium protococcarum*, forms a monophyletic group with *Rozella* and microsporidia as a sister group to Fungi. Several subsequent studies confirmed the findings of Karpov et al. (2013) and confirmed that *Aphelidiomycota* and *Rozellomycota* reside in the Kingdom *Fungi* (Tedersoo et al. 2018, Voigt et al. 2021, Wijayawardene et al. 2024). Furthermore, novel species have been introduced with MycoBank numbers (e. g. Letcher et al. 2015b, Corsaro et al. 2016) but later listed in Index Fungorum or both MycoBank and ZooBank identifiers (Seto et al. 2020a, 2022).

Taxa introduced with sequences as the type (or eDNA as the type)

It is mandatory to follow the rules and guidelines provided by ICNafp when introducing new species. Designating type materials (Art. 40, Shenzhen Code) and indicating the identifiers obtained from a repository (i.e., Index Fungorum, MycoBank or Fungal Names) in the protologue (Art. F.5.1, San Juan Chapter F) are two important rules that are necessary to follow. However, currently, taxonomists and mycologists focus on Next Generation Sequencing and reveal dark taxa that lack any phenotypes. Hence, sequence-based nomenclature is being promoted for naming the dark taxa (Lücking et al. 2021); however, it is still not concluded as different opinions are prevailing among the mycology community.

Tedersoo et al. (2024) is a recent study focused on the classification of *Glomeromycota* and *Endogonomycetes* (in *Mucoromycota*), based on combined SSU, ITS and LSU sequences. In this study, Tedersoo et al. (2024) introduced several taxa (including novel species and new combinations) based on eDNA samples and sequence data. However, ICNafp does not accept eDNA as the type material, thus all new species are invalid (see Index Fungorum 2025). Nevertheless, we list all genera and supra-generic ranks separately (not in the outline section) in this compilation to gather all prevailing data (Table 2). We regard it as necessary to adapt the use of eDNA samples and sequence data by the code and implement its use as a type material in the future.

Table 2 Invalid genera and super-generic ranks in Tedersoo et al. (2024)

Classes	Orders	Families	Genera
Glomeromycetes	*Entrophosporales*	*Pseudoentrophosporaceae* Tedersoo & Magurno	*Pseudoentrophospora* Tedersoo & Magurno

Table 2 Continued

Classes	Orders	Families	Genera
Endogonomycetes	*Hoforsales* Tedersoo	*Hoforsaceae* Tedersoo	*Hoforsa* Tedersoo
	Kahvenales Tedersoo	*Kahvenaceae* Tedersoo	*Kahvena* Tedersoo
	Kelottijaerviales Tedersoo	*Kelottijaerviaceae* Tedersoo	*Kelottijaervia* Tedersoo
	Kungsaengenales Tedersoo	*Kungsaengenaceae* Tedersoo	*Kungsaengena* Tedersoo
	Langduoales Tedersoo	*Langduoaceae* Tedersoo	*Langduoa* Tedersoo
	Lehetuales Tedersoo	*Lehetuaceae* Tedersoo	*Lehetua* Tedersoo
	Lokrumales Tedersoo	*Lokrumaceae* Tedersoo	*Lokruma* Tedersoo
	Moosteales Tedersoo	*Moosteaceae* Tedersoo	*Moostea* Tedersoo
	Nikkaluoktales Tedersoo	*Nikkaluoktaceae* Tedersoo	*Nikkaluokta* Tedersoo
	Parniguales Tedersoo	*Parniguaceae* Tedersoo	*Parnigua* Tedersoo
	Riederbergales Tedersoo	*Riederbergaceae* Tedersoo	*Riederberga* Tedersoo
	Ruuales Tedersoo	*Ruuaceae* Tedersoo	*Ruua* Tedersoo
	Tammsaareales Tedersoo	*Tammsaareaceae* Tedersoo	*Tammsaarea* Tedersoo
	Unemaeeales Tedersoo	*Unemaeeaceae* Tedersoo	*Unemaeea* Tedersoo
	Densosporales Tedersoo*	*Densosporaceae* Desirò et al.*	
		Planticonsortiaceae Tedersoo	
	Endogonales Jacz. & P.A. Jacz.#	*Jimgerdemanniaceae* Tedersoo*	

*Indicates taxa that are validated in this study and # indicates valid taxa that have been introduced previously.

Fossil non-*Dikarya* fungi

The lower fungi are frequently found as fossils in rocks of all ages. The most important fossil genera of this group are as follows.

***Chytridiomycota*:** *Brijax* M. Krings & C.J. Harper, *Cultoraquaticus* Strullu-Derr., *Globicultrix* M. Krings et al., *Grilletia* Renault & C.E. Bertrand, *Guizhounema* X. Mu, *Illmanomyces* M. Krings & T.N. Taylor, *Krispiromyces* T.N. Taylor et al., *Lyonomyces* T.N. Taylor et al., *Milleromyces* T.N. Taylor et al., *Nimbosphaera* C.J. Harper & M. Krings, *Oochytrium*

Renault, *Palaeozoosporites* Strullu-Derr., *Perexiflasca* M. Krings et al., *Rhizophydites* M. Krings & C.J. Harper and *Trewinomyces* M. Krings et al.

***Glomeromycota*:** *Archaeosporites* C. Walker et al., *Gigasporites* Carlie J. Phipps & T.N. Taylor, *Glomites* T.N. Taylor et al., *Glomorphites* Garcia Mass., *Helmutella* M. Krings & T.N. Taylor, *Kryphiomyces* M. Krings et al., *Mycokidstonia* D. Pons & Locq., *Palaeogigaspora* R. Kar et al., *Palaeoglomus* R. Redecker et al., *Palaeomyces* D. Ellis, *Scutellosporites* Dotzler, M. Krings, T.N. Taylor and Agerer, *Udaria* A. Gupta and *Zwergimyces* M. Krings & T.N. Taylor.

***Mucoromycota*:** *Lithomucorites* R. Kar et al. and *Palaeomycites* Mesch.

We provide all the species belonging to the above-mentioned genera in the taxonomy section.

Aim of the study

In this study, we list the latest classification of non-*Dikarya* fungi based on recent publications and our phylogenetics and phylogenomic analyses. We provide descriptions for all families of non-*Dikarya* fungi, notes including life modes, distribution, important previous studies and descriptions and notes of the type genera. Moreover, we validate several taxa that have been introduced erroneously in the original protologues. We recognise that several taxa in *Rozellomycota* have not been registered in any of the fungal repositories, and therefore, we registered them in Index Fungorum (2025).

MATERIALS AND METHODOLOGY

Data collection and arrangements of the families

We follow Wijayawardene et al. (2018, 2020, 2022) and Hyde et al. (2024) to gather the list of genera of non-*Dikarya* fungi and follow the same for higher-level rankings. Tedersoo et al. (2018), Galindo et al. (2021), Strassert & Monaghan (2022), Mikhailov et al. (2022a), Hyde et al. (2024) and Wijayawardene et al. (2024) are some of the studies that we follow to compare the arrangements of the classification of non-*Dikarya* fungi.

The descriptions of the families and their type genera and illustrations (microscopic images or line drawings) are based on previous publications. The species number is based on Species Fungorum (2025).

Registration of novel taxa and validation of invalid taxa (including proposing new names)

We obtained Index Fungorum Identifiers for the novel taxa, invalid taxa and previously unregistered taxa such as *Rozellomycota,* including *Microsporidia,* which were regarded as protists following ICNafp.

Phylogenomic tree of non-*Dikarya* fungi

The dataset for phylogenomic analysis was assembled using 300 orthologous groups, which were used in an earlier study of fungal phylogeny (Wijayawardene et al. 2024). The original dataset was updated to include all families of non-dikaryan fungi with at least one representative with a sequenced genome. The genomic data were acquired from public repositories of the National Center for Biotechnology Information and Joint Genome Institute, utilizing the MycoCosm portal (Grigoriev et al. 2014) and the NCBI Taxonomy browser (Schoch et al. 2020) to survey the available fungal species. The protein datasets for *Capillidium heterosporum*, *Cochlonema odontosperma*, *Thermomucor indicae-seudaticae*, *Protomycocladus faisalabadensis*, and *Densosporaceae* sp. MVC-580 were prepared with the help of the protein-to-genome searches of the exonerate 2.2.0 program (Slater & Birney 2005) using a set of orthologous sequences from the related species. The genomes of *Protomycocladus faisalabadensis*, and *Densosporaceae* sp. MVC-580 were assembled from the WGS data available in the NCBI Sequence Read Archive (SRA accessions: SRR10127521 and SRR17035067) with SPAdes 4.0.0 (Prjibelski et al. 2020). The proteome of *Metchnikovella incurvata* was obtained using ORF prediction of TransDecoder v5.7.1 (https://github.com/TransDecoder/TransDecoder) with the genome assembly in GenBank

(GCA_003600395.1). Orthologous sequences were identified in the proteomes using HMMER searches (Eddy 2011) with the alignment profiles, and reciprocal BLAST searches (Altschul et al. 1997). The orthologous sequences were aligned with MAFFT 7.525 using the localpair (L-INS-i) algorithm (Katoh & Standley 2013), and trimmed using the trimAl 1.5 program (Capella-Gutierrez et al. 2009) with a gap threshold of 0.1, followed by processing with 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 176 species and 120K amino acid sites. Maximum likelihood analysis with the concatenated alignment was performed with IQ-TREE 1.6.12 (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. The tree was visualized using the MEGA software (Kumar et al. 2016).

Phylogenomic analyses of *Mucoromycota*

Genomes collected

A total of 58 genomes were downloaded from the NCBI database, including 56 genomes from *Mucoromycota* and two genomes from *Mortierella* as outgroups. The 56 *Mucoromycota* genomes represented 19 families. However, no genome from the family *Pygmaeomycetaceae* was obtained in this study.

Phylogenomic analysis

In this study, the phylogenomic relationships of *Mucoromycota* were reanalyzed following previous studies (Spatafora et al. 2016, Vandepol et al. 2020, Zhao et al. 2023). Briefly, 434 clusters of orthologous proteins (COPs) were retrieved using HMMER v3.3.1 (http://hmmer.org/download.html) and trimmed with Trimal v1.4.4 (Chimal-Sánchez et al. 2011) according to the methods of Spatafora et al. (2016). Phylogenetically informative protein markers followed those identified by Vandepol et al. (2020). Maximum likelihood (ML) phylogenomic analysis was performed using RAxML v8 (Ronquist et al. 2012), with the optimal model estimated by ModelTest-NG v0.1.7 (Darriba et al. 2020). For the ML analysis, 1,000 bootstrap replications were conducted under the best-fit model. The ML tree was visualized using Figtree v1.4.4 (http://tree.bio.ed.ac.uk/software/figtree/), and nodes with ML bootstrap values below 50% were not considered.

Phylogenetic analyses of the phylum *Glomeromycota*

Maximum likelihood (ML) and Bayesian inference (BI) analyses were performed using a dataset including all the *Glomeromycota* species in possession of partial 45S or partial 28S sequences. Overall, the dataset included 235 species and 48 genera represented by 664 sequences. Sequence alignment was performed in three steps: a) for each order separately, sequences were aligned using MAFFT 7.243 (Katoh et al. 2019), strategy E-INS-i; b) after trimming the ITS, the alignments were aligned together using the MAFFT function 'Merge', preserving the “intra-order” alignments; c) for each order in the alignment, it's related ITS block was concatenated, not overlapping ITS blocks of other orders. In such a way, the information of ITS was preserved but used only to infer phylogenetic relationships among taxa in each order. In both ML and BI analyses, the alignment was divided into two partitions (18S+5.8S, 28S), plus additional partitions for ITS1 and ITS2 exclusive to each order. GTR+I+G was chosen in both BI and ML analyses as a nucleotide substitution model for each nucleotide partition (Abadi et al. 2019). The ML tree was estimated using RAxML-NG 1.0.1 (Kozlov et al. 2019), using a maximum likelihood/1000 bootstrapping run, and ML estimated proportion of invariable sites and base frequencies. In the BI analysis, four Markov chains were run over fifteen million generations in MrBayes 3.2 (Ronquist et al. 2012), sampling every 1000 generations, with a burn-in at 25% sampled trees. The order *Paraglomerales*, as the earliest diverging lineage in *Glomeromycota*, was used to root the tree.

Results

Phylogenomic tree of non-*Dikarya* fungi

The phylogenomic analysis was carried out using a previously assembled 300-gene dataset (Wijayawardene et al. 2024), updated to include every family of non-*Dikarya* fungi with sequenced genomes. To properly sample the available data, we collected all genomic datasets for non-*Dikarya* fungi and reconstructed individual phylogenies for major fungal phyla or subkingdoms. In total, the current tally of nearly 400 non-dikaryan species with available genomes covers 85 families and several *incertae sedis* taxa, which is less than half of the registered families for these groups of fungi. Particularly poorly represented are groups such as *Chytridiomycota* and *Rozellomycota*, where 30 to 40 known families have no sequenced representatives.

For the combined phylogeny, we reduced the initial dataset to 141 non-dikaryan species by excluding closely related species, while preserving one to several representatives per family. The ML tree reconstructed for this condensed dataset using the site-heterogeneous profile mixture model of IQ-TREE reproduces the earlier result of ML inference for fungal phyla (Wijayawardene et al. 2024), lending full support to many early nodes of fungal phylogeny, including the controversial grouping of *Mucoromycota* and *Glomeromycota* (Fig. 2). Relationships between families of non-*Dikarya* fungi likewise receive high support values. Notably, the improved sampling within *Chytridiomycota* provides better resolution for the positions of *Caulochytrium* and *Polychytrium*, which were conflicting in the previous analysis. Yet, several nodes of this new phylogeny remain poorly supported. The sister group position of *Lentamyces* to *Cunninghamellaceae* in *Mucoromycota* receives only 60% support – the distinctly divergent sequences of *Lentamyces* likely impel its placement closer to the root in 40% of replicates, sister to the group that includes families *Phycomycetaceae*, *Cunninghamellaceae* and *Mucoraceae*. Among microsporidians, the early branching of *Edhazardia* (fam. *Amblyosporidae*) is not well supported, and the alternative position, sister to *Astathelohania*, is observed in 37% of replicates. The relative branching within *Aphelidiomycota* is uncertain, with the two *Aphelidium* species competing with *Amoeboaphelidium protococcarum* for the sister group position to other aphelids. The exact placement of *Basidiobolomycota* also remains ambiguous, with 79% of replicates supporting a sister relationship to a group uniting *Entomophthoromycota* and *Kickxellomycota*, 18% of replicates supporting a closer relationship to *Zoopagomycota*, and the remaining 3% placing *Basidiobolomycota* as the earliest branch of the subkingdom *Zoopagomyceta*. Among chytrids, the alternative placement of *Nowakowskiellaceae* and *Cladochytrium replicatum* closer to the root of the group is observed in 9% of replicates.

Several families emerge as paraphyletic in the reconstruction. The family *Cladochytriaceae*, represented in the dataset by *Cladochytrium replicatum* and *Cladochytrium tenue*, is particularly problematic. The two *Cladochytrium* species are not closely related, with *C. replicatum* branching sister to *Nowakowskiellaceae*, while *C. tenue* branches with *Cladochytrium polystomum* that was redescribed as *Zopfochytrium polystomum* of family *Chytridiaceae* (Fig. 2). As pointed out in the study that introduced *Zopfochytrium polystomum*, family *Cladochytriaceae* is paraphyletic and requires revision following a clearer ultrastructural investigation of type species *C. tenue* (Powell et al. 2018a). The current phylogenomic reconstruction, however, also refutes the inclusion of *Zopfochytrium* in *Chytridiaceae* – the group of *Z. polystomum* and *C. tenue* is close to the family *Chytriomycetaceae* and several *incertae sedis* chytrids, rendering the *Chytridiaceae* paraphyletic. Therefore, the taxonomic affinities of *Z. polystomum* and *Cladochytrium* species conflict with the phylogeny, and the delineations of both families, *Cladochytriaceae* and *Chytridiaceae*, need further reassessment.

Phylogenomic tree of *Mucoromycota*

In this study, phylogenomic analysis was performed on 58 genomes using the PROTGAMMALGX model. The resulting ML tree indicated strong support for 18 families within the *Mucoromycota* (Fig. 3). However, the family *Densosporaceae* did not form a clade with

Endogonaceae, as both families belong to the order *Endogonales* (Desirò et al. 2017, Zhao et al. 2023). Within the family *Mucoraceae*, the genus *Mucor* was also found to be polyphyletic. Additionally, the family *Pygmaeomycetaceae* was classified under the order *Umbelopsidales* based on ITS sequences (Walsh et al. 2021). However, the taxonomic status of some groups could not be determined from the phylogenomic analysis due to the lack of published genome data.

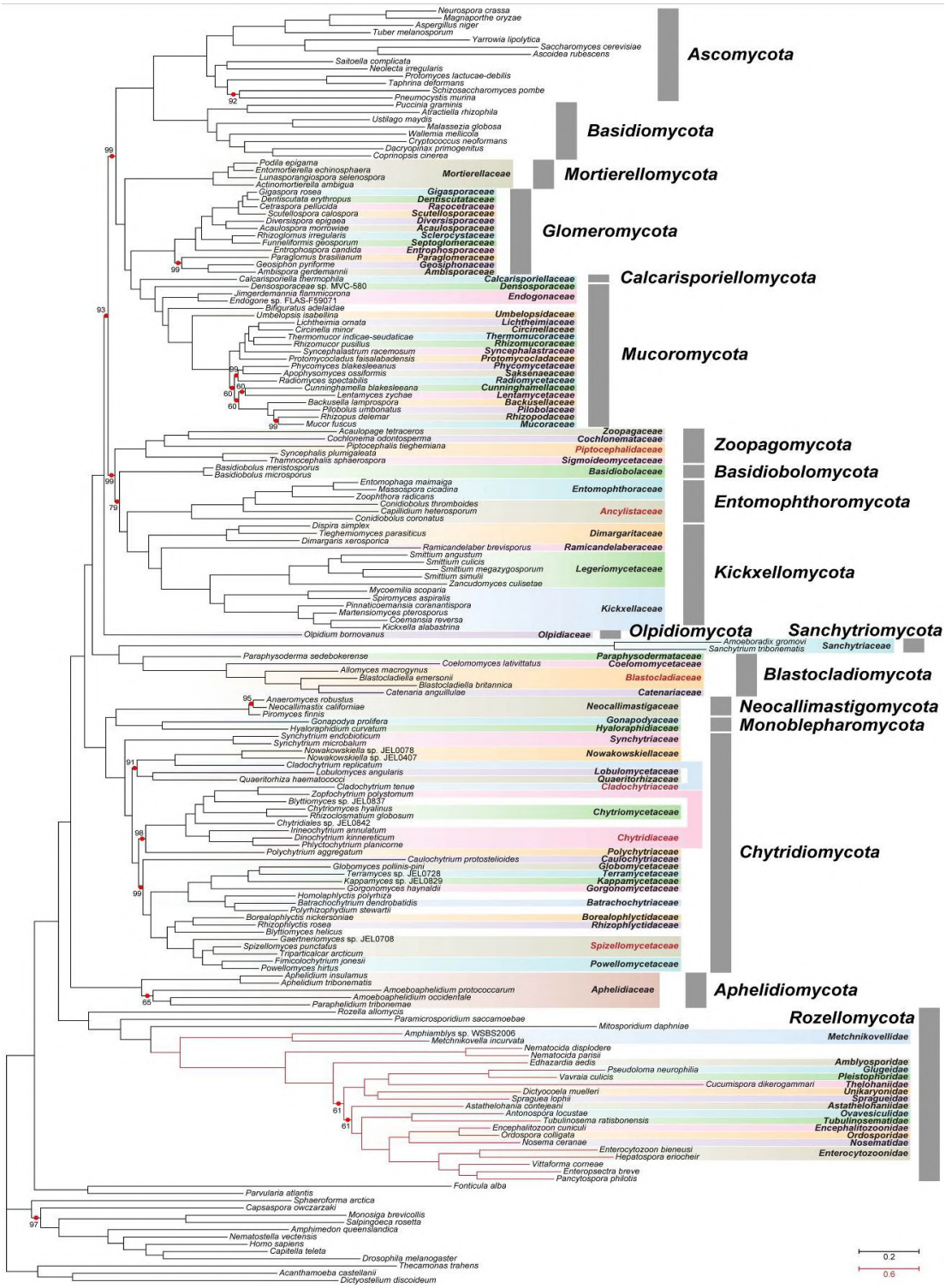


Figure 2 – Phylogenomic analysis of relationships between families of non-*Dikarya* fungi. The phylogeny was reconstructed using the maximum likelihood approach of IQ-TREE with a 300-gene dataset, featuring representatives of all families of non-dikaryan fungi where sequenced genomes were available; the inference utilized the profile mixture evolutionary model LG+C60+F+G4, with

support values estimated by ultrafast bootstrap approximation; only nodes that fail to achieve full support have the support values shown – indicated by a red circle and the corresponding bootstrap percentage; the branches of the microsporidian subtree were shortened to a third of their actual length for the illustration (the branches drawn in red); families that emerge as paraphyletic in the reconstruction have their names highlighted with a red colour.

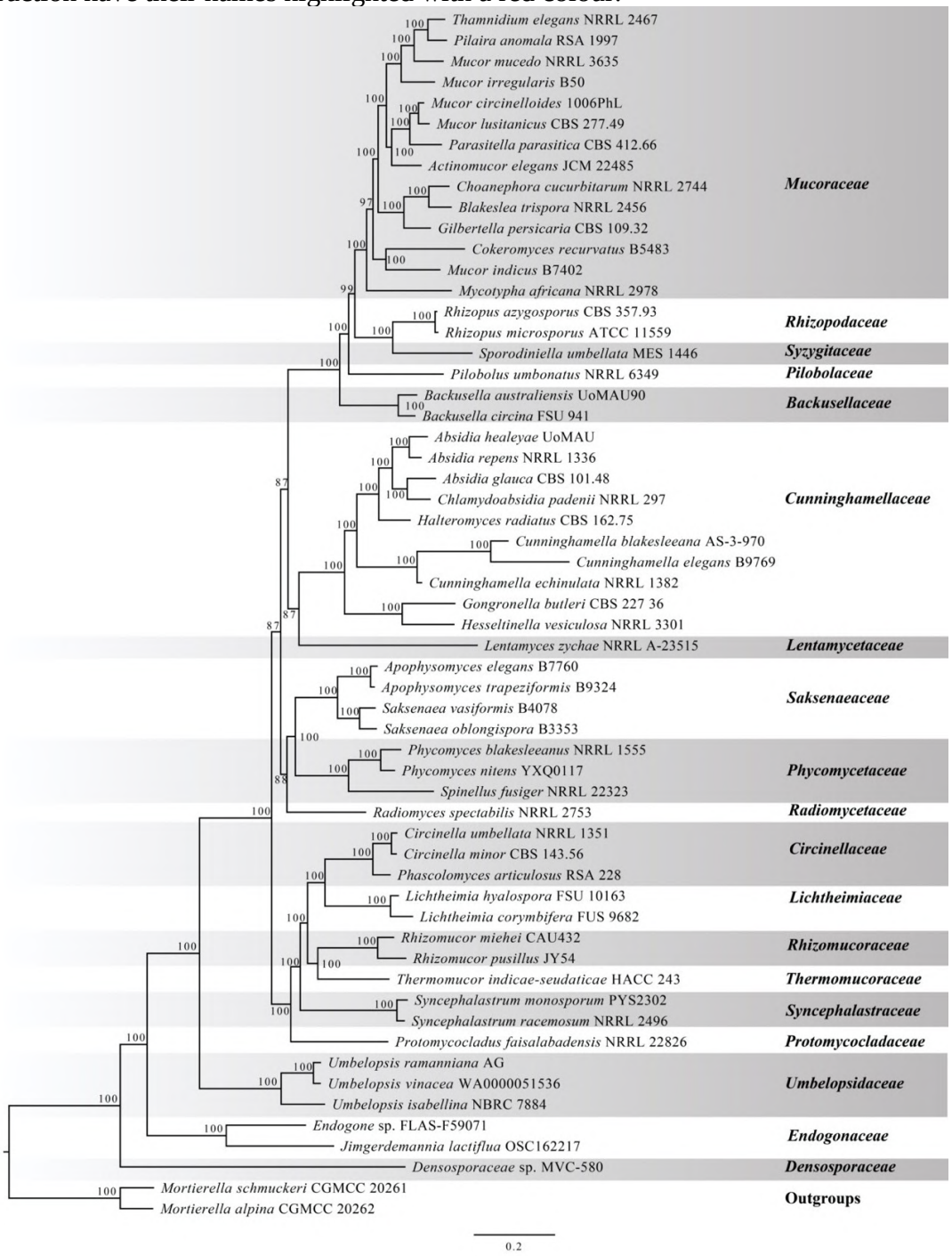


Figure 3 – A maximum likelihood tree of 56 genomes of *Mucoromycota*, and two genomes of *Mortierella* as outgroups. The ML bootstrap values are shown at the branch nodes. The scale bar at the bottom left indicates the number of substitutions per site.

Phylogenetic analyses of *Glomeromycota*

Tree topology of the ML analysis at genus or higher taxonomic rank was mostly identical to the one recovered in the BI analysis, generally in agreement with previous phylogenies shown by recent phylogenetic analysis (da Silva et al. 2024), involving also data from environmental

sequences (Tedersoo et al. 2024). Among the 22 *Glomeromycota* families considered, 16 received full ML and BI support. All families included in the analysis were placed in the expected order clades, except for *Pacisporaceae* (*Diversisporales sensu* Oehl, G.A. Silva & Sieverd) that clustered, very weakly supported, with *Gigasporales*. The phylogenetic placement of this family, as proposed by Walker et al. (2004), is unlikely to be contentious, as its species are the only ones reported to form both intraradical vesicles and extraradical auxiliary cells, structures which are characteristic of *Diversisporales* and *Gigasporales*, respectively (Błaszkowski 2012). The current affiliation of *Pacisporaceae* to *Diversisporales sensu* Oehl, G.A. Silva & Sieverd should be considered uncertain, requiring further investigation.

Furthermore, the analysis showed the clade populated by *Bulbospora minima* sequences represents an independent clade at the family level. The previous inclusion of *Bulbospora* in *Scutellosporaceae* (Marinho et al. 2014) rendered this family unsupported. Based on the phylogenetic analyses presented here (Fig. 4) and in Tedersoo et al. (2024, Supplementary material 2), *Bulbospora* does not show any sister relationship with either *Scutellosporaceae* clade or other family clades in *Gigasporales*. Therefore, considering also the morphology of *Bulbospora minima*, the new family *Bulbosporaceae* is erected to accommodate the monospecific genus.

Among the families not fully supported, those with the weakest were *Gigasporaceae* and *Scutellosporaceae*, both in *Gigasporales*. *Gigasporaceae* "suffered" the introduction of *Gigaspora siqueirae*, recently added into the genus (Manawasinghe et al. 2025), occupying a sister position to the clade formed by the other *Gigaspora* species. The new species was retained as *Gigaspora*, based on the spore morphology, undoubtedly resembling those of the genus. Potential emendations of the *Gigasporaceae-Intraornatosporaceae* clade should be considered once additional molecular data become available, especially for *Intraornatospora* and *Paradentiscutata* genera, whose SSU-ITS-LSU sequences are still lacking, as well as alternative molecular markers (as *rpb1*).

Outline of non-*Dikarya* fungi (The number of species of each genus is given inside the brackets)
APHELIDIOMYCOTA Tedersoo, Sanchez-Ramirez, Kõljalg, Bahram, M. Döring, Schigel, T.W. May, M. Ryberg & Abarenkov
Aphelidiomycetes Tedersoo, Sanchez-Ramirez, Kõljalg, Bahram, M. Döring, Schigel, T.W. May, M. Ryberg & Abarenkov
Aphelidiales Tedersoo, Sanchez-Ramirez, Kõljalg, Bahram, M. Döring, Schigel, T.W. May, M. Ryberg & Abarenkov
Aphelidiaceae Tedersoo, Sanchez-Ramirez, Kõljalg, Bahram, M. Döring, Schigel, T.W. May, M. Ryberg & Abarenkov
Amoeboaphelidium Scherff. (5)
Aphelidium Zopf (10)
Paraphelidium Karpov, Moreira, López-García (2)
Protaphelidium Seliuk & Karpov (1)
Pseudaphelidium Schweikert & Schnepf (1)

BASIDIOBOLOMYCOTA Doweld
Basidiobolomycetes Doweld
Basidiobolales Jacz. & P.A. Jacz.
Basidiobolaceae Engl. & E. Gilg
Basidiobolus Eidam (7)
Schizangiella J. Dwyer, B. Burwell, Humber, C. Mcleod, M. Fleetwood & T. Johnson bis (1)

BLASTOCLADIOMYCOTA T.Y. James
Blastocladiomycetes Doweld
Blastocladiales H.E. Petersen
Blastocladiaceae H.E. Petersen
Allomyces E.J. Butler (10)

Blastocladia Reinsch (30)
Blastocladiopsis Sparrow (2)

Catenariaceae Couch
Catenophlyctis Karling (2)
Nematoceromyces Doweld (3)

Paraphysodermataceae Doweld
Paraphysoderma Boussiba, Zarka & T.Y. James (1)

Sorochytriaceae Dewel
Sorochytrium Dewel (1)

Callimastigales Doweld
Callimastigaceae Fonseca
Callimastix Weissenb. (2)

Catenomycetales Doweld
Catenomycetaceae Doweld
Catenomyces A.M. Hanson (2)

Coelomomycetaceae Couch
Coelomomyces Keilin (66)
Coelomycidium Debais. (2)

Physodermatomycetes Tedersoo, Sanchez-Ramirez, Kõljalg, Bahram, M. Döring, Schigel, T.W. May, M. Ryberg & Abarenkov
Physodermatales Caval.-Sm.
Physodermataceae Sparrow
Physoderma Wallr. (99)

CALCARISPORIELLOMYCOTA Tedersoo, Sanchez-Ramirez, Kõljalg, Bahram, M. Döring, Schigel, T.W. May, M. Ryberg & Abarenkov
Calcarisporiellomycotina Tedersoo, Sanchez-Ramirez, Kõljalg, Bahram, M. Döring, Schigel, T.W. May, M. Ryberg & Abarenkov
Calcarisporiellomycetes Tedersoo, Sanchez-Ramirez, Kõljalg, Bahram, M. Döring, Schigel, T.W. May, M. Ryberg & Abarenkov
Calcarisporiellales Tedersoo, Sanchez-Ramirez, Kõljalg, Bahram, M. Döring, Schigel, T.W. May, M. Ryberg & Abarenkov
Calcarisporiellaceae Tedersoo, Sanchez-Ramirez, Kõljalg, Bahram, M. Döring, Schigel, T.W. May, M. Ryberg & Abarenkov
Calcarisporiella de Hoog (1)
Echinochlamydosporium X.Z. Jiang, H.Y. Yu, M.C. Xiang, X.Y. Liu & Xing Z. Liu (1)

CHYTRIDIOMYCOTA Doweld (= *Caulochytriomycota* Doweld)
Caulochytriomycetes Doweld
Caulochytriales Doweld
Caulochytriaceae Subram.
Caulochytrium Voos & L.S. Olive (2)

Chytridiomycetes Caval.-Sm.

Chytridiales Cohn
Asterophlyctaceae Doweld
Asterophlyctis H.E. Petersen (2)
Wheelerophlyctis P.M Letcher, M.J. Powell, W.J. Davis (2)
Chytridiaceae Nowak.
Chytridium A. Braun (143)
Dendrochytridium Letcher, Longcore & M.J. Powell (1)
Dinochytrium Lesham, Letcher & M.J. Powell (1)
Irineochytrium Letcher, Longcore & M.J. Powell (1)
Phlyctochytrium J. Schröt. (ca. 50)
Polyphlyctis Karling (3)
Zopfochytrium M.J. Powell, Longcore, Letcher (1)

Chytriomycetaceae Letcher (= *Phlyctorhizaceae* Doweld**)**
Avachytrium Vélez & Letcher (1)
Chytriomyces Karling (33)
Entophlyctis A. Fisch. (29)
Fayochytriomyces W.J. Davis, Letcher, Longcore & M.J. Powell (1)
Obelidium Nowak. (3)
Odontochytrium Vélez & Letcher (1)
Pendulichytrium K. Seto & Degawa (1)
Phlyctorhiza A.M. Hanson (1)
Physocladia Sparrow (1)
Podochytrium Pfitzer (7)
Rhopalophlyctis Karling (1)
Rhizidium A. Braun (34)
Rodmanochytrium M.J. Powell & Letcher (2)
Rhizoclosmatium H.E. Petersen (4)
Siphonaria H.E. Petersen (3)

Pseudorhizidiaceae Doweld
Delfinachytrium Vélez & Letcher (1)
Pseudorhizidium M.J. Powell, Letcher & Longcore (1)

Scherffeliomycetaceae Doweld
Scherffeliomyces Sparrow (4)

Nephridiophagales Doweld
Nephridiophagaceae R. Radek, Letcher, Wijayaw., P.M. Kirk & K.D. Hyde
Coleospora Gibbs (1)
Malpighivinco Radek & Strassert (1)
Nephridiophaga Ivanić (12)
Nephridiochytrium Radek & Strassert (1)
Oryctospora Purrini & Weiser (1)
Peltomyces Léger (1)

Polyphagales Doweld
Polyphagaceae F. Maekawa
Polyphagus Nowak. (15)
Volvorax Doweld (1)

Saccopodiales Doweld
Saccopodiaceae Jacz. & P.A. Jacz.
Saccopodium Sorokīn (1)

Zygophlyctidales K. Seto
Zygophlyctidaceae K. Seto
Zygophlyctis Doweld (3)

Zygorhizidiales K. Seto
Zygorhizidiaceae Doweld
Zygorhizidium Löwenthal (9)

Chytridiomycetes families *incertae sedis*
Amoebochytriaceae Doweld
Amoebochytrium Zopf (1)

Sparrowiaceae Doweld
Sparrowia Willoughby (2)

Sphaeromonadaceae Doweld
Sphaeromonas E. Liebet. (3)

Tetrachytriaceae Doweld
Tetrachytrium Sorokīn (1)
Zygochytrium Sorokīn (1)

Thalassochytriaceae Doweld
Thalassochytrium Nyvall, M. Pedersén & Longcore (1)

Cladochytriomycetes Tedersoo, Sanchez-Ramirez, Kõljalg, Bahram, M. Döring, Schigel, T.W. May, M. Ryberg & Abarenkov
Cladochytriales Mozl.-Standr.
Cladochytriaceae J. Schröt.
Cladochytrium Nowak. (51)
Karlingiella (Karling) G.H. Jerônimo, A.L. Jesus & Pires-Zottar. (1)

Endochytriaceae Sparrow ex D.J.S. Barr
Endochytrium Sparrow (7)

Nowakowskiellaceae Sparrow ex Mozl.-Standr.
Nowakowskiella J. Schröt. (18)

Septochytriaceae Mozl.-Standr. (= ?*Catenochytridiaceae*)
Allochytridium D.J.S. Barr & Desauln (3)
Catenochytridium Berdan (6)
Cylindrochytridium Karling (2)
Dogmamyces G.H. Jerônimo, C.L.A. Pires-Zottar., T.Y. James & J.E. Longcore (1)
Nephrochytrium Karling (4)
Phytochytrium Longcore & G.H. Jerônimo (1)
Septochytrium Berdan (5)
Sparrowiella Longcore & G.H. Jerônimo (1)

Cladochytriales* genera *incertae sedis
?*Diplophlyctis* J. Schröt. (12)
Thomasia G.H. Jerônimo (1)

Lobulomycetes Tedersoo, Sanchez-Ramirez, Kõljalg, Bahram, M. Döring, Schigel, T.W. May, M. Ryberg & Abarenkov
Lobulomycetales D.R. Simmons
Lobulomycetaceae D.R. Simmons (= *Alogomycetaceae* Doweld)
Algochytrops Doweld (1)
Algomyces Van den Wyngaert, K. Rojas & K. Seto (1)
Alogomyces D.R. Simmons & Letcher (1)
Clydaea D.R. Simmons (1)
Cyclopsomyces K. Seto & Degawa (1)
Lobulomyces D.R. Simmons (2)
Maunachytrium D.R. Simmons (1)

Mesochytriomycetes Tedersoo, Sanchez-Ramirez, Kõljalg, Bahram, M. Döring, Schigel, T.W. May, M. Ryberg & Abarenkov
Gromochytriales Karpov & Aleoshin
Gromochytriaceae Karpov & Aleoshin
Apiochytrium Karpov & D. Moreira (1)
Gromochytrium Karpov & Aleoshin (1)

Mesochytriales Doweld
Mesochytriaceae Doweld
Mesochytrium B.V. Gromov, Mamkaeva & Pljusch (1)

Polychytriomycetes Tedersoo, Sanchez-Ramirez, Kõljalg, Bahram, M. Döring, Schigel, T.W. May, M. Ryberg & Abarenkov
Polychytriales Longcore & D.R. Simmons
Polychytriaceae Doweld (= ?*Arkayaceae* Doweld)
Arkaya Longcore & D.R. Simmons (2)
Karlingiomyces Sparrow (8)
Lacustromyces Longcore (1)
Neokarlingia Longcore & D.R. Simmons (1)
Polychytrium Ajello (1)

Rhizophlyctidomycetes Tedersoo, Sanchez-Ramirez, Kõljalg, Bahram, M. Döring, Schigel, T.W. May, M. Ryberg & Abarenkov
Rhizophlyctidales Letcher
Arizonaphlyctidaceae Letcher
Arizonaphlyctis Letcher (1)

Borealophlyctidaceae Letcher
Borealophlyctis Letcher (2)

Rhizophlyctidaceae H.E. Petersen
Rhizophlyctis A. Fisch. (31)

Sonoraphlyctidaceae Letcher
Sonoraphlyctis Letcher (1)

Rhizophydiomycetes Tedersoo, Sánchez-Ramírez, Kõljalg, Bahram, Döring, Schigel, T. May, M. Ryberg & Abarenkov
Rhizophydiales Letcher
Alphamycetaceae Letcher
Alphamyces Letcher (2)
Betamyces Letcher (1)
Gammamyces Letcher (1)

Angulomycetaceae Letcher
Angulomyces Letcher (1)

Aquamycetaceae Letcher
Aquamyces Letcher (1)

Batrachochytriaceae Doweld
Batrachochytrium Longcore, Pessier & D.K. Nichols (2)

Collimycetaceae K. Seto & Degawa
Collimyces K. Seto & Degawa (1)

Coralloidiomycetaceae Doweld
Coralloidiomyces Letcher (1)

Dinomycetaceae Karpov & Guillou
Dinomyces Karpov & Guillou (2)
Paradinomyces Reñé & Karpov (2)

Ericiomycetaceae Karpov & Reñé
Ericiomyces Karpov & Reñé (1)

Globomycetaceae Letcher
Globomyces Letcher (1)
Urceomyces Letcher (1)

Gorgonomycetaceae Letcher
Gorgonomyces Letcher (5)

Halomycetaceae Letcher & M.J. Powell
Halomyces Letcher & M.J. Powell (1)
Paludomyces Letcher & M.J. Powell (1)
Paranamyces Letcher & M.J. Powell (1)
Ulkenomyces Letcher & M.J. Powell (1)

Kappamycetaceae Letcher
Kappamyces Letcher & M.J. Powell (2)

Operculomycetaceae Doweld
Operculomyces M.J. Powell, Letcher & Longcore (1)

Pateramycetaceae Letcher
Pateramyces Letcher (2)

Protrudomycetaceae Letcher
Protrudomyces Letcher (1)

Rhizophydiaceae Letcher
Rhizophydium Schenk ex Rabenh. (ca. 150)

Staurastromycetaceae S. Van den Wyngaert, K. Seto & K. Rojas
Staurastromyces Van den Wyngaert, K. Seto & K. Rojas (1)

Terramycetaceae Letcher
Boothiomyces Letcher (1)
Terramyces Letcher (4)

Uebelmesseromycetaceae M.J. Powell & Letcher
Uebelmesseromyces M.J. Powell & Letcher (1)

Rhizophydiales* genera *incertae sedis
Homolaphlyctis Longcore, Letcher & T.Y. James (1)
Polyrhizophydium Longcore & D.R. Simmons (1)

Spizellomycetes Tedersoo, Sanchez-Ramirez, Kõljalg, Bahram, M. Döring, Schigel, T.W. May, M. Ryberg & Abarenkov
Spizellomycetales D.J.S. Barr
Powellomycetaceae D.R. Simmons
Fimicolochytrium D.R. Simmons & Longcore (2)
Geranomyces D.R. Simmons (4)
Powellomyces Longcore (1)
Thoreauomyces D.R. Simmons & Longcore (1)

Spizellomycetaceae D.J.S. Barr
Barromyces M.J. Powell & Letcher (1)
Brevicalcar Letcher & M.J. Powell (1)
Bulbosomyces Letcher & Longcore (1)
Gaertneriomyces D.J.S. Barr (4)
Gallinipes Letcher & M.J. Powell (3)
Kochiomyces D.J.S. Barr (1)
Spizellomyces D.J.S. Barr (7)
Triparticalcar D.J.S. Barr (1)

Synchytriomycetes Tedersoo, Sanchez-Ramirez, Kõljalg, Bahram, M. Döring, Schigel, T.W. May, M. Ryberg & Abarenkov
Synchytriales Doweld
Synchytriaceae J. Schröt.
Carpenterophlyctis Doweld (2)
Endodesmidium Canter (1)
Johnkarlingia Pavgi & S.L. Singh (1)
Micromyces P.A. Dang. (11)
?*Micromycopsis* Scherff. (6)
Synchytrium de Bary & Woronin (ca. 200)

Chytridiomycota* family *incertae sedis
Quaeritorhizaceae Longcore, D.R. Simmons & T.Y. James
Quaeritorhiza Longcore, D.R. Simmons & T.Y. James (1)

ENTOMOPHTHOROMYCOTA Humber
Entomophthoromycotina Humber
Entomophthoromycetes Humber
Entomophthorales G. Winter
Ancylistaceae J. Schröt.
Ancylistes Pfitzer (4)
Macrobiotophthora Reukauf (1)

Batkoaceae Gryganskyi, A.E. Hajek & Stajich
Batkoa Humber (10)

Capillidiaceae Y. Nie, Stajich & K.T. Hodge
Capillidium B. Huang & Y. Nie (7)

Completoriaceae Humber
Completoria Lohde (1)

Conidiobolaceae B. Huang, Stajich & K.T. Hodge
Azygosporus B. Huang & Y. Nie (2)
Conidiobolus Bref. (ca. 30)
Microconidiobolus B. Huang & Y. Nie (3)

Entomophthoraceae Nowak.
Entomophaga A. Batko (22)
Entomophthora Fresen. (63)
Erynia (Nowak. ex A. Batko) Remaud. & Hennebert (27)
Eryniopsis Humber (5)
Furia (A. Batko) Humber (16)
Massospora Peck (15)
Orthomyces Steinkr., Humber & J.B. Oliv. (1)
Strongwellsea A. Batko & J. Weiser (3)
Tarichium Cohn *sensu stricto* (26)
Zoophthora A. Batko (38)

Meristacraceae Humber
Meristacrum Drechsler (2)

Neoconidiobolaceae X.Y. Liu, Stajich & K.T. Hodge
Neoconidiobolus B. Huang & Y. Nie (13)

Neozygitomycetes Humber
Neozygitales Humber
Neozygitaceae Ben-Ze'ev , R.G. Kenneth & Uziel
Apterivorax S. Keller (2)
Neozygites Witlaczil (22)

GLOMEROMYCOTA C. Walker & A. Schüßler
Archaeosporomycetes Sieverd., G.A. Silva, B.T. Goto & Oehl
Archaeosporales C. Walker & A. Schüssler
Ambisporaceae C. Walker, Vestberg & A. Schüssler (= *Appendicisporaceae* C. Walker, Vestberg & A. Schüssler)
Ambispora C. Walker, Vestberg & A. Schüssler (basionym *Appendicispora* Spain, Oehl & Sieverding) (11)

Archaeosporaceae J.B. Morton & D. Redecker
Archaeospora J.B. Morton & D. Redecker (6)
Palaeospora Oehl, Palenz., Sánchez-Castro & G.A. Silva (1)

Geosiphonaceae Engl. & E. Gilg
Geosiphon F. Wettst. (1)

Polonosporaceae Błaszk., Niezgoda, B.T. Goto, Magurno
Polonospora Błaszk., Niezgoda, B.T. Goto, Magurno (1)

Glomeromycetes Caval.-Sm. emend. Oehl, G.A. Silva, B.T. Goto & Sieverd.
Diversisporales C. Walker & A. Schüssler emend. Oehl, G.A. Silva & Sieverd.
Acaulosporaceae J.B. Morton & Benny
Acaulospora Gerd. & Trappe (= *Kuklospora* Oehl & Sieverd.) (58)

Diversisporaceae C. Walker & A. Schüessler
Corymbiglomus Błaszk. & Chwat (3)
Desertispora Błaszk., Kozłowska, Ryszka, Al-Yahya'ei & Symanczik (1)
Diversispora C. Walker & A. Schüssler (21)
Redeckera C. Walker & A. Schüssler (6)
Sieverdingia Błaszk., Niezgoda & B.T. Goto (1)

Pacisporaceae C. Walker, Błaszk., A. Schüssler & Schwarzott
Pacispora Sieverd. & Oehl (7)

Sacculosporaceae Oehl, Sieverd., G.A. Silva, B.T. Goto, Sánchez-Castro & Palenz.
Sacculospora Oehl, Sieverd., G.A. Silva, B.T. Goto, I.C. Sánchez & Palenz. (2)

Entrophosporales Błaszk., Sánchez-García, B.T. Goto & Magurno
Entrophosporaceae s. str. Oehl & Sieverd.
Entrophospora R.N. Ames & R.W. Schneid. (2)

Gigasporales S.P. Gautam & U.S. Patel (= *Gigasporales* Sieverd., G.A. Silva, B.T. Goto & Oehl)
Bulbosporaceae Magurno, F.A. de Souza, N.V.L. Oliveira & B.T. Goto
Bulbospora Oehl& G.A. Silva (1)

Dentiscutataceae F.A. Souza, Oehl & Sieverd.
Dentiscutata Sieverd., F.A. Souza & Oehl (9)
Fuscutata Oehl, F.A. Souza & Sieverd. (7)

Gigasporaceae J.B. Morton & Benny
Gigaspora Gerd. & Trappe (7)

Intraornatosporaceae B.T. Goto & Oehl
Intraornatospora B.T. Goto, Oehl & G.A. Silva (1)
Paradentiscutata B.T. Goto, Oehl & G.A. Silva (2)

Racocetraceae Oehl, Sieverd. & F.A. Souza
Cetraspora Oehl, F. A. Souza & Sieverd. (9)
Racocetra Oehl, F.A. Souza & Sieverd. (13)

Scutellosporaceae Sieverd., F.A. Souza & Oehl
Orbispora Oehl, G.A. Silva & D.K. Silva (2)
Scutellospora C. Walker & F.E. Sanders (14)

Glomerales J.B. Morton & Benny emend. Oehl, G.A. Silva, B.T. Goto & Sieverd.
Glomeraceae Piroz. & Dalpé emend. Oehl, G.A. Silva & Sieverd.
Complexispora Błaszk., B.T. Goto, Niezgoda & Magurno (2)
Glomus Tul. & C. Tul. emend. Oehl, G.A. Silva & Sieverd. (58)
Sclerocarpum B.T. Goto, Błaszk., Niezgoda, Kozłowska & Jobim (1)

Dominikiaceae G.A. Silva, Sieverd. & Oehl
Dominikia Błaszk., Chwat &Kovács (14)
Macrodominikia Oehl, Sieverd. & G.A. Silva (1)
Microdominikia Oehl, Corazon-Guivin & G.A. Silva (1)
Nanoglomus Corazon-Guivin, G.A. Silva & Oehl (1)
Orientoglomus G.A. Silva, Oehl & Corazon-Guivin (1)

Kamienskiaceae G.A. Silva, Sieverd. & Oehl
Kamienskia Błaszk., Chwat & Kovács (1)
Epigeocarpum Błaszk., B.T. Goto, Jobim, Niezgoda & Marguno (2)
Microkamienskia Corazon-Guivin, G.A. Silva & Oehl (3)

Sclerocystaceae Oehl, G.A. Silva, & Sieverd.
Sclerocystis Berk. & Broome (13)
Halonatospora Błaszk., Niezgoda, B.T. Goto & Kozłowska (1)
Oehlia Błaszk., Kozłowska, Niezgoda, B.T. Goto & Dalpé (1)
Rhizoglomus Sieverd., G.A. Silva & Oehl (23)
Silvaspora Błaszk., Niezgoda, B.T. Goto, Crossay & Magurno (1)
Parvocarpum Magurno (1)

Septoglomeraceae Oehl, G.A. Silva & Sieverd.
Septoglomus Sieverd., G.A. Silva & Oehl (14)
Blaszkowskia G.A. Silva & Oehl (1)
Funneliformis C. Walker & A. Schüssler emend. Oehl, G.A. Silva & Sieverd. (13)
Funneliglomus Corazon-Guivin, G.A. Silva & Oehl (1)
Viscospora Sieverd., G.A. Silva & Oehl (3)

Paraglomeromycetes Oehl, G.A. Silva, B.T. Goto & Sieverd.
Paraglomerales C. Walker & A. Schüssler
Paraglomeraceae J.B. Morton & D. Redecker
Paraglomus J.B. Morton & D. Redecker (8)
Innospora Błaszk., Kovács, Chwat & Kozłowska (1)

Pervetustaceae Błaszk., Chwat, Kozłowska, Symanczik & Al-Yahya'ei
Pervetustus Błaszk., Chwat, Kozłowska, Symanczik & Al-Yahya'ei (1)

KICKXELLOMYCOTA Tedersoo, Sanchez-Ramirez, Kõljalg, Bahram, M. Döring, Schigel, T.W. May, M. Ryberg & Abarenkov
Asellariomycetes Tedersoo, Sanchez-Ramirez, Kõljalg, Bahram, M. Döring, Schigel, T.W. May, M. Ryberg & Abarenkov
Asellariales Manier ex Manier & Lichtw.
Asellariaceae Manier ex Manier & Lichtw.
Asellaria R.A. Poiss. (9)

Asellariales* genus *incertae sedis
Baltomyces Cafaro (1)

Barbatosporomycetes Tedersoo, Sanchez-Ramirez, Kõljalg, Bahram, M. Döring, Schigel, T.W. May, M. Ryberg & Abarenkov
Barbatosporales Doweld
Barbatosporaceae Doweld
Barbatospora M.M. White, Siri & Lichtw. (1)

Dimargaritomycetes Tedersoo, Sanchez-Ramirez, Kõljalg, Bahram, M. Döring, Schigel, T.W. May, M. Ryberg & Abarenkov
Dimargaritales R.K. Benj.
Dimargaritaceae R.K. Benj.
Dimargaris Tiegh. (7)
Dispira Tiegh. (4)
Tieghemiomyces R.K. Benj. (2)

Harpellomycetes Tedersoo, Sanchez-Ramirez, Kõljalg, Bahram, M. Döring, Schigel, T.W. May, M. Ryberg & Abarenkov
Harpellales Lichtw. & Manier
Harpellaceae L. Léger & Duboscq ex P.M. Kirk & P.F. Cannon
Carouxella Manier, Rioux & Whisler (2)
Harpella L. Léger & Duboscq (7)
Harpellomyces Lichtw. & S.T. Moss (4)
Klastostachys Lichtw., M.C. Williams & M.M. White (1)
Stachylina L. Léger & M. Gauthier (40)
Stachylinoides Lichtw. & López-Lastra (1)

Legeriomycetaceae Pouzar
Austrosmittium Lichtw. & M.C. Williams (Nom. Inval.) (6)
Bactromyces William & Strongman (1)
Baetimyces L.G. Valle & Santam. (1)
Bojamyces Longcore (3)
Capniomyces S.W. Peterson & Lichtw. (3)
Caudomyces Lichtw., Kobayasi & Indoh (3)
Coleopteromyces Ferrington, Lichtw. & López-Lastra (1)
Dacryodiomyces Lichtw. (1)
Ejectosporus S.W. Peterson, Lichtw. & M.C. Williams (1)
Ephemerellomyces M.M. White & Lichtw. (1)
Furculomyces Lichtw. & M.C. Williams (3)

Gauthieromyces Lichtw. (3)
Genistelloides S.W. Peterson, Lichtw. & B.W. Horn (5)
Genistellospora Lichtw. (6)
Glotzia M. Gauthier ex Manier & Lichtw. (7)
Graminella L. Léger & M. Gauthier ex Manier (3)
Laculus William & Strongman (1)
Lancisporomyces Santam. (5)
Legerioides M.M. White (1)
Legeriomyces Pouzar (14)
Legeriosimilis M.C. Williams, Lichtw., M.M. White & J.K. Misra (8)
Pennella Manier (8)
Plecopteromyces Lichtw., Ferrington & López-Lastra (3)
Pseudoharpella Ferrington, M.M. White & Lichtw. (1)
Pteromaktron Whisler (2)
Simuliomyces Lichtw. (1)
Sinotrichium Juan Wang (1)
Smittium R.A. Poiss. (1)
Spartiella Tuzet & Manier ex Manier (3)
Stipella L. Léger & M. Gauthier (2)
Stypomyces Doweld (2)
Tectimyces L.G. Valle & Santam. (3)
Trichozygospora Lichtw. (1)
Trifoliellum Strongman & M.M. White (1)
Zancudomyces Yan Wang, Tretter, Lichtw. & M.M. White (1)
Zygopolaris S.T. Moss, Lichtw. & Manier (2)
Zygopolaropsis Hirok. Sato & Degawa (1)

Kickxellomycetes Tedersoo, Sanchez-Ramirez, Kõljalg, Bahram, M. Döring, Schigel, T.W. May, M. Ryberg & Abarenkov
Kickxellales Kreisel ex R.K. Benj.
Kickxellaceae Linder
Coemansia Tiegh. & G. Le Monn. (25)
Dipsacomyces R.K. Benj. (1)
Kickxella Coem. (1)
Linderina Raper & Fennell (2)
Martensella Coem. (1)
Martensiomyces J.A. Mey. (1)
Mycoemilia Kurihara, Degawa & Tokum. (1)
Myconymphaea Kurihara, Degawa & Tokum. (1)
Pinnaticoemansia Kurihara & Degawa (1)
Unguispora T. Ri & Degawa (1)

Kickxellales* genus *incertae sedis
Spirodactylon R.K. Benj. (1)

Orphellales Doweld
Orphellaceae Doweld
Orphella L. Léger & M. Gauthier (12)

Kickxellomycetes* genus *incertae sedis
Spiromyces R.K. Benj. (2)

Ramicandelaberomycetes Tedersoo, Sanchez-Ramirez, Kõljalg, Bahram, M. Döring, Schigel, T.W. May, M. Ryberg & Abarenkov
Ramicandelaberales Doweld
Ramicandelaberaceae Doweld
Ramicandelaber Y. Ogawa, S. Hayashi, Degawa & Yaguchi (4)

MONOBLEPHAROMYCOTA Doweld
Hyaloraphidiomycetes Doweld
Hyaloraphidiales Doweld
Hyaloraphidiaceae Doweld
Hyaloraphidium Korshikov (1)

Monoblepharidomycetes J.H. Schaffn.
Monoblepharidales Sparrow
Gonapodyaceae H.E. Petersen ex P.M. Kirk, P.F. Cannon & J.C. David
Gonapodya A. Fisch. (5)
Monoblepharella Sparrow (5)

Harpochytriaceae Wille
Harpochytrium Lagerh. (12)

Monoblepharidaceae A. Fisch.
Monoblepharis Cornu (13)

Oedogoniomycetaceae D.J.S. Barr
Oedogoniomyces Kobayasi & M. Ôkubo (1)

Telasphaerulaceae Longcore & T.Y. James
Telasphaerula Longcore & T.Y. James (1)

MORTIERELLOMYCOTA Tedersoo, Sanchez-Ramirez, Kõljalg, Bahram, M. Döring, Schigel, T.W. May, M. Ryberg & Abarenkov
Mortierellomycotina Kerst. Hoffm., K. Voigt & P.M. Kirk
Mortierellomycetes Doweld
Mortierellales Caval.-Sm.
Mortierellaceae A. Fisch.
Actinomortierella Chalab. (5)
Aquamortierella Embree & Indoh (1)
Benniella Vandepol & Bonito (1)
Dissophora Thaxt. (4)
Entomortierella Vandepol & Bonito (10)
Gamsiella (R.K. Benj.) Benny & M. Blackw. (2)
Gryganskiella Vandepol & Bonito (2)
Linnemannia Vandepol & Bonito (24)
Lobosporangium M. Blackw. & Benny (1)
Lunasporangiospora Vandepol & Bonito (2)
Modicella Kanouse (4)
Mortierella Coem. (112)
Necromortierella Vandepol & Bonito (1)
Podila Stajich, Vandepol & Bonito (7)

MUCOROMYCOTA Doweld
Mucoromycotina Benny
Endogonomycetes Doweld
Bifiguratales Tedersoo
Bifiguratacеae Tedersoo
Bifiguratus Torres-Cruz & Porras-Alfaro (1)

Densosporales Tedersoo, ex Madrid, P.M. Kirk & Wijayaw.
Densosporaceae Desirò, M.E. Sm., Bidartondo, Trappe & Bonito ex Madrid, Kirk & Wijayaw.
Densospora McGee (9)

Endogonales Jacz. & P.A. Jacz.
Endogonaceae Paol.
Endogone Link (26)
Jimwhitea M. Krings &T.N. Taylor (1)
Peridiospora C.G. Wu & Suh J. Lin (2)
Sclerogone Warcup (1)

Jimgerdemanniaceae Tedersoo ex Madrid, P.M. Kirk & Wijayaw.
Jimgerdemannia Trappe, Desirò, M.E. Sm., Bonito & Bidartondo (2)

Vinositunicaceae Tedersoo
Vinositunica Koh. Yamam., Degawa & A. Yamada (2)

Mucoromycetes Doweld
Mucorales Fr.
Backusellaceae K. Voigt & P.M. Kirk
Backusella Hesselt. & J.J. Ellis (26)

Circinellaceae H. Zhao, Y.C. Dai, B.K. Cui, F. Wu, Yuan Yuan & X.Y. Liu
Circinella Tiegh. & G. Le Monn. (11)
Fennellomyces Benny & R.K. Benj. (4)
Phascolomyces Boedijn ex Benny & R.K. Benj. (1)
Thamnostylum Arx & H.P. Upadhyay (4)
Zychaea Benny & R.K. Benj. (1)

Cunninghamellaceae Naumov ex R.K. Benj.
Absidia Tiegh. (70)
Chlamydoabsidia Hesselt. & J.J. Ellis (1)
Cunninghamella Matr. (123)
Gongronella Ribaldi (26)
Halteromyces Shipton & Schipper (1)
Hesseltinella H.P. Upadhyay (1)

Lentamycetaceae K. Voigt & P.M. Kirk
Lentamyces Kerst. Hoffm. & K. Voigt (4)

Lichtheimiaceae Kerst. Hoffm., Walther & K. Voigt
Dichotomocladium Benny & R.K. Benj. (5)
Lichtheimia Vuill. (11)

Mucoraceae Dumort.
Actinomucor Schostak. (1)
Ambomucor R.Y. Zheng & X.Y. Liu (3)
Benjaminiella Arx (3)
Blakeslea Thaxt. (2)
Chaetocladium Fresen. (2)
Choanephora Curr. (2)
Cokeromyces Shanor (1)
Dicranophora J. Schröt. (1)
Ellisomyces Benny & R.K. Benj. (1)
Gilbertella Hesselt. (2)
Helicostylum Corda (2)
Hyphomucor Schipper & Lunn (1)
Isomucor J.I. Souza, Pires-Zottar. & Harakava (2)
Kirkiana L.S. Loh, Kuthub. & Nawawi (1)
Kirkomyces Benny (1)
Mucor Fresen. (98)
Mycotypha Fenner (4)
Nawawiella L.S. Loh & Kuthub. (1)
Parasitella Bainier (1)
Pilaira Tiegh. (10)
Pirella Bainier (2)
Poitrasia P.M. Kirk (1)
Rhizopodopsis Boedijn (1)
Thamnidium Link (1)
Tortumyces L.S. Loh (2)

Mycocladaceae Kerst. Hoffm.
Mycocladus Beauverie (1)

Mycotyphaceae Benny & R.K. Benj.
Mycotypha Fenner (4)

Phycomycetaceae Arx
Phycomyces Kunze (3)
Spinellus Tiegh. (5)

Pilobolaceae Corda
Pilobolus Tode (8)
Utharomyces Boedijn ex P.M. Kirk & Benny (1 sp. and 1 subspecies)

Protomycocladaceae H. Zhao, Y.C. Dai, B.K. Cui, F. Wu, Yuan Yuan & X.Y. Liu
Protomycocladus Schipper & Samson (1)

Radiomycetaceae Hesselt. & J.J. Ellis
Radiomyces Embree (3)

Rhizomucoraceae H. Zhao, Y.C. Dai, B.K. Cui, F. Wu, Yuan Yuan & X.Y. Liu
Rhizomucor Lucet & Costantin (6)

Rhizopodaceae K. Schum.
Rhizopus Ehrenb. (13)

Saksenaeaceae Hesselt. & J.J. Ellis
Apophysomyces P.C. Misra (6)
Saksenaea S.B. Saksena (5)

Syncephalastraceae Naumov ex R.K. Benj.
Syncephalastrum J. Schröt. (3)
Neofennellomyces Hyang B. Lee & T.T.T. Nguyen (1)

Syzygitaceae H. Zhao, Y.C. Dai, B.K. Cui, F. Wu, Yuan Yuan & X.Y. Liu
Sporodiniella Boedijn (1)
Syzygites Ehrenb. (1)

Thermomucoraceae H. Zhao, Y.C. Dai, B.K. Cui, F. Wu, Yuan Yuan & X.Y. Liu
Thermomucor Subrahm., B.S. Mehrotra & Thirum. (1)

Umbelopsidomycetes Tedersoo, Sanchez-Ramirez, Kõljalg, Bahram, M. Döring, Schigel, T.W. May, M. Ryberg & Abarenkov
Umbelopsidales Spatafora & Stajich
Pygmaeomycetaceae E. Walsh & N. Zhang
Pygmaeomyces E. Walsh & N. Zhang (2)

Umbelopsidaceae W. Gams & W. Mey.
Umbelopsis Amos & H.L. Barnett (17)

NEOCALLIMASTIGOMYCOTA M.J. Powell
Neocallimastigomycetes M.J. Powell
Neocallimastigales J.L. Li, I.B. Heath & L. Packer
Anaeromycetaceae Doweld
Anaeromyces Breton, Bernalier, Dusser, Fonty, B. Gaillard & J. Guillot (4)
Capellomyces Hanafy, Lanjekar, Dhakephalkar, T.M. Callaghan, Dagar, G.W. Griff., Elshahed & N.H. Youssef (2)
Liebetanzomyces Joshi, G.W. Griff. & Dagar (1)
Oontomyces Dagar (1)

Caecomycetaceae R.A. Hanafy, Yan Wang, Stajich, C.J. Pratt, N.H. Youssef & Elshahed
Caecomyces J.J. Gold (5)
Cyllamyces Ozkose, B.J. Thomas, D.R. Davies, G.W. Griff. & Theodorou (1)

Neocallimastigaceae I.B. Heath (= *Piromonadaceae* Doweld)
Aestipascuomyces Stabel, R. Hanafy, Schweitzer, Greif, Aliyu, Flad, D. Young, Lebuhn, Elshahed, Ochsenreither & N.H. Youssef (1)
Feramyces Radwa Hanafy, Mostafa Elshahed & Noha Youssef (1)
Ghazallomyces Hanafy, Lanjekar, Dhakephalkar, T.M. Callaghan, Dagar, G.W. Griff., Elshahed & N.H. Youssef (1)
Neocallimastix Vávra & Joyon ex I.B. Heath (7)
Orpinomyces D.J.S. Barr, H. Kudo, Jakober & K.J. Cheng (2)
Paucimyces R.A. Hanafy, N.H. Youssef & Elshahed (1)
Pecoramyces Hanafy, N.H. Youssef, G.W. Griff. & Elshahed (1)

Piromycetaceae R.A. Hanafy, Yan Wang, Stajich, C.J. Pratt, N.H. Youssef & Elshahed
Piromyces J.J. Gold, I.B. Heath & Bauchop

Neocallimastigales* genera *incertae sedis
Agriosomyces Hanafy, Lanjekar, Dhakephalkar, T.M. Callaghan, Dagar, G.W. Griff., Elshahed & N.H. Youssef (1)
Aklioshbomyces Hanafy, Lanjekar, Dhakephalkar, T.M. Callaghan, Dagar, G.W. Griff., Elshahed & N.H. Youssef (1)
Buwchfawromyces T.M. Callaghan & G.W. Griff. (1)
Joblinomyces Hanafy, Lanjekar, Dhakephalkar, T.M. Callaghan, Dagar, G.W. Griff., Elshahed & N.H. Youssef (1)
Khoyollomyces Hanafy, Lanjekar, Dhakephalkar, T.M. Callaghan, Dagar, G.W. Griff., Elshahed & N.H. Youssef (1)
Tahromyces Hanafy, Lanjekar, Dhakephalkar, T.M. Callaghan, Dagar, G.W. Griff., Elshahed & N.H. Youssef (1)

OLPIDIOMYCOTA Doweld
Olpidiomycetes Doweld
Olpidiales Caval.-Sm.
Olpidiaceae J. Schröt.
Chytridhaema Moniez (1)
Cibdelia Juel (1)
Leiolpidium Doweld (5)
Olpidium (A. Braun) J. Schröt. (ca. 50)

ROZELLOMYCOTA Doweld
Rozellidea Cavalier-Smith
Rozellida Cavalier-Smith
Rozellidae Cavalier-Smith
Rozella Cornu (ca 27)

Chytridiopsea Weiser
Chytridiopsida Weiser
Burkeidae Sprague
Burkea V. Sprague (2)

Buxtehudiidae J.I.R. Larss.
Jiroveciana J.I.R. Larss. (1)
Buxtehudea J.I.R. Larss. (1)

Chytridiopsidae R. Sprague, Ormières & Manier
Acarispora R. Radek, M. Kariton, J. Dabert & G. Alberti (1)
Chytridiopsis W.G. Schneid. (11)
Intexta J.I.R. Larss., M.Y. Steiner & Bjørnson (1)
Nolleria C.B. Beard, J.F. Butler & J.J. Becnel (1)
Sheriffia J.I.R. Larss. (1)

Hesseidae Ormières & R. Sprague
Hessea Ormières & R. Sprague (1)

Rudimicrosporea V. Sprague
Metchnikovellida Caullery & Mesnil
Amphiacanthidae J.I.R. Larss.
Amphiacantha Caullery & Mesnil (3)

Metchnikovellidae Caullery & Mesnil emend. Larsson
Amphiamblys Caullery & Mesnil (7)
Caulleryetta V.A. Dogiel (8)
Desportesia I.V. Issi & Voronin (1)
Metchnikovella Caullery & Mesnil (8)

Metchnikovellida* genus *incertae sedis
Mesnilivella Frolova & Nassonova (1)

Microsporidea Corliss & Levine
Amblyosporida Y.S. Tokarev & Issi
Amblyosporidae Weiser emend. Y.S. Tokarev & Issi
Aedispora P.J. Kilochitskii (1)
Amblyospora Hazard & Oldacre (90)
Andreanna A.V. Simakova, C.R. Vossbrinck & Andreadis (1)
Becnelia T. Tonka & J. Weiser (1)
Crepidulospora A.V. Simakova, T.F. Pankova & I.V. Issi (1)
Cristulospora L.F. Khodzhaeva & I.V. Issi (3)
Culicospora Weiser (2)
Culicosporella Weiser (1)
Dimeiospora A.V. Simakova, T.F. Pankova & I.V. Issi (1)
Edhazardia Becnel, V. Sprague & Fukuda (1)
Hyalinocysta Hazard & Oldacre (1)
Intrapredatorus Chen, Kuo & Wu (1)
Novothelohania Andreadis, Simakova, Vossbrinck, Shepard & Yurchenko (1)
Parastempellia Khodzhaeva (2)
Parathelohania Codreanu (25)
Trichoctosporea J.I.R. Larss. (1)
Tricornia J.K. Pell & E.U. Canning (1)

Caudosporidae Weiser emend. Y.S. Tokarev & I.V. Issi
Binucleospora A.M. Bronnvall & J.I.R. Larss. (1)
Caudosporina (J. Weiser) Y.S. Tokarev & I.V. Issi (1)
Flabelliforma E.U. Canning, R. Killick-Kendrick & M. Killick-Kendrick (4)
Myrmecomorba R.M. Plowes, J.J. Becnel, E.G. LeBrun, D.H. Oi, S.M. Valles, N.T. Jones & L.E. Gilbert (1)
Neoflabelliforma D.J. Morris & M.A. Freeman (2)
Octosporea Flu (18)
Polydispyrenia E.U. Canning & E.I. Hazard (2)
Ringueletium J.J. Garcia (1)
Scipionospora E.K.C. Bylén & J.I.R. Larss. (1)
Weiseria J.M. Doby & F. Saguez (3)

Gurleyidae Sprague emend. Y.S. Tokarev & I.V. Issi
Agglomerata J.I.R. Larss. & N.D. Yan (6)
Binucleata D. Refardt, E. Decaestecker, P.T.J. Johnson & Vávra (1)

Conglomerata I. Vávra, P. Fiala, Krylová, Petrusek & Hyliš (1)
Episeptum J.I.R. Larss. (6)
Gurleya Doflein (10)
Lanatospora Voronin (4)
Larssonia S.S. Vidtmann & Y.Y. Sokolova (2)
Marssoniella Lemmermann (1)
Norlevinea Vávra (1)
Paraepiseptum M. Hyliš, Oborník, J. Nebesářová & Vávra (4)
Pseudoberwaldia Vávra, I. Fiala, P. Krylová, Petrusek & Hyliš (1)
Senoma A.V. Simakova, T.F. Pankova, Y.S. Y.S. Tokarev & I.V. Issi (1)
Zelenkaia M. Hyliš, Oborník, J. Nebesářová & Vávra (1)

Neopereziida Y.S. Tokarev & I.V. Issi
Berwaldiidae Simakova, Y.S. Tokarev & I.V. Issi
Berwaldia Larsson (4)
Fibrillanosema G.M.J. Slothouber Galbreath, J.E. Smith, R.S. Terry, J.J. Becnel & A.M. Dunn (1)

Neopereziidae Voronin emend. I.V. Issi, Y.S. Tokarev, Seliverstova & Voronin
Bryonosema E.U. Canning, D. Refardt, C.R. Vossbrinck, B. Okamura & A. Curry (2)
Neoperezia I.V. Issi & Voronin (2)
Pseudonosema E.U. Canning, D. Refardt, C.R. Vossbrinck, B. Okamura & A. Curry (1)
Schroedera D.J. Morris & A. Adams (2)
Trichonosema E.U. Canning, D. Refardt, C.R. Vossbrinck, B. Okamura & A. Curry (2)

Tubulinosematidae C. Franzen, S. Fisch., Schröd., J. Schölmerich & S. Schneuwly emend. Y.S. Tokarev & I.V. Issi
Anncaliia I.V. Issi, S.V. Krylova & V.M. Nikolaeva (6)
Kneallhazia Sokolova & Fuxa (2)
Tubulinosema C. Franzen, S. Fisch., Schröd., J. Schölmerich & S. Schneuwly (5)

Ovavesiculida Y.S. Y.S. Tokarev & I.V. Issi
Ovavesiculidae R. Sprague, J.J. Becnel & E.I. Hazard emend. Y.S. Tokarev & I.V. Issi
Antonospora I. Fr., R.J. Paxton, J. Tengö, J.A. da Silva, S.B. Slemenda & N.J. Pieniazek (2)
Ovavesicula Andreadis & Hanula (1)
Paranosema Sokolova, Dolgikh, E.V. Morzhina, Nassonova, I.V. Issi, R.S. Terry, J.E. Ironside, J.E. Sm. & Vossbr. (4)

Glugeida Gurley emend. Y.S. Tokarev & I.V. Issi
Facilisporidae S.R.M. Jones, Prosperi-Porta & E. Kim
Facilispora S.R.M. Jones, Prosperi-Porta & E. Kim (1)

Glugeidae Gurley emend. Y.S. Tokarev & I.V. Issi
Alloglugea I. Paperna & R. Lainson (1)
Amazonspora C. Azevedo & E. Matos (1)
Cambaraspora Bojko, C.E. Stratton, Moler, Stratton & Reisinger (1)
Glugea Thélohan (41)
Ichthyosporidium Caullery & Mesnil (5)
Johenrea C.E. Lange, J.J. Becnel, E. Razafindratiana, J. Przybyszewski & H. Razafindrafara (1)
Loma C.M. Morrison & R. Sprague (12)
Parapleistophora I.V. Issi, Kadyrova, Pushkar, Khodzhaeva & S.V. Krylova (1)

Pseudoloma J.L. Matthews, A.M.V. Br., K. Larison, J.K. Bishop-Stewart, P. Rogers & M.L. Kent (6)

Myosporidae G.D. Stentiford, K.S. Bateman, H.J. Small, J. Moss, Shields, Reece & I. Tuck
Myospora G.D. Stentiford, K.S. Bateman, H.J. Small, J. Moss, Shields, Reece & I. Tuck (1)

Pereziidae Loubes, Maurand, Comps & Campillo emend. Y.S. Tokarev & I.V. Issi
Ameson V. Sprague (2)
Nadelspora Olson, Tiekotter & Reno (1)
Perezia L. Léger & Duboscq (12)
Pernicivesicula E.K.C. Bylén & J.I.R. Larss. (1)

Pleistophoridae Doflein emend. Y.S. Tokarev & I.V. Issi
Dasyatispora A. Diamant, Goren, M.B. Yokeş, B.S. Galil, Y. Klopman, D. Huchon, A. Szitenberg & S.Ü. Karhan (1)
Heterosporis G. Schub. (4)
Myosporidium E. Baquero, M. Rubio, I.N.S. Moura, N.J. Pieniazek & R. Jordana (1)
Ovipleistophora Pekkar., Lom & F. Nilsen (2)
Pleistophora Gurley (10)
Trachipleistophora W.S. Hollister, E.U. Canning, E. Weidner, A.S. Field, J. Kench & D.J. Marriott (4)
Vavraia J. Weiser (10)

Spragueidae Weissenberg emend. Y.S. Tokarev & I.V. Issi
Apotaspora Sokolova & R.M. Overstreet (1)
Inodosporus R.M. Overstreet & E. Weidner (2)
Kabatana Lom, Dyková & Tonguthai (5)
Microgemma J.R. Ralphs & R.A. Matthews (6)
Potaspora G. Casal, E. Matos, M.L. Teles-Grilo & C. Azevedo (3)
Pseudokabatana Xing H. Liu, G.D. Stentiford, V.N. Voronin, H. Sato, A.H. Li & Jin Y. Zhang (1)
Spraguea R. Weissenb. (2)
Tetramicra R.A. Matthews & A.B.F. Matthews (1)

Thelohaniidae Hazard & Oldacre emend. Y.S. Tokarev & I.V. Issi
Bohuslavia J.I.R. Larsson (1)
Chapmanium E.I. Hazard & Oldacre (4)
Coccospora R.R. Kudo (1)
Cucumispora M.O. Ovcharenko, K. Bącela-Spychalska, T. Wilkinson, J.E. Ironside, T. Rigaud & Wattier (2)
Hyperspora G.D. Stentiford, Ramilo, E. Abollo, R. Kerr, K.S. Bateman, Feist, D. Bass & A. Villalba (1)
Napamichum J.I.R. Larss. (3)
Octotetraspora I.V. Issi, Kadyrova, Pushkar, Khodzhaeva & S.V. Krylova (1)
Ormieresia C.P. Vivarès, Bouix & Manier (1)
Orthothelohania Codreanu & Codreanu-Balcescu (1)
Paradoxium G.D. Stentiford, S.H. Ross, R. Kerr, D. Bass & K.S. Bateman (1)
Pegmatheca E.I. Hazard & Oldacre (2)
Resiomeria J.I.R. Larss. (1)
Spherospora J.J. Garcia (1)
Systenostrema E.I. Hazard & Oldacre (5)

Thelohania Henneguy (50)
Unikaryonidae Sprague emend. Y.S. Tokarev & I.V. Issi
Canningia Weiser, Wegensteiner & Žižka (2)
Dictyocoela R.S. Terry, J.E. Sm., R.G. Sharpe, T. Rigaud, D. Littlew., J.E. Ironside, Rollinson, Bouchon, MacNeil, J.T.A. Dick & A.M. Dunn (8)
Larssoniella J. Weiser & L. David (2)
Unikaryon E.U. Canning, P.F. Lai & J.K. Lie (19)

Nosematida Labbe emend. Y.S. Tokarev & I.V. Issi
Encephalitozoonidae Voronin
Encephalitozoon C. Levaditi, Nicolau & R. Schoen (12)
Mockfordia Sokolova, I.M. Sokolov & C.E. Carlton (1)

Enterocytozoonidae Cali & Owen emend. Y.S. Tokarev & I.V. Issi
Desmozoon M.A. Freeman & C. Sommerville (3)
Enterocytozoon I. Desp., Le Charpentier, Galian, F. Bernard, Cochand-Priollet, Lavergne, Ravisse & Modigliani (2)
Enterospora Stentiford, K.S. Bateman, Longshaw & Feist (2)
Hepatospora G.D. Stentiford, K.S. Bateman, Dubuffet, E. Chambers & D.M. Stone (1)
Nucleospora R.P. Hedrick, J.M. Groff & D.V. Baxa (3)
Obruspora A. Diamant, S.B.S. Rothman, Goren, B.S. Galil, M.B. Yokeş, A. Szitenberg & D. Huchon (1)

Heterovesiculidae C.E. Lange, C.M. Macvean, J.E. Henry & D.A. Streett
Heterovesicula C.E. Lange, C.M. Macvean, J.E. Henry & D.A. Streett (1)

Mrazekiidae L. Léger & E. Hesse
Agmasoma E.I. Hazard & Oldacre (3)
Anostracospora N.O. Rode, J. Landes, E.J.P. Lievens, E. Flaven, A. Segard, R. Jabbour-Zahab, Michalakis, P. Agnew, C.P. Vivarès & T. Lenormand (1)
Euplotespora Fokin, Di Giuseppe, Erra & Dini (1)
Globosporidium Y. Yakovleva, Nassonova, N.A. Lebedeva, O. Lanzoni, G. Petroni, A. Potekhin & E. Sabaneyeva (5)
Hrabyeia Lom & Dyková (1)
Jirovecia J. Weiser (8)
Mrazekia L. Léger & E. Hesse (17)
Rectispora J.I.R. Larss. (1)

Nosematidae Y.S. Tokarev, Huang, Solter, Malysh, Becnel & Vossbrinck
Nosema Nägeli (20)
Vairimorpha B.M. Pilley (15)

Ordosporidae J.I.R. Larss., D. Ebert & Vávra
Ordospora J.I.R. Larss., D. Ebert & Vávra (2)

Microsporidia* families *incertae sedis
Abelsporidae C. Azevedo
Abelspora C. Azevedo (1)

Areosporiidae G.D. Stentiford, S. Bateman, Feist, S. Oyarzún, J.C. Uribe, Palacios Vargas & D.M. Stone
Areospora G.D. Stentiford, S. Bateman, Feist, S. Oyarzún, J.C. Uribe, M. Palacios & D.M. Stone (1)

Burenellidae Jouvenaz & E.I. Hazard
Burenella Jouvenaz & E.I. Hazard (1)
Pilosporella E.I. Hazard & Oldacre (2)
Tabanispora H.I. Bykova, Sokolova & I.V. Issi (2)

Cougourdellidae R.A. Poiss
Cougourdella E. Hesse (7)

Cylindrosporidae I.V. Issi & Voronin
Cylindrospora I.V. Issi & Voronin (2)

Duboscqiidae V. Sprague
Duboscqia C. Pérez (11)
Mitoplistophora Codreanu (1)
Pulicispora Vedmed, S.V. Krylova & I.V. Issi (1)
Tardivesicula J.I.R. Larss. & E.K.C. Bylén (1)
Trichoduboscqia L. Léger (1)

Golbergiidae I.V. Issi
Golbergia J. Weiser (1)
Krishtalia P.J. Kilochitskii (1)
Simuliospora Khodzhaeva, S.V. Krylova & I.V. Issi (2)

Microfilidae R. Sprague, J.J. Becnel & E.I. Hazard
Microfilum N. Faye, B.S. Toguebaye & Bouix (1)

Neonosemoidiidae N. Faye, B.S. Toguebaye & Bouix
Neonosemoides N. Faye & B.S. Toguebaye (4)

Pleistosporidiidae Codr.-Balc. & Codreanu
Pleistosporidium Codr.-Balc. & Codreanu (1)

Pseudopleistophoridae V. Spragu
Pseudopleistophora V. Sprague (1)
Steinhausia R. Sprague, Ormières & Manier (4)

Striatosporidae I.V. Issi & Voronin
Striatospora I.V. Issi & Voronin (1)
Toxospora Voronin (2)

Telomyxidae L. Léger & E. Hesse
Telomyxa L. Léger & E. Hesse (4)

Toxoglugeidae J.I.R. Larss.
Toxoglugea L. Léger & E. Hesse (15)

Tuzetiidae V. Sprague, Tuzet & Maurand
Nelliemelba J.I.R. Larss. (1)
Pankovaia A.V. Simakova, Y.S. Y.S. Tokarev & I.V. Issi (1)
Paratuzetia L.G. Poddubnaya, Y.S. Y.S. Tokarev & I.V. Issi (1)
Tuzetia Maurand, Fize, Fenwick & R. Michel (7)

Rozellomycota **orders** ***incertae sedis***
Paramicrosporidiales D. Corsaro
Paramicrosporidiaceae D. Corsaro
Paramicrosporidium D. Corsaro, J. Walochnik, D. Venditti, J. Steinmann, K.D. Müller & R. Michel (2)

Morellosporales D. Corsaro
Morellosporaceae D. Corsaro
Morellospora D. Corsaro, J. Walochnik, D. Venditti, B. Hauröder & R. Michel (1)

Mitosporidiaceae D. Corsaro
Mitosporidium K.L. Haag, T.Y. James, Pombert, R. Larsson, T.M.M. Schaer, D. Refardt & D. Ebert (1)

Nucleophagales D. Corsaro
Nucleophagaceae D. Corsaro
Nucleophaga Dangeard 1895, emend. D. Corsaro, J. Walochnik, D. Venditti, K.-D. Müller, B. Hauröder & R. Michel 2014 (8)

Microsporidia **genera** ***incertae sedis***
Auraspora J. Weiser & K. Purrini (1)
Baculea Loubès & Akbarieh (1)
Burkea V. Sprague (2)
Chytridioides Trégouboff (1)
Ciliatosporidium I. Foissner & W. Foissner (1)
Cryptosporina E.I. Hazard & Oldacre (1)
Evlachovaia Voronin (1)
Geusia V.H. Rühl & H. Korn (1)
Gurleyides Voronin (1)
Hamiltosporidium K.L. Haag, J.I.R. Larss., D. Refardt & D. Ebert (2)
Hirsutosporos B.S. Batson (1)
Holobispora Voronin (1)
Issia Weiser (3)
Kinorhynchospora Adrianov & Rybakov (1)
Mariona Stempell (1)
Merocinta Pell & Canning (1)
Myxocystis Mrazek (1)
Nematocenator Sapir, Dillman, Connon, Grupe, Ingels, Mundo-Ocampo, Levin, Bladwin, Orphan & Sternberg (1)
Nosemoides Vinckier (5)
Pyrotheca Hesse (4)
Sheriffia Larsson (1)
Spiroglugea Léger & Hesse (1)
Stempellia Léger & Hesse (19)

Wittmannia Czaker (1)
[#]*Microsporidium* is a collective genus which incorporates species with uncertain genus allocation

SANCHYTRIOMYCOTA Galindo, López-García, Torruella, Karpov & Moreira
Sanchytriomycetes Tedersoo, Sanchez-Ramirez, Kõljalg, Bahram, M. Döring, Schigel, T.W. May, M. Ryberg & Abarenkov
Sanchytriales Tedersoo, Sanchez-Ramirez, Kõljalg, Bahram, M. Döring, Schigel, T.W. May, M. Ryberg & Abarenkov
Sanchytriaceae Karpov & Aleoshin
Amoeboradix Karpov, López-García, Mamkaeva & Moreira (1)
Sanchytrium Karpov & Aleoshin (1)

ZOOPAGOMYCOTA Gryganskyi, M.E. Sm., Spatafora & Stajich
Zoopagomycetes Doweld
Zoopagales Bessey ex R.K. Benj.
Cochlonemataceae Dudd.
Amoebophilus P.A. Dang. (4)
Aplectosoma Drechsler (1)
Bdellospora Drechsler (1)
Cochlonema Drechsler (11)
Endocochlus Drechsler (4)
Euryancale Drechsler (4)

Helicocephalidaceae Boedijn
Brachymyces G.L. Barron (1)
Helicocephalum Thaxt. (6)
Rhopalomyces Corda (11)
Verrucocephalum Degawa (1)

Piptocephalidaceae J. Schröt.
Kuzuhaea R.K. Benj. (1)
Piptocephalis de Bary (ca. 25)
Syncephalis Tiegh. & G. Le Monn. (ca. 55)

Sigmoideomycetaceae Benny, R.K. Benj. & P.M. Kirk
Reticulocephalis Benny, R.K. Benj. & P.M. Kirk (2)
Sigmoideomyces Thaxt. (1)
Sphondylocephalum Stalpers (1)
Thamnocephalis Blakeslee (3)

Zoopagaceae Drechsler
Acaulopage Drechsler (27)
Cystopage Drechsler (9)
Lecophagus M.W. Dick (2)
Stylopage Drechsler (17)
Tentaculophagus Doweld (1)
Zoopage Drechsler (11)
Zoophagus Sommerst. (4)

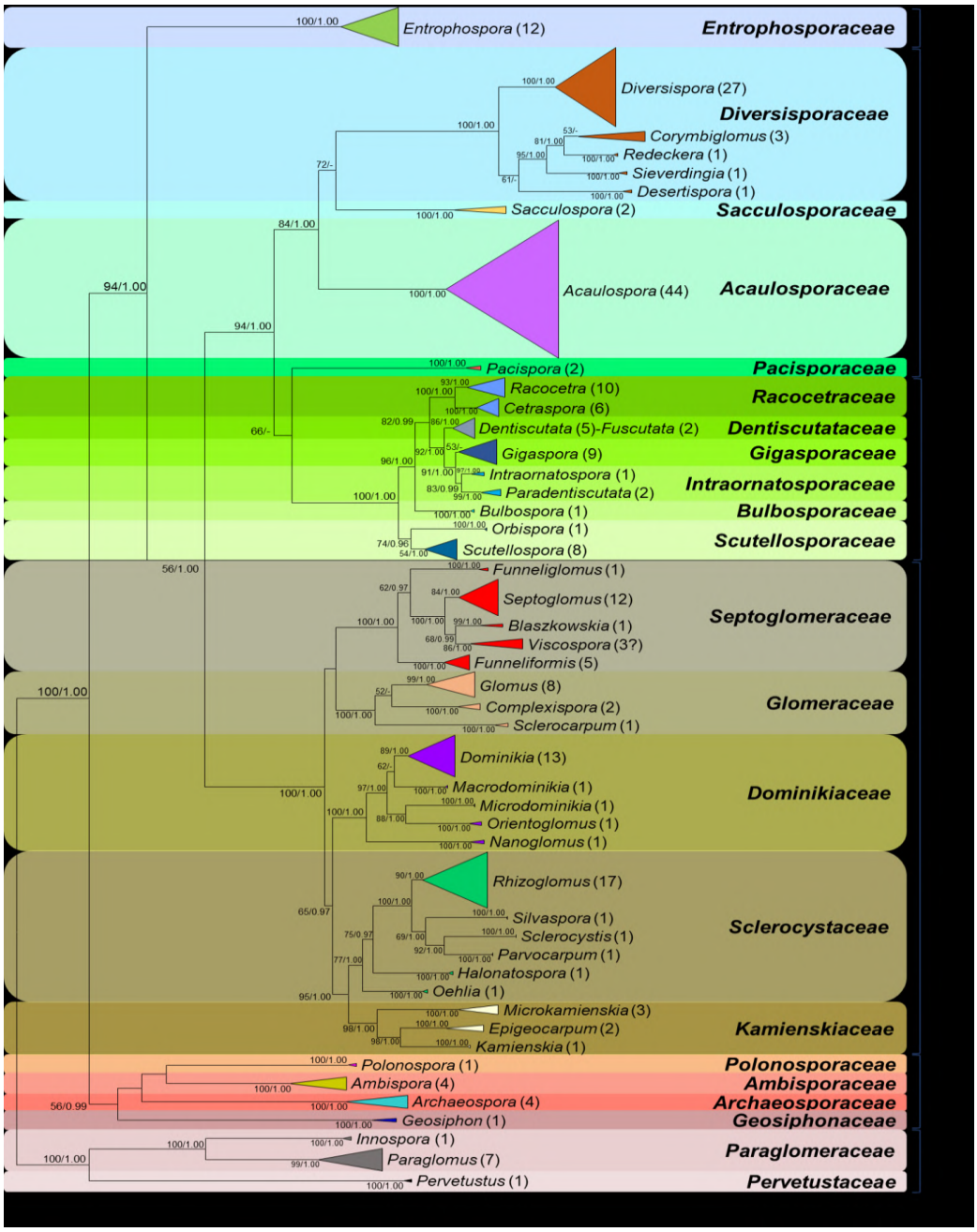


Figure 4 – Phylogram generated from maximum likelihood and Bayesian inference analyses displaying the relationships among the 22 families described in *Glomeromycota*, including the newly introduced family *Bulbosporaceae* (*). The order *Paraglomerales* was used to root the tree. Standard ML bootstrap support values and posterior probabilities greater than 50% and 0.97, respectively, are indicated above or below the nodes. Clades were collapsed at genus rank for clear visualisation of the tree. For each genus, the number of species represented is indicated in brackets. Families are shown in coloured boxes. The bar indicates 0.2 expected change per site per branch.

Validation of orders

In this section, we validate orders and higher taxa that are regarded as invalid. However, validation of families and genera is included in the section "families of non-dikaryan fungi".

Densosporales Tedersoo ex Madrid, P.M. Kirk & Wijayaw.

Index Fungorum Identifier IF903313

= *Densosporales* Tedersoo, in Tedersoo, Magurno, Alkahtani & Mikryukov, MycoKeys 107: 308 (2024) **Nom. inval.,** Art. 38.1(a) (Shenzhen); Index Fungorum Identifier 853690

Chlamydospores one-celled, (sub)globose to ellipsoidal, produced directly from hyphae or inside sporophores. Sporophores, when produced, epigeous or hypogeous, usually (sub)globose, sometimes pubescent due to the presence of superficial hyphal clusters, with or without a peridium. Hyphae sometimes producing appressoria and arbuscules involved in symbiotic relationships with plants (McGee 1996, Yamamoto et al. 2015, Walker et al. 2018, Tedersoo et al. 2024).

Type family – *Densosporaceae* Desirò, M.E. Sm., Bidart., Trappe & Bonito ex Madrid, P.M. Kirk & Wijayaw.

Type genus – *Densospora* McGee Aust. Syst. Bot. 9(3): 330 (1996)

Families of non-dikaryan fungi

In this section, we list the families according to the above outline. Each family is provided with descriptions, illustrations, genera included and notes for the type genus.

APHELIDIOMYCOTA Tedersoo et al.
Aphelidiomycetes Tedersoo et al.
Aphelidiales Tedersoo et al.
Aphelidiaceae Tedersoo, Sánchez-Ramírez, Kõljalg, Bahram, Döring, Schigel, T. May, M. Ryberg & Abarenkov, Fungal Diversity 90: 147 (2018)
Index Fungorum Identifier 553993

Amoeboid endobiotic parasitoids 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, which 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 present (Karpov et al. 2014a).

Family type – *Aphelidium* Zopf

Ecology & life modes – Intracellular parasitoids of algae in fresh water and marine.

Notes – The aphelids are a small group of intracellular parasitoids of algae, including three freshwater genera, *Aphelidium* (Zopf) Gromov, *Amoeboaphelidium* Scherff., *Paraphelidium* Karpov, Tcvetkova, Mamkaeva, Torruella, Timpano, Moreira, Mamanazarova & López-García (Karpov et al. 2017b), and two marine genera, *Pseudaphelidium* Schweikert & Schnepf, *Protaphelidium* Seliuk & Karpov (Gromov 2000, Karpov et al. 2017a, Seliuk & Karpov 2024).

Only the asexual morph of the life cycle is known for aphelids: amoeboid zoospore attaches to the host algae, involves a flagellum and encysts. A cyst germinates and penetrates the host cell wall with an infection tube and uses the latter to inject the cyst contents into the host. The parasitoid becomes the intracellular phagotrophic amoeba, which engulfs the host cytoplasm with pseudopodia and forms a central digestive vacuole containing a red residual body. The parasitoid grows to form an endobiotic multinucleate plasmodium with the residual body in a large central vacuole while it consumes the cytoplasm of the host cell. The mature plasmodium then divides into several uninucleate cells. After maturation, the amoeboid zoospores release the empty host cell through the hole made previously by the infection tube and infect other algae.

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

A new genus and species *Protaphelidium rhizoclonii* were described as the marine parasite of green algae (Seliuk & Karpov 2024). Annotated genomes of three (Mikhailov et al. 2022a) and transcriptomes of four aphelid species (Torruella et al. 2018, Galindo et al. 2023) have been received, and the multigene phylogenies unambiguously showed a sister position of the *Aphelida* and *Fungi*. Genomic analyses of *Holozoa* and *Holomycota* revealed more differences between *Fungi* and *Aphelidiomycota* in the genes encoding proteins involved in osmotrophy and

phagotrophy, and in the development of multicellularity in *Fungi* and *Metazoa* (Mikhailov et al. 2022a, Pozdnyakov et al. 2023, 2024).

Aphelidium Zopf, Encyklop. Naturwiss. (Breslae): 30 (1885)
Fig. 5
Index Fungorum Identifier 13159

Parasitoids of various species of algae. Forms rounded to oval zoospores, able to produce pseudopodia, with one posteriorly directed flagellum and one or several lipid globules (refractile granules). Vegetative development as described for the class. Resting spores rounded to oval with a thick smooth cell wall, and without an excretory body, which is ejected from the spore before spore wall synthesis.

Type species – *Aphelidium deformans* Zopf, Encyklop. Naturwiss. (Breslae): 30 (1885)

Notes – *Aphelidium* was described as *Aphelidium deformans* parasitizing green algae *Coleochaete soluta* and causing a deformation of the host cell (Zopf 1885). Later, Bruyne (1890) described *Aph. lacerans,* which has zoospores with an anterior flagellum and grains of chlorophyll, thus cannot be a parasitic opisthokont, and become a doubtful species (Gromov 2000, Letcher & Powell 2019). Several species of *Aphelidium* were described by Scherffel (1925), *viz.*, *Aph. melosirae, Aph. tribonematis* and *Aph. chaetophorae*. The latter species is similar to *Aph. deformans,* however, neither the formation of a cyst nor penetration of the parasite into the host cell and the resting spores were observed. Subsequently, they observed the parasite plasmodium within the host, with multiple digestive vacuoles (Letcher & Powell 2019). We agree with the opinion of Letcher & Powell (2019) that *Aph. chaetophorae* is not a doubtful species as Gromov (2000) considered. It is a typical aphelid similar to *Aph. deformans* (the type species) accordingly zoospore dimensions and this infection also cause the host deformation (cell enlargement). It might be a younger synonym of *Aph. deformans*, but in the absence of essential information in *Aph. chaetophorae* description, we have to leave *Aph. chaetophorae* as valid.

Fott (1957) described *Aph. chlorococcorum*, but Gromov & Mamkaeva (1970) found bigger zoospores studying similar species and established a new form *Aph. chlorococcorum* f. *majus.* Consequently, Fott's species became *Aph. chlorococcorum* f. *chlorococcorum* (Letcher & Powell 2019).

Electron microscopic studies (Schnepf et al. 1971, Gromov & Mamkaeva 1975) revealed high similarity of *Aphelidium* spp. in the general structure of zoospores, cysts, young trophonts, and multinuclear plasmodium. Close attention to zoospore flagellar apparatus structure uncovered some interspecific differences in the root structure of kinetosome and centriole/kinetosome orientation (Karpov et al. 2014c, 2016a, 2019a, Letcher et al. 2017b, Seto et al. 2020a, 2022). Molecular phylogenetic investigations based on 18S rRNA gene sequences combined with light and electron microscopic studies showed a new species: *Aph. occidentale* (Letcher et al. 2017b), *Aph. arduennense* (Tcvetkova et al. 2019), *Aph. insulamus* (Karpov et al. 2020), *Aph. collabens* (Seto et al. 2020a), *Aph. parallelum* (Seto et al. 2022).

Other genera in *Aphelidiaceae*

Amoeboaphelidium Scherff., Arch. Protistenk. 52: 52 (1925)
Index Fungorum Identifier 20022; five epithets in Index Fungorum (2025); sequence data are available in GenBank

Type species – *Amoeboaphelidium achnanthis* Scherff.

Paraphelidium Karpov, Moreira & López-García, Journal of Eukaryotic Microbiology. 64(2): 204-212 (2017)
Index Fungorum Identifier 92121; two epithets in Index Fungorum (2025); sequence data are available in GenBank

Type species – *Paraphelidium tribonematis* Karpov, Moreira & Lopez-Garcia

Protaphelidium Seliuk & Karpov, Mycol. Prog. 23(no. 57): 8 (2024)
Index Fungorum Identifier: 902058; one epithet in Index Fungorum (2025); sequence data available in GenBank

Type species – *Protaphelidium rhizoclonii* Seliuk & Karpov

Pseudaphelidium Schweik. & Schnepf, Arch. Protistenk. 147(1): 11-17 (1996)
Index Fungorum Identifier 560205; one epithet in Index Fungorum (2025); no sequence data in GenBank

Type species – *Pseudaphelidium drebesii* Schweik. & Schnepf

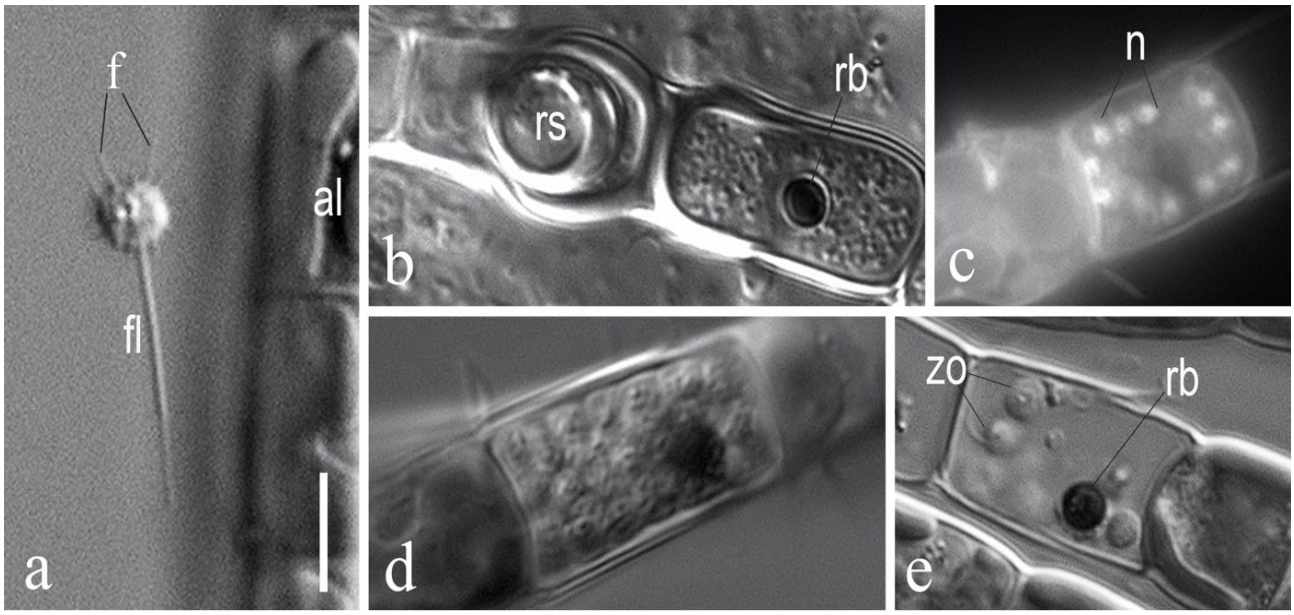


Figure 5 – Light microscopic images of the life cycle of *Aphelidium melosirae*. a crawling zoospore in the alga (al) vicinity, with anterior filopodia (f) and posterior flagellum (fl). b resting spore (rs) and plasmodium with residual body (rb) in the host cell. c DAPI stained nuclei in plasmodium. d zoospores just appeared from mature plasmodium. e host cell with several zoospores (zo) and residual body (rb) left. Scale bars: a-e 5 µm.

BASIDIOBOLOMYCOTA Doweld
Basidiobolomycetes Doweld
Basidiobolales Jacz. & P.A. Jacz
Basidiobolaceae Engl. & E. Gilg, Syllabus, Edn 9 & 10 (Berlin): 45 (1924)
Index Fungorum Identifier 80514

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 tears from 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. The formation of a subsporangial vesicle, sporangiolar dehiscence resulting from rupture of the subsporangial vesicle, the presence of multispored sporangiola (and, in some species, vegetative cells) due to internal protoplast production, the formation of accessory cells on gametangia, the uninucleate nature of all cells, and the relatively large size of the nucleus which contains a nucleolus but no heterochromatin (Eidam 1886, Benjamin 1979, Humber 1981, Ben-Ze'ev & Kenneth 1982a, b).

Family Type – *Basidiobolus* Eidam

Ecology & life modes – Saprophytic in the intestines of vertebrates and amphibians (Nickerson et al. 1971, Coremans-Pelseneer 1973, Gugnani & Okafor 1980, Okafor et al. 1984, Dykstra & Bradley-Kerr 1994), in the intestinal contents of bat (Chaturvedi et al. 1984), kangaroos (Speare & Thomas 1985), spiders (Dykstra & Bradley-Kerr 1994), compost heaps, decaying plant material and soil (Drechsler 1956, 1958, Clark 1968), Pathogenic (Gugnani1999, Mendiratta et al. 2012, Hamid et al. 2015, Mousavi et al. 2021)

Notes – Jensen et al. (1998) sequenced the nuclear small subunit of ribosomal DNA (18S rDNA) from seven species in the *Entomophthorales*, and excluding *Basidiobolus ranarum*, they formed a monophyletic group. Additionally, they discovered that *B. ranarum* was more closely related to chytrids from the *Chytridiales* and *Neocallimasticales* rather than the *Entomophthorales*. According to a phylogenetic analysis of *Zygomycota* using combined 18S, 28S, and 5.8S rDNA by White et al. (2006), *Basidiobolus* was found to be placed within the *Zygomycota*, but not within the *Entomophthorales* as previously shown (Hawksworth et al. 1995). White et al (2006) conducted a phylogenetic analysis of *Zygomycota* using 18S+28S+5.8S rDNA, and found that *Basidiobolus* was within the *Zygomycota* but not within the *Entomophthorales* as in Hawksworth et al. (1995). Using molecular data, Benny et al. (2012) developed a classification system for *Basidiobolaceae*, placing it as a member of the *Entomophthorales* within the "*Zygomycota*".

Basidiobolus Eidam, Krypt.-Fl. Schlesien (Breslau) 3.1(9–16): 225. 1886;
Fig. 6
Index Fungorum Identifier 20068

Conidial structures are thread-like, about 15 μm wide, strongly heliotropic, undivided, and swollen at the upper end into an elliptical club approximately 60 μm long and 40 μm wide. Conidia are spherical or short-ellipsoid, up to 48 μm long and 46 μm wide, colourless, filled with uniform cytoplasm, and lacking oil droplets. Chlamydospores are spherical or elliptical, 23–43 μm in diameter, with a thick, multi-layered, yellow-brown or colourless membrane of wavy surface, sometimes (in cultures in late autumn) covered with a thick, dark brown, brittle crust, and up to 50 μm in diameter. The chlamydospores are crowned with a fairly long, pointed beak formed from two closely adjacent hyphal ends; each tip of the beak is divided by a cross-wall. No sexual morphs were observed (Saccardo 1886).

Type species – *Basidiobolus ranarum* Eidam 1886

Other genera in *Basidiobolaceae*
Schizangiella J. Dwyer, B. Burwell, Humber, C. Mcleod, M. Fleetwood & T. Johnson bis, Veter. Pathol. 43(5): 819 (2006)
Index Fungorum Identifier 542002; Index Fungorum (2025) lists one epithet and Species Fungorum (2025) lists one species

Type species – *Schizangiella serpentis* J. Dwyer, B. Burwell, Humber, C. Mcleod, M. Fleetwood & T. Johnson bis (2006)

BLASTOCLADIOMYCOTA T.Y. James
Blastocladiomycetes Doweld
Blastocladiales H.E. Petersen
Blastocladiaceae Petersen, Botanisk Tidsskrift 29: 357 (1909)
Index Fungorum Identifier 80521

Thalli vary markedly in size and extent or degrees of complexity, with some monocentric and chytrid-like, usually a non-septate or septate stalked reproductive structure and radiating or basal branched rhizoids; while in others larger, more extended and distally branched as in *Allomyces* and *Blastocladia*, bearing reproductive structures, typically with a basal cell anchored to the substratum with branched rhizoids at its proximal end. Zoospores produced in thin-walled zoosporangia, emerging through one or more exit papilla or pores at times, either in an evanescent vesicle after

the deliquescence or individually. The resistant sporangia or resting spores are borne in thin-walled container cells, punctate, usually brown with thick, smooth or variously ornamented, distinctly pitted walls; germination by wall cracking open. Separate, equal or unequal gametophytic and sporophytic phases occur. Sexuality may be pronounced or lacking and may be anisogamous or isogamous. Fusion occurs between pairs of iso- or aniso-zoospores to form a biflagellate zygote; upon germination, it gives rise to the sporophyte. The sporophyte is diploid throughout, and meiosis occurs at the time of resistant sporangia germination. The resistant sporangia zoospores are haploid and give rise to gametophytes (Sparrow 1960, Emerson & Robertson 1974).

Family type – *Blastocladia* P.F. Reinsch

Ecology & life modes – This family is composed entirely of saprophytes in the aquatic and terrestrial ecosystem on a wide variety of animal and plant debris (Sparrow 1960). Representatives within the family may be monoecious or dioecious with a life history ranging from Brachyallomyces, Cystogenes or Euallomyces type (Emerson 1938, 1941).

Notes – This family is composed of three saprophytic genera living in water and soil on a variety of decaying animal and plant matter, with *Blastocladia* as the type genus. *Blastocladiaceae* currently includes three genera: *Allomyces*, *Blastocladia*, and *Blastocladiopsis* (Wijayawardene et al. 2018). It is the largest family in *Blastocladiales* with approximately 36 species (Calabon et al. 2022). The motile zoospore ultrastructure characters from this family were extensively studied by numerous researchers (Reichle & Fuller 1967, Fuller & Olson 1971, Robertson 1972, Olson 1973, Lingle & Barstow 1983, Aliaga & Pommerville 1990). Porter et al. (2011) and James et al. (2014) showed that the members of this family are polyphyletic and thus need revision.

Blastocladia Reinsch, Jahrbücher für Wissenschaftliche Botanik 11(2): 291 (1877).
Index Fungorum Identifier 20077

Thallus large tree-like, consisting of often irregular, cylindrical, short or long, more or less elongated, swollen trunk-like basal cell or central axis, bearing short or long branches at its apex on which reproductive organs borne, delimited by septa and the whole attached to the substratum through a system of branched rhizoids. The branches arising from a simple, lobed or branched basal cell, often with secondary axes; distal part expanded, short or clavate, slightly tapering, lacking pseudosepta, and not definitely constricted like in *Allomyces*, arranged in dichotomous to subdichotomous, or sympodial manner. In addition to the reproductive organs, simple, and branched sterile setae, generally bulbous at the base, may be present among the zoosporangia and resting spores. Zoosporangia irregularly clustered on the apical region or sympodially arranged, elongated, thin-walled, smooth, sessile with a broad, truncate base and a single apical exit papilla, often with an inwardly projecting refractive peglike plug; sometimes deciduous, disappearing after discharge, leaving a scar at the point of attachment or sometimes persistent. Zoospores posteriorly uniflagellate, with a clearly visible subtriangular nuclear cap, emerging at times in an evanescent vesicle after the deliquescence or individually. Resistant zoosporangia or resting bodies thick-walled, minutely pitted or punctate, brown, predominantly ovoid, ellipsoid, fusiform, spherical to subspherical or broadly clavate with a rounded or beaked apex and narrowly or broadly truncate base, persistent or deciduous, terminal, filling the thin-walled case in which it is borne on the same or different thalli. Gametophyte not observed. Sexual reproduction unknown (Sparrow 1960).

Type species – *Blastocladia pringsheimii* P.F. Reinsch [as "pringsheimi"], Jahrbücher für Wissenschaftliche Botanik 11(2): 367 (1877).

Notes – *Blastocladia* is the earliest known and established genus from which the order derives its name. According to Sparrow (1960), the genus differs from the other genera of its family in zoosporangia bearing an apical papilla or exit pore with a downwardly projecting peg, thallus with distally expanded lobes or short branches or without branches, and the absence of a sexual stage in the life cycle (Sparrow 1960). *Blastocladia* contain approximately twenty *saprophytic* species in water and soil habitats on a large variety of submerged plant substrates and found growing over other zoosporic fungi, specifically *Gonapodya*, in the form of pustules or crisp white tufts (Sparrow 1960, Wijayawardene et al. 2018). Representatives of this genus are cosmopolitan

and composed entirely of obligate fermenters that thrive in stagnant water with lower dissolved oxygen levels, functioning as facultative anaerobes (Whisler 1987, Gleason et al. 2002); less readily cultured than *Allomyces* and need B group vitamins for growth under laboratory conditions (Sparrow 1960, Emerson & Natvig 1981). Zoospore ultrastructural character examined by Lingle and Barstow (1983) in the anaerobic genus *Blastocladia*, revealed that the internal contents of the spores contain sparse lipid globules and mitochondria, with the complete absence of the backing membrane and microbodies. In addition, the study also provided strong evidence for the presence of abundant stored visible glycogen granules in the zoospores of blastoclad anaerobic members (Lingle & Barstow 1983). Further, in contrast to obligatory anaerobic rumen fungi, it encompasses mitochondria and lacks hydrogenosomes (Lingle & Barstow 1983, Gleason et al. 2002). According to the molecular phylogeny of Porter et al. (2011), representatives of *Blastocladia* form a monophyletic sister group to the clade encompassing *Allomyces* and a well-supported clade in *Blastocladiaceae*. Cultures and sequences available (Porter et al. 2011).

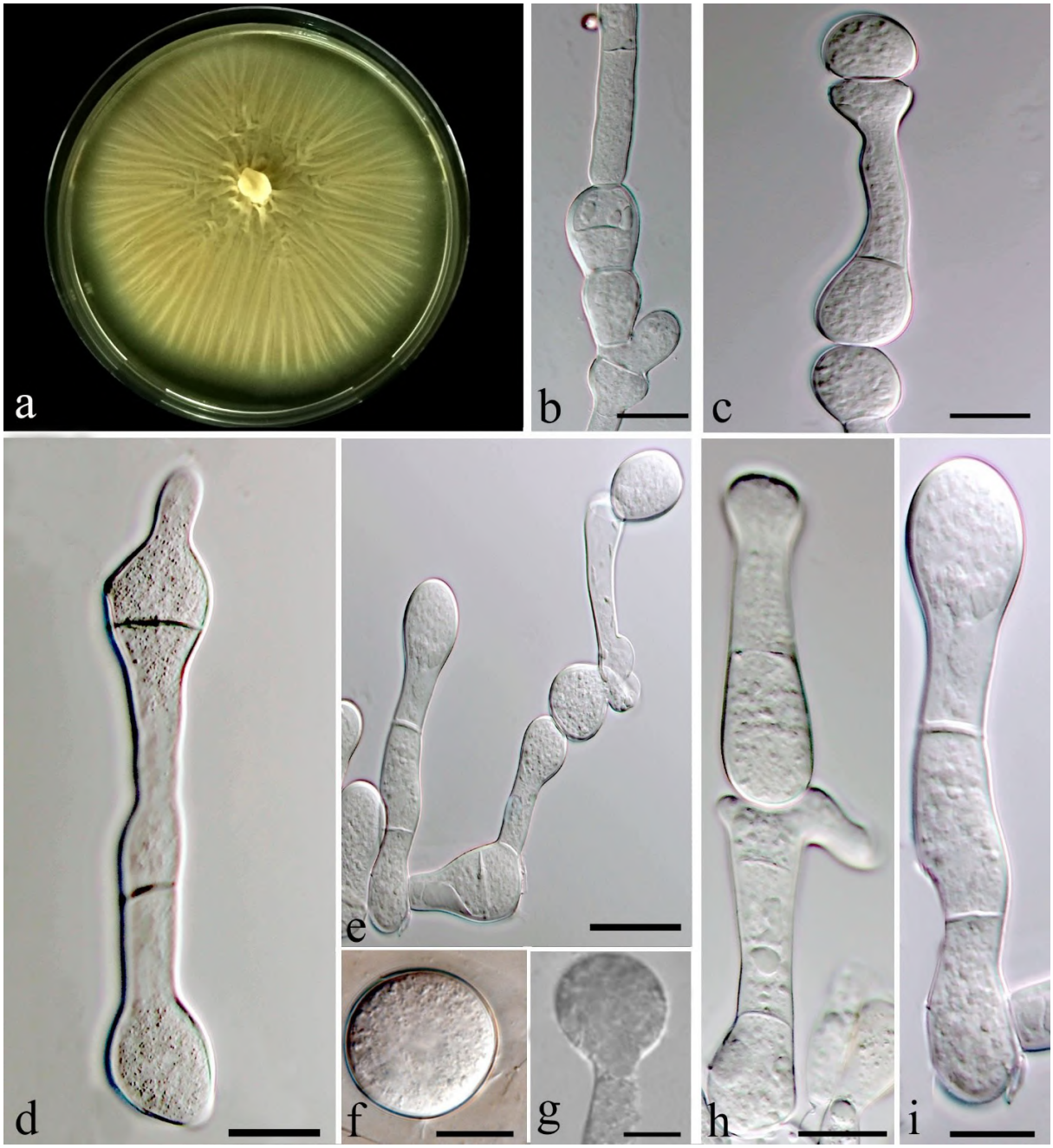


Figure 6 – *Basidiobolus haptosporus*. a Colony after 7 days of incubation at 28°C on MEA front. b-i hyphal elements with spore cells. Scale bars: b-i = 10 µm.

Other genera in *Blastocladiaceae*

Allomyces E.J. Butler, Ann. Bot., Lond. 25: 1027 (1911); Fig. 7

Index Fungorum Identifier 20017; Index Fungorum (2025) lists 23 epithets however, Species Fungorum (2025) accepted only ten

Type species – *Allomyces arbusculus* E.J. Butler 1911

Blastocladiopsis Sparrow, J. Wash. Acad. Sci. 40: 52 (1950)

Index Fungorum Identifier 20080; two epithets are listed in Index Fungorum (2025) and both are accepted in Species Fungorum (2013*).*

Type species – *Blastocladiopsis parva* (Whiffen) Sparrow 1950

Catenariaceae Couch, Mycologia 37(2): 187 (1945)

Index Fungorum Identifier 80558

Thallus predominantly polycentric, eucarpic, extra-intramatrical. Rhizomycelium extensive, composed of tubular or cylindrical catenulate swellings, unbranched or branched, bearing numerous rhizoids along its length, with sparingly developed septa/cross walls delimiting reproductive structures and sterile isthmi. Zoosporangia intercalary, formed from aforementioned swellings, arranged in a linear series in the rhizomycelium, separated by sterile isthmi, spherical or oval, occasionally irregular, smooth-walled, variable in size, dehiscing by the development of short or long exit papillae or release tube; formed as local enlargements in the rhizomycelium filaments and separated by short or long, narrow, rarely septate or non-septate isthmi. Zoospores are posteriorly uniflagellate, with a hyaline, clearly visible, distinctive nuclear cap; germinating directly to produce a new thallus (asexual plants) or encysting; the cyst serves as a gametangium discharging to release four uniflagellate isogamous gametes, fusing in pairs to produce a biflagellate zygote, which reestablishes the sporophytic thallus. Resting spores are sometimes formed in place of zoosporangia through enlargements in the filaments, connected by isthmi, usually, the content contracts and becomes enveloped by a pale brown, thick wall, which may be smooth or minutely pitted (Sparrow 1960, Karling 1977).

Family type – *Catenaria* Sorokīn, Revue mycologique (Toulouse) 11: 139 (1889); Fig. 8

Ecology & life modes – *Catenariaceae* is a ubiquitous family and contains many parasites of various soil-inhabiting small invertebrates and fungi. They are also saprobic on a variety of plant and animal substrates in water-logged soil or water. This family also includes two fungicolous (biotrophic) blastocladialean fungi, *Catenaria anguillulae* and *C. allomyci* (Sun et al. 2019a). Both representatives were reported as endobiotic fungal parasites of species associated with *Allomyces* or *Blastocladiella* in aquatic or terrestrial ecosystems (Couch 1945), however, can parasitize any saprolegnialean hosts under *in vitro* conditions (Whipps 1997).

Notes – *Catenariaceae* differs from *Blastocladiaceae* in having catenulate (chain-like) rhizomycelium. The *Catenariaceae* includes three genera: *Catenaria*, *Catenophlyctis*, and *Nematoceromyces* (Doweld 2014f, Wijayawardene et al. 2018). Several studies have described the ultrastructural organization of the zoospores of different taxa from this family and presented several new observations on their side body complex organization (Chong & Barr 1974, Olson & Reichle 1978, Olson et al. 1978, Lange & Olson 1979). DNA sequence-based phylogenetic studies have shed light on establishing the species boundaries and relationships within the family (James et al. 2006a, Porter et al. 2011). Molecular phylogeny studies suggested that representatives of the *Catenariaceae* group form a well-supported clade corresponding to *lastocladiella*, while representatives of *Allomyces*, *Blastocladia* and *Microallomyces* form a clade with representatives of *Blastocladiaceae* (Porter et al. 2011).

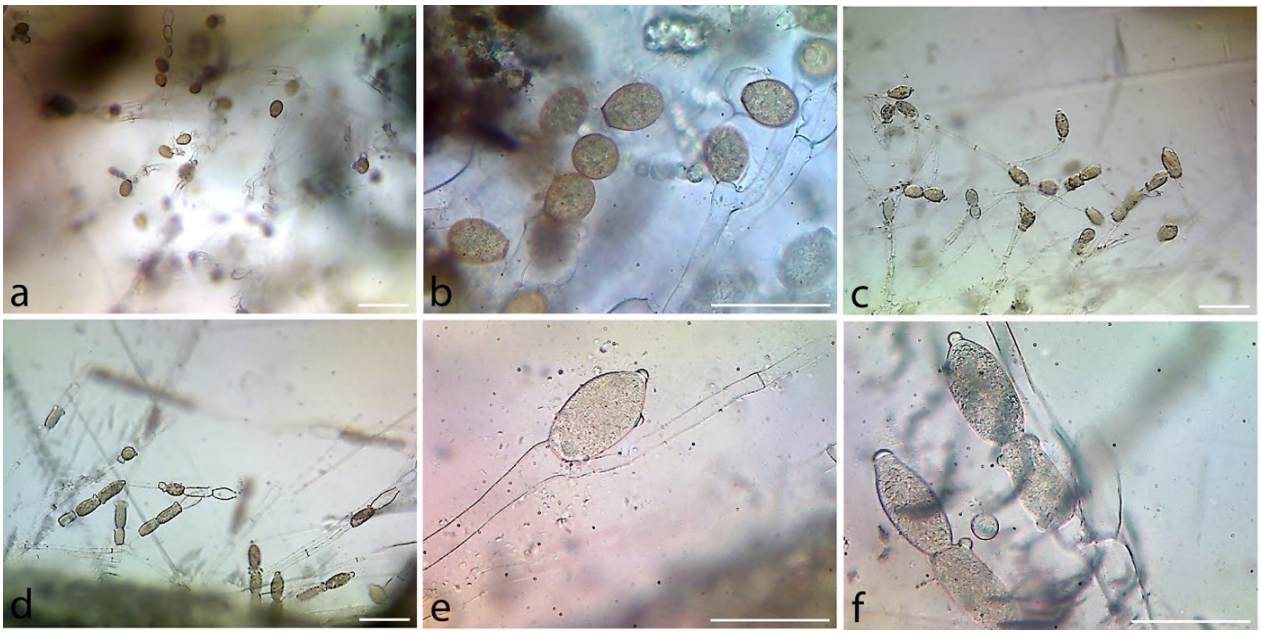


Figure 7 – Microscopic features associated with *Allomyces* species. **a, b** Mature thallus of *Allomyces neomoniliformis* showing septate vegetative hyphae and numerous brown, thick-walled resistant sporangia/resting spores. **c** Developed thallus of *Allomyces moniliformis* **d** Young and empty zoosporangia of *Allomyces moniliformis* in chains **e, f** Septate vegetative hyphae of *Allomyces moniliformis* showing thin-walled zoosporangia with various sites of exit papillae/pores. Scale bars: **a, c, d** = 100 µm; **b, e, f** = 50 µm.

Catenaria Sorokīn, Annales des Sciences Naturelles; Botanique, sér. VI, 4: 67 (1876).
Index Fungorum Identifier 213424

Eucarpic, predominantly polycentric, endobiotic, intramatrical, branched or unbranched, septate thallus with septa or cross walls delimiting the reproductive structures (zoosporangia and resistance sporangia) or short sterile isthmuses at more or less regular intervals. Rhizomycelium branched, extensive. Zoosporangia variable in shape, spherical, or oval, occasionally irregular or spindle shaped, often intercalary, arranged in a linear series in the rhizomycelium (catenulated arrangement), typically separated from each other by alternating sterile isthmuses delimited through cross walls or septa; smooth walled, hyaline; usually with a single long curved or irregular tapering release/discharge tube, variable in size, help in the release of posteriorly uniflagellate zoospores with numerous globules fully formed within the zoosporangia. Resting spores or resistance sporangia borne like the zoosporangia, thick-walled, upon germination can give rise to either uniflagellate zoospores which directly establish the new asexual plants or encyst to represent the gametophytic thallus that function as gametangia, which produce posteriorly uniflagellate isogametes (haploid) that fuse in pairs forming biflagellate zygotes to reestablish the sporophytic thalli (Sparrow 1960, Milanez et al. 2003).

Type species – *Catenaria anguillulae* Sorokīn, Annales des Sciences Naturelles; Botanique, sér. VI, 4: 67 (1876); Fig. 8

Notes – The presence of variable-shaped zoosporangia arranged in a series linear in the rhizomycelium with a long exit tube and blastocladiaceous zoospores with numerous globules readily serve as identifying unique characters for the genus (Sparrow 1960, Milanez et al. 2003). Several *Catenaria* spp. are common parasites or saprobes on amphibian eggs, small or microscopic animals like nematodes, rotifers, mites, liver flukes, flies and in other *Chytridiomycetes* and *Blastocladiomycetes*. In addition, they are saprobes in water algae and plant debris in freshwater or terrestrial ecosystems throughout the world (Sparrow 1960, Gleason et al. 2010, James et al. 2014, Powell 2017). One estuarine ecotype of *Catenaria* was also reported from marine ecosystems in New Zealand (Ulken 1977). Like the species of *Allomyces*, sexual reproduction also occurs in

certain species of *Catenaria* through the fusion of posteriorly uniflagellate isogamous gametes. This mode of the life cycle is known as cystogenes (with the dominant sporophytic stage and the restricted gametophyte stage represented by cysts and gametes). However, in some species, such as *Catenaria anguillulae*, the Brachyallomyces type of life cycle (no fusion of gametes) is also reported (Olson & Reichle 1978).

Other genera in *Catenariaceae*

Catenophlyctis Karling, American Journal of Botany, 52: 133–138 (1965)
Index Fungorum Identifier 20108; four epithets are listed in Index Fungorum (2025), however, only three species are accepted in Species Fungorum (2025)

Type species – *Catenophlyctis variabilis* (Karling) Karling 1965

Nematoceromyces Doweld, Index Fungorum 48: 1 (2014)
Index Fungorum Identifier 550338; three epithets are listed in Index Fungorum (2025), and all species are accepted in Species Fungorum (2025)

Type species – *Nematoceromyces spinosus* (W. Martin) Doweld 2013

Paraphysodermataceae Doweld, Index Fungorum 52:1 (2014)
Index Fungorum Identifier 550350

Thallus monocentric, eucarpic, epibiotic. Rhizoidal system arising from a single axis at the base of the zoosporangium, apophysis inside the host. Zoosporangium inoperculate, sessile, varying in shape and size, smooth and thin-walled. Zoospore (flagellated spore) stage is absent. Aplanospores (aflagellate spores) or pseudopodiate spores, with several minute refractive lipid globules or bodies coalescing upon encystment, exiting through the collapse in the zoosporangium wall, crawl about actively in an amoeboid fashion on the host cell surface before encysting; germinating endogenously. Resting spores or dormant sporangia epibiotic, similar to the zoosporangia in size and shape, developing to discharge aplanospores by the crack opening of the wall (James et al. 2011, Doweld 2014h).

Family type – *Paraphysoderma* Boussiba, Zarka & T.Y. James, Mycotaxon 118: 178 (2011).

Ecology & life modes – Generally parasitic on green algae in nature.

Notes – *Paraphysodermataceae* was introduced by Doweld (2014h) based on DNA sequence data (Hoffman et al. 2008, Porter et al. 2011) and zoospore ultrastructure studies (Letcher et al. 2016). According to Porter et al. (2011), *Physodermataceae* occupy the most basal branch in the *Blastocladiomycota*. Strittmatter et al. (2016) observed the rapidly swimming flagellated spores (uniflagellate zoospores), their dispersion stage and conjugation of amoeboid swarmer (aflagellate pseudopodiate spores). *Paraphysodermataceae* is a monotypic family which is typified by *Paraphysoderma* (James et al. 2011).

Paraphysoderma Boussiba, Zarka & T.Y. James, Mycotaxon 118: 178 (2011).
Index Fungorum Identifier 561750

Thallus monocentric, eucarpic, epibiotic. Rhizoidal system is intracellular, with the apophysis inside the host. Zoosporangium inoperculate, sessile, apophysate, globular, smooth and thin-walled; occasionally with subsporangial swelling. Zoospore stage absent. Aplanospores (aflagellate spores), few to dozens per zoosporangium, swarming before release, emerging concurrently through a tear in the zoosporangium wall, crawl in an amoeboid fashion on the host cell surface before encysting; germinating and developing endogenously. Resting spores or dormant sporangia epibiotic, darker, thick-walled, similar to the thin-walled zoosporangia in size and shape, developing to release aplanospores (James et al. 2011, Letcher et al. 2016).

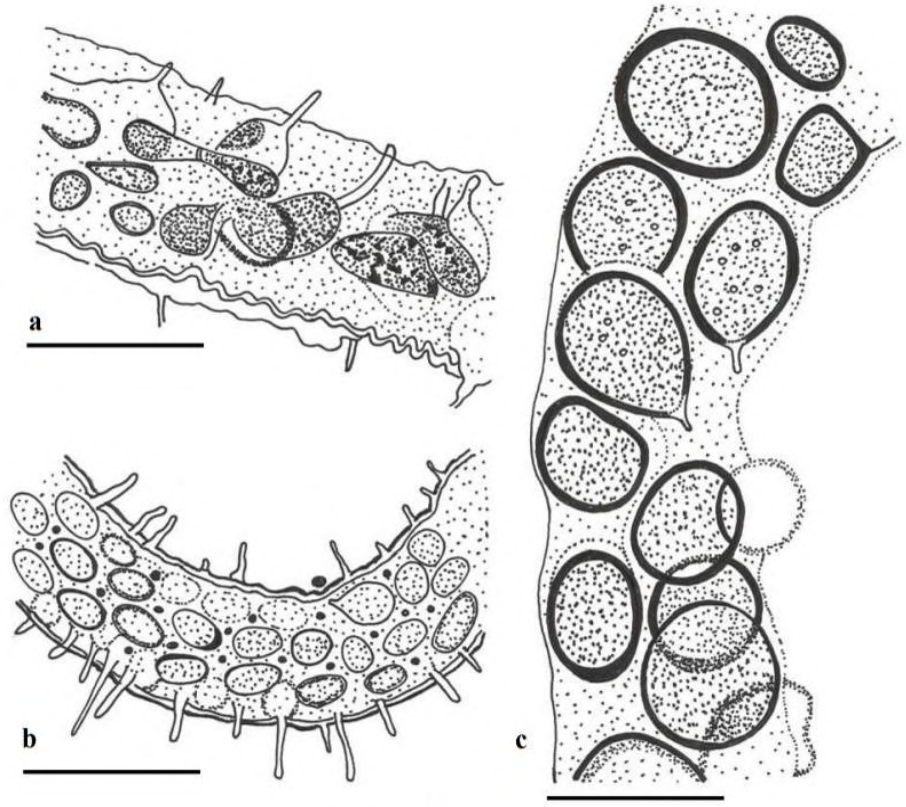


Figure 8 – *Catenaria anguillulae* in *Romanomermis culicivorax*. a Maturing zoosporangia. b Exit tubes from zoosporangia. c Resting sporangia. Scale bars: a-c 100 µm (Redrawn from Stirling & Platzer 1978).

Type species – *Paraphysoderma sedebokerense* Boussiba, Zarka & T.Y. James, Mycotaxon 118: 178 (2011); Fig. 9

Notes – *Paraphysoderma* was established with *P. sedebokerense* (James et al. 2011). The 18S ribosomal RNA gene phylogenetic analysis suggests that this species was closely related but basal to the obligately biotrophic plant parasitic zoosporic blastocladialean genus *Physoderma* (Hoffman et al. 2008). On the contrary, it differs morphologically and in host preference. In this sense, Letcher et al. (2016) examined the ultrastructure of *P. sedebokerense* for the first time and compared its ultrastructural characteristics with those of a sister taxon, *Physoderma maydis*. This study revealed the presence of synaptonemal complexes (SCs) in resting spores, indicating the site of meiosis. Moreover, both aflagellated and flagellated spores were observed in resting spores, thus, their role in the life history of this blastocladialean fungus remains to be elucidated. Asatryan et al. (2019) developed a method for the stimulation and isolation of *P. sedebokerense* propagules and their development under different conditions. The genus has only been reported from Asia, Europe and North America as a parasite on green algae in aquatic habitats (James et al. 2011, Letcher et al. 2016, Alors et al. 2021), and little is known about their occurrence and abundance throughout the world. Cultures are available in the University of Alabama Chytrid Culture Collection (UACCC) and CZEUM (Collection of Zoosporic Eufungi at the University of Michigan).

Sorochytriaceae Dewel, Joines & Bond, Canadian Journal of Botany 63(9): 1533 (1985)
Index Fungorum Identifier 81385

Thallus monocentric or polycentric, eucarpic, endobiotic and extra-intramatrical. In the colonial endobiotic phase, usually polysporangiate thallus with sequential septation, sorus generally transitory and cleaves into segmentsthat separate and round up to produce incipient zoosporangia.

Zoosporangium inoperculate, smooth, thin-walled, bearing branched rhizoids with short discharge tube or exit papilla. Zoospore ovoid, entirely formed within the zoosporangium, with a structure similar to a clearly visible, distinctive nuclear cap and peripheral granules; germinating intramatrically after encystment on the host to produce appressorium or penetration tube; otherwise, the cyst forms germ tube extramatrically in case of polycentric thallus. Polycentric phase extramatrical on the host with branched rhizomycelium consisting of sequential septation or constrictions, bearing rhizoids; usually form zoosporangia either from swelling in the rhizoid or enlargement of a segment of septate intercalary swelling. Zoosporangia and flagellated spores similar in shape and size to those in the colonial endobiotic phase (Dewel et al. 1985).

Family type – *Sorochytrium* Dewel Canadian Journal of Botany 63(9): 1533 (1985).

Ecology & life modes – Parasitizes the moss-inhabiting small carnivorous invertebrate tardigrade, *Milnesium tardigradum* (Dewel et al. 1985). Known only from the USA.

Notes – *Sorochytriaceae* is generally known to produce two thallus forms. The parasitic endobiotic colonial phase formed under the host cells, consisting of a sorus with several zoosporangia that scatter throughout the living host body cavity. The polycentric phase occurs epibiotically as a saprotroph with rhizomycelium upon the dead host cells (Dewel et al. 1985).

Sorochytrium Dewel, Canadian Journal of Botany 63:1525–1534. 1985
Index Fungorum Identifier 25736

In an endobiotic colonial cycle, the thallus spherical, holocarpic (until host death), generally polysporangiate, cleaves sequentially into a persistent or transitory sorus; incipient zoosporangium inoperculate, smooth, thin-walled, spherical, bearing branched and delicate rhizoids with short discharge papillae. Zoospore ovoid, completely formed within the zoosporangium, with prominently visible nuclear cap-like structure, occasionally with sluggish movement, or amoeboid; germinating intramatrically to develop appressorium inside the host after encystment; otherwise in polycentric thallus, extramatrically form germ tube. Polycentric phase on a dead host extrametrical, with numerous zoosporangia and branched rhizomycelium consisting of sequential septation, bearing rhizoids; zoospores relatively larger and multiflagellate (Dewel 1985).

Type species – *Sorochytrium milnesiophthora* Dewel, Canadian Journal of Botany 63(9): 1533 (1985); Fig. 10

Notes – *Sorochytrium* is a monotypic genus with *Sorochytrium milnesiophthora* growing endobiotically as a parasite within the tardigrade *Milnesium tardigradum* and exhibits unusual morphological variability in development by forming a polycentric thallus with rhizomycelium. No molecular phylogeny studies on the genus have been published. Dewel & Dewel (1990) examined the ultrastructure features of the zoospore and supported their taxonomic inclusion in the *Blastocladiales* based on a number of notable differences from those in other members. There are no recent information, cultures and sequences are available for this genus.

Callimastigales Doweld
Callimastigaceae Fonseca, Estudos sobre os flagellados parasitos dos Mammiferos do Brazil: 104 (1915)
Index Fungorum Identifier 816546

Protoplasmic body is globular. The protoplasm is of coarsely granulated creation and closes on the outside with a fine membrane. The rest of the body has no appendages. The pole pointing backwards when swimming wears a crest of long flagella, up to nine, that arise from basal bodies that are close together, stand at equal intervals, and a single straight or form a slightly curved row.

Family type – *Callimastix* Weissenb.

Ecology & life modes – Terrestrial and parasitic in crustaceans.

Notes – Fonseca (1915) introduced this family to accommodate *Callimastix*, a monotypic genus (*fide* Species Fungorum 2025).

Callimastix Weissenb., Sber. Gesellschaft naturf. Freunde Berlin 5: 299 (1912)

Type species – *Callimastix cyclopis* Weissenb., Sber. Gesellschaft naturf. Freunde Berlin 5: 299 (1912)

Protoplasmic body globular, 8–12 μm in diameter. The protoplasm is of coarsely granulated creation and closes on the outside with a fine membrane. The rest of the body has no appendages, and the pole, pointing backwards when swimming, wears a crest of long flagella. Flagella 24–30 μm long, up to nine, arise from basal bodies that are close together and stand at equal intervals, with a single straight or slightly curved row.

Notes – *Callimastix* contains only one species, *C. cyclopis,* which was originally described as a parasite in *Cyclops* (Weissenberg 1912). Braune (1913) introduced the second species, *C. frontalis* R.A. Braune, which is transferred to a new genus as *Neocallimastix frontalis* (R.A. Braune) Vávra & Joyon ex I.B. Heath (Heath et al. 1983).

Catenomycetales Doweld

Catenomycetaceae Doweld 2014, Index Fungorum 81: 1 (2014)

Index Fungorum Identifier 550388

Thallus polycentric to rarely monocentric, diffusely organized, intra- and extramatrical; intramatrical portion branched or unbranched, septate; septa delimiting the rudiments of the sporangia or sterile isthmuses; extramatrical portion branched, aseptate and sterile. Zoosporangia intercalary, smooth, pyriform, with strongly developed discharge tubes with endoopercula. Zoospores spherical, with multiple golden lipid globules, a single flagellum, forming a temporary group near the orifice, intermittently amoeboid; zoospore germination bipolar.

Family type – *Catenomyces* A.M. Hanson, Torreya 44: 30 (1944)

Ecology & life modes – Saprophyte on cellulosic substrates and also found in the human gastrointestinal tract (Hanson 1945, Kirk et al. 2013, Hillman et al. 2017)

Notes – Phylogenetic analyses based on 18S rRNA, 5.8S and 28S sequence data, James et al. (2006b) and Porter et al. (2011) accommodated *Catenomyces* in *Chytridiomycota*. However, phylogenetic analysis of Wijayawardene et al. (2018) and Galindo et al. (2021) placed this family in order *Catenomycetales* of *Blastocladiomycota*.

Catenomyces A.M. Hanson, Torreya 44: 30 (1944)

Index Fungorum Identifier 20107

Sporangia variable in size and shape; uteriform, pyriform, ovoid, cylindrical, spherical, elliptical, rectangular, triangular, or irregular, up to 8 exit tubes. Zoospore spherical, 3.7–4.5 μm in diameter, contains 5–18 golden refractive globules which may be nearly uniform or variable in size, flattened; 1–6, up to 30 μm long. Zoospores germinate and produce a germ tube that penetrates the substrate or grows on the surface. Germ tube thick, blunt, branched and developed to sporangia.

Notes – *Catenomyces* is a monotypic genus and *Ca. persicinus* was originally described as a saprophyte in cellophane, bleached corn and grass leaves, and dried onion skin suspended in samples of water (Hanson 1945).

Type species – *Catenomyces persicinus* A.M. Hanson, Torreya 44: 30 (1944); Fig. 11

Coelomomycetaceae Couch, Journal of the Elisha Mitchell Scientific Society 78: 135.1962

Index Fungorum Identifier 80619

Thallus endobiotic. Mycelium aseptate, coenocytic, usually naked (lack demonstrable walls or unwalled), well developed, thick, dichotomously branched and without the rhizoids, breaking up into hyphal bodies which develop into resting spores ingeniously utilizing the reproductive system of the host (mosquito). The sporophytic phase primarily consists of resting spore or resistant sporangia, developed from hyphal bodies and serving as reproductive structures, numerous, consisting of two distinct layers: the inner thin-walled and smooth whereas the outer thick-walled with smooth or outer wall variously ornamented with vast numbers of minute anastomosing pits and a longitudinal slit; the entire mycelial network generally used up in resting spore formation in the insect's hemocoel; releasing in the environment after insect host death followed by meiosis to

discharge numerous uniflagellate zoospores, capable of infecting the alternate host (other than insects). In this alternate host, the gametophytic phase ingeniously develops to produce uniflagellate male and female gametes for dispersion inside the host environment, upon fusion of compatible gametes (plasmogamy) leading to the formation of biflagellate zygotes, capable of encysting in an aquatic dipteran host (Sparrow 1960, Karling 1977).

Family type – *Coelomomyces* Keilin

Ecology & life modes – The members of *Coelomomycetacea* are entomopathogenic and distributed in freshwater ecosystems worldwide. The family comprise a highly specialized group of obligate parasites that occur commonly within the body cavity (coelom) of aquatic dipteran larvae, especially larvae of mosquitoes, midges and black flies. Many of its members exhibit an Euallomyces type of complex life cycle, especially within the genus *Coelomomyces* with sporophyte and gametophyte generations alternating between the mosquito and copepod host (crustacean), respectively, to complete its reproduction cycle (Sparrow 1960, Karling 1977, Powell 2017, Wijayawardene et al. 2018, Shen et al. 2020).

Notes – Compared to the *Blastocladiaceae*, in a broader context, the members of this family are accompanied by striking structural changes in their naked, branched, coenocytic, vegetative thallus, such as a lack of hyphal walls and specialized food-absorbing structures called rhizoids. This family includes two entomopathogenic genera: *Coelomomyces* and *Coelomycidium*, covering about 76 species pathogenic to specific groups of insects, such as flies and mosquitoes, with life histories that usually include alternation of haploid (gametophyte) sexual generation with a diploid (sporophyte) asexual generation or life stage in their life cycle (Powell 2017, Wijayawardene et al. 2018, Shen et al. 2020). Because they are parasites of medically important haematophagous *Diptera* (arthropods), there has been considerable interest in the last few decades in developing them for use as biocontrol or biological control agents, specifically in mosquito-control operations. However, the use of their members seems impractical since no species known from this blastocladiaceous family has been successfully cultivated *in vitro*, and the situation is furthermore complicated because of the presence of heteroecious life cycle complexity. Nevertheless, encouraging results have been obtained with a few field trials and experiments that have been conducted in the past. Porter et al. (2011) examined the molecular phylogeny of phylum *Blastocladiomycota* based on nuclear rDNA sequences, and the results revealed the monophyly of *Physodermataceae* and *Coelomomycetaceae* lineages. On the other hand, two invertebrate pathogenic genera of the family, *Coelomycidium* and *Coelomomyces* are reciprocally monophyletic sister clades (James et al. 2014).

Coelomomyces Keilin, emend. Couch, Journal of the Elisha Mitchell Scientific Society 61: 128 (1945).

Index Fungorum Identifier 20136

Thallus endobiotic comprising of coenocytic, aseptate, poorly developed, irregularly or dichotomously branched, anastomosing mycelium, without cell walls and rhizoids, enclosed by a plasma membrane to absorb the nutrients directly through its entire surface from the mosquito larvae hemocoel. Thin-walled zoosporangia apparently lacking. Sporophytic thalli reproduce asexually in the insect host (mosquitoes or chironomids) via smooth or variously sculptured, thick-walled resting spores or resistant sporangia formed from the hyphal bodies or segments, behaving as zoosporangia after a period of rest; splitting apart from the mycelium before the maturation of a definite wall to complete the development and filling the body cavity inside the insect's hemocoel; enclosed by an exceedingly thin, smooth outer membrane developed from the old plasma membrane; wall two layered; a smooth inner thin layer and the outer thicker, smooth or pitted or elaborately sculptured, ridged or ornamented wall; dehiscing by a preformed longitudinal slit to discharge posteriorly uniflagellate zoospores capable of infecting only the alternate host, particularly copepods or ostracods. Gametophytic thalli develop within these alternate hosts (small crustaceans) and produce uniflagellate male and female gametes. The resulting biflagellate zygotes (kariogamy= 2n) formed, capable of infecting mosquito larval cuticle via a germinating penetration

tube to re-establish the sporophytic thalli. Overall, it follows the Euallomyces mode of the life cycle with the heterothallic gametophyte (haploid) and sporophyte (diploid) bearing resting sporangia stages alternating between an intermediate host (crustacean) and a definitive host (dipteran) (Sparrow 1960, Travland 1979, Whisler 1985, Couch & Bland 1985).

Type species – *Coelomomyces stegomyiae* Keilin, Parasitology 13: 225 (1921); Fig. 12

Notes – *Coelomomyces* is essentially worldwide in distribution and comprises over 75 highly fastidious aquatic species. These species are obligately parasitize aquatic (freshwater) dipteran insects (Chironomidae, Psychodidae, Tabanidae and Simuliidae), primarily mosquitoes' larvae (more rarely chironomids) and require an essential alternate microcrustacean host consisting of either cyclopoid copepods, ostracods or harpacticoid copepods to complete its complex alternating life cycle (Wijayawardene et al. 2018, Shen et al. 2020, Ettinger et al. 2023). Although the species probably do not display host-specificity, they are relatively restricted in their host range (Federici 1981). Over the past hundred years, the obligate fatal parasites of this genus are generally found infecting all major medically important genera of mosquitoes, like *Aedes*, *Anopheles* and *Culex* and are easily recognized by the yellow to golden-brown colour of the relatively large resting sporangia which may fill the hemocoel and other body parts of the insect host (Federici & Lucarotti 1986, Whisler et al. 2009). The genus has attracted considerable interest because of its significant potential use in the biological control of vector mosquitoes (Shen et al. 2020), which transmit medically important human diseases such as Zika fever, West Nile fever, Chikungunya, yellow fever, filariasis, dengue fever, hemorrhagic dengue, malaria and various viral encephalitides all over the world causing millions of deaths every year. Presently, the generic characters primarily host specificity, ornamentation, unique wall structure, placement of the dehiscence slit and size and structure of their resting spores as viewed by light microscopy are largely used in the taxonomy of *Coelomomyces*. Recently, Ettinger et al. (2023) reported the genomes and transcriptomes of *C. lativittatus* as a valuable genomic resource that can be leveraged toward providing a comprehensive insight for understanding the biology of this blastoclad fungus and other important and unique, largely understudied early diverging zoosporic (flagellated) fungal lineages. Within the *Blastocladiomycota*, molecular phylogeny based on nuclear ribosomal DNA suggests that the branches leading to *Coelomycidium* and *Coelomomyces* taxa were relatively long and further molecular phylogenetic estimation with both groups is warranted to break up these long branches and improve the accuracy of analyses by including the sample of many additional taxa (Porter et al. 2011). This study also pointed out that numerous *Coelomomyces* spp. have many unique large insertions in their sequences of the rDNA that could be used reliably as a tool to facilitate rapid species identification based on rDNA sequence data. Several investigators observed and described the ultrastructure of *Coelomomyces* spp. (Martin 1971, Lucarotti & Federici 1984, Federici & Lucarotti 1986). Nevertheless, Madelin & Beckett (1972) studied the thin-wall sporangia of *Coelomomyces indicus* at the ultrastructural level, while Couch & Bland (1985) provided scanning electron micrographs (SEM) of resistant sporangia of *Coelomomyces iliensis* var. *iliensis*. Despite these reports, a survey of the literature suggests that we know remarkably little about the biology, biochemistry and genomics of this very large group of fungi. These lacunae in the existing knowledge are largely due to the failure, despite numerous attempts, to axenically obtain the culture of any species of *Coelomomyces* for detailed investigations. Nevertheless, this potential has not been realised or even accurately evaluated due to the lack of a cell wall for growing hyphae in the vegetative stages on their definitive (mosquito) and intermediate (copepod) hosts. Cultures are unavailable, but sequences are available on DDBJ/ENA/GenBank.

Other genus in *Coelomomycetaceae*

Coelomycidium Debais., C. r. Séanc. Mém. Soc. Biol. 82: 899 (1919)

Index Fungorum Identifier 20138; Index Fungorum (2025) lists two epithets; however, Species Fungorum (2025) accepted only one.

Type species – *Coelomycidium* simulii Debais. 1919

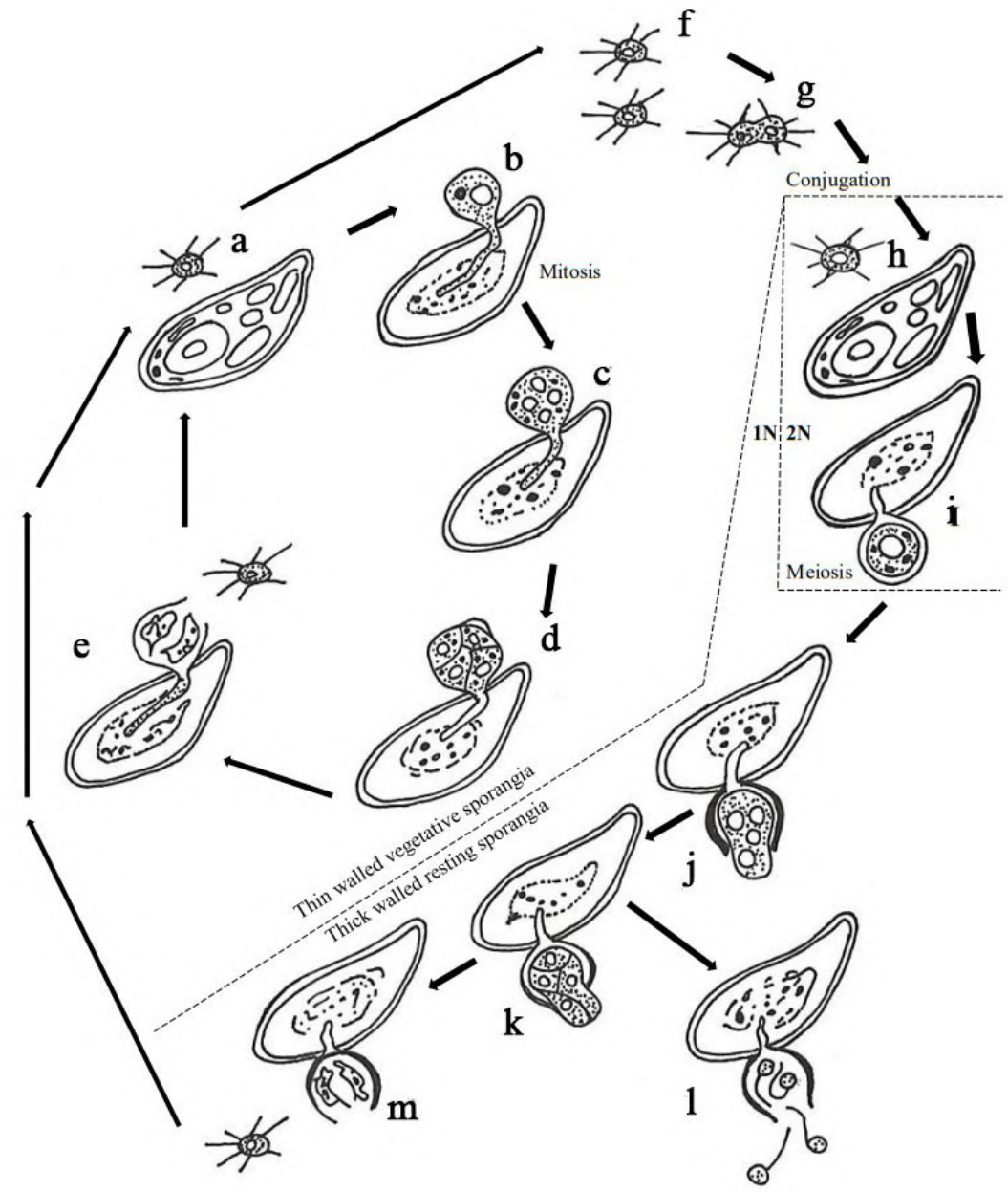


Figure 9 – A putative life cycle of *Paraphysoderma sedebokerense* based on the hypothesis of Hoffman et al. (2008) and Strittmatter et al. (2016). a. A haploid amoeboid swarmer contacts algal host. b. Swarmer encysts on the host surface, producing a thin-walled vegetative sporangium and a rhizoid, which invades the host. c. Mitosis produces multiple nuclei in the developing sporangium. d. Cytoplasmic cleavage into amoeboid swarmers. e. Amoeboid swarmers discharged from a thin-walled vegetative sporangium and continue the asexual life cycle (A). f. Two amoeboid swarmers approach each other. g. Conjugation between amoeboid swarmers results in a diploid zygote. h. Zygote encysts on the host surface. i. Zygote develops into a thick-walled resting sporangium, which invades the host with a rhizoid; meiosis occurs in the resting sporangium. j. Haploid nuclei as a product of meiosis. k. Cytoplasmic cleavage into either flagellated zoospores or amoeboid swarmers. l. Flagellated zoospores discharged from resting sporangium. m. Amoeboid swarmers discharged from resting sporangium (modified drawing from Letcher et al. 2016).

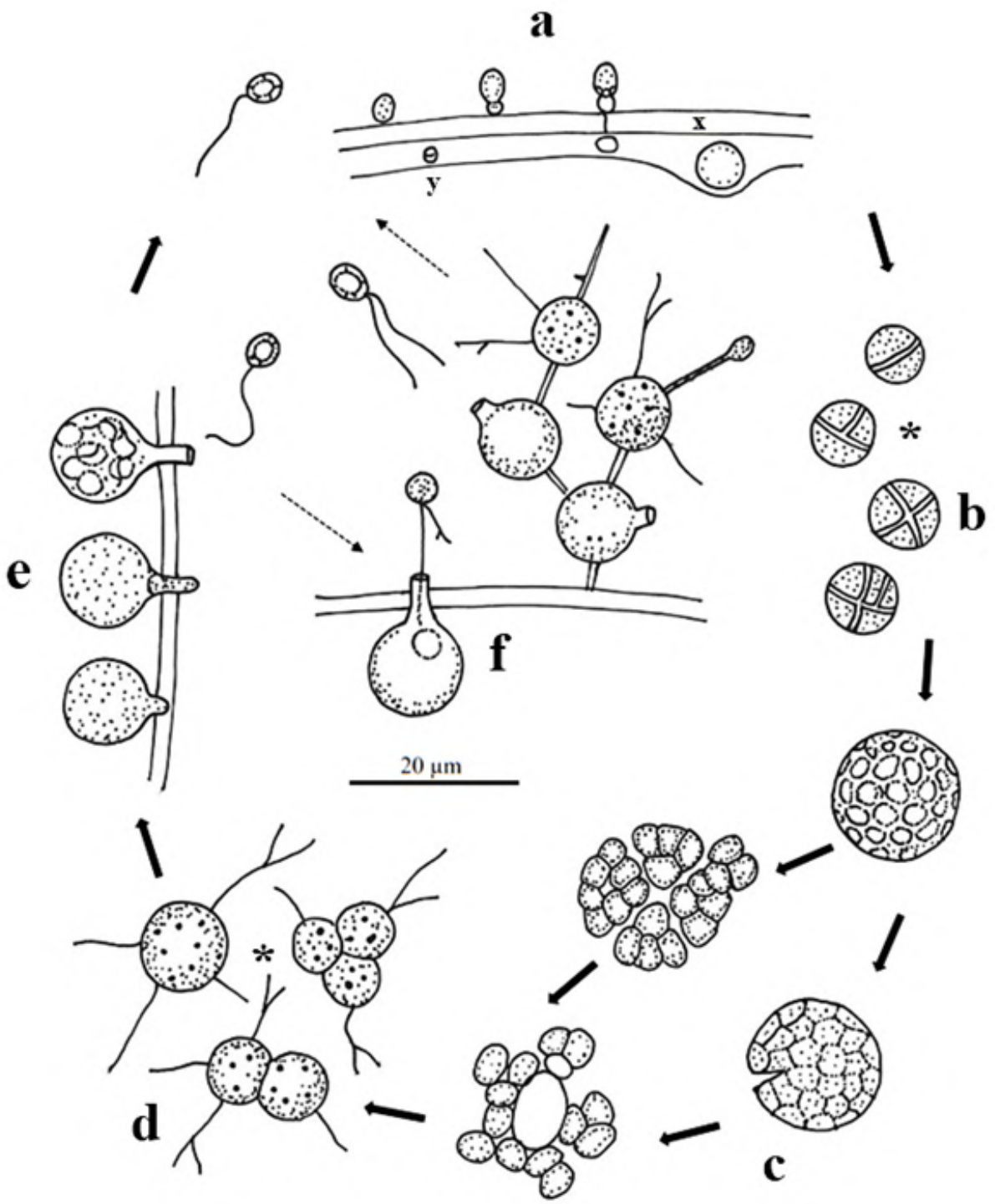


Figure 10 – Summary of endobiotic, colonial phase (solid arrows), and extrametrical, polycentric phase (broken arrows). a Initial infection stage of the endobiotic cycle. x, host cuticle; y, host epidermis. b Cleavage of thallus into segments. If the host dies prematurely, the sporangia developing from early cleavage stages will remain opposed (*). c Breakup of the cleavage segments. d Maturing sporangia. e Formation of exit papilla and zoospores. f Polycentric phase. The origin of the extramatrical growth from spores encysted within sporangia and the infectivity of motile spores from this phase is tentative. matrical growth from spores encysted within sporangia and the infectivity of motile spores from this phase is tentative (Redrawn from Dewel et al. 1985).

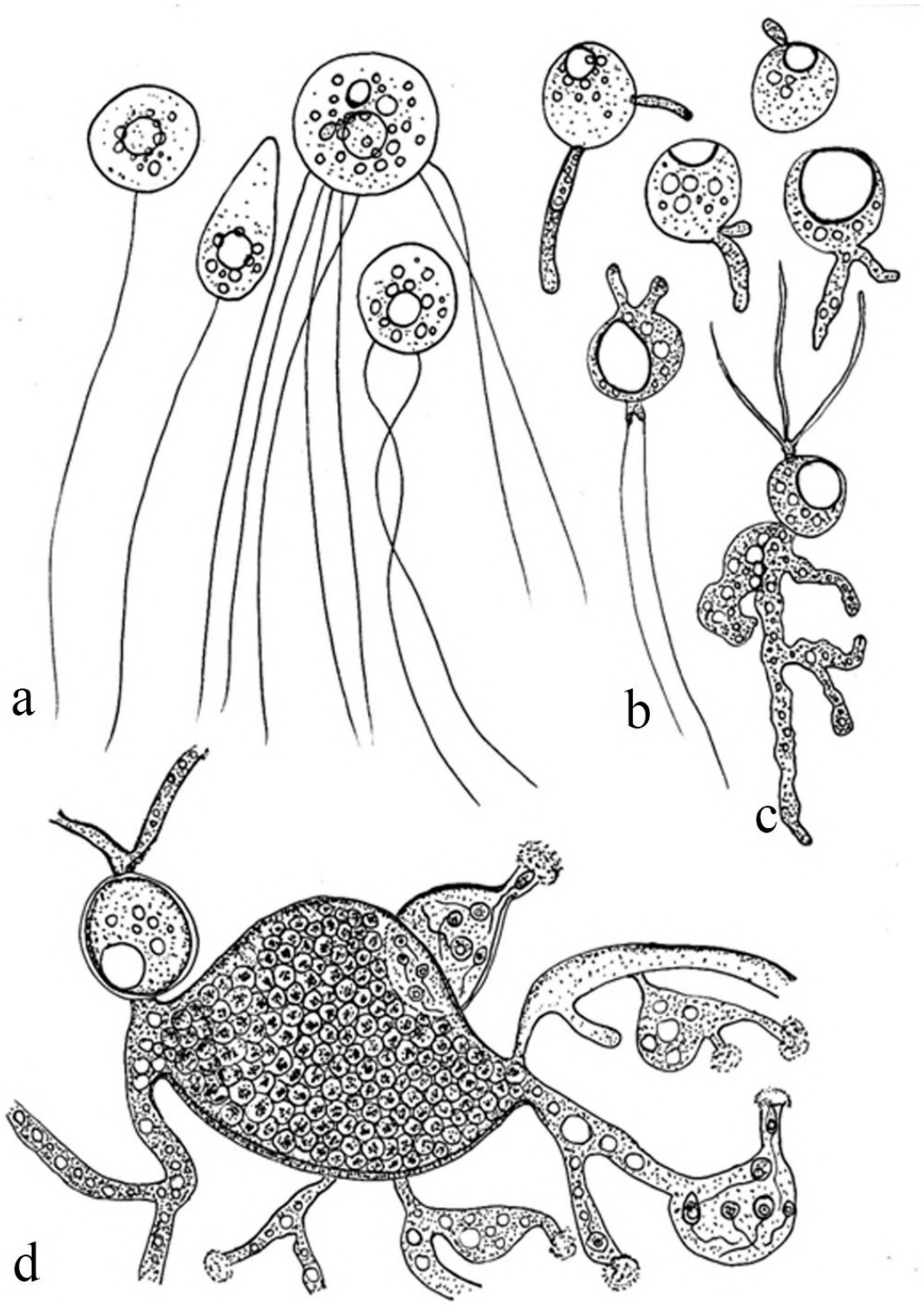


Figure 11 – *Catenomyces persicinus*. a Zoospores. b Germinating of zoospores. c Germinating of zoospores and developing of extrametrical hypgae. d Sporangium and zoospores (modified from Hanson 1945).

Physodermatomycetes Tedersoo et al.
Physodermatales Caval.-Sm.
Physodermataceae Sparrow, Mycologia 44(6): 768 (1952)
Index Fungorum Identifier 81168

Thallus two-forms, first a monocentric system of endobiotic and epibiotic sporangium clothed in a thin membrane standing; other polycentric, completely endobiotic, numerous persistent spores

and cells carrying turbines. Spores persist in the germination of individual zoosporangia forming a thinly clad membrane.

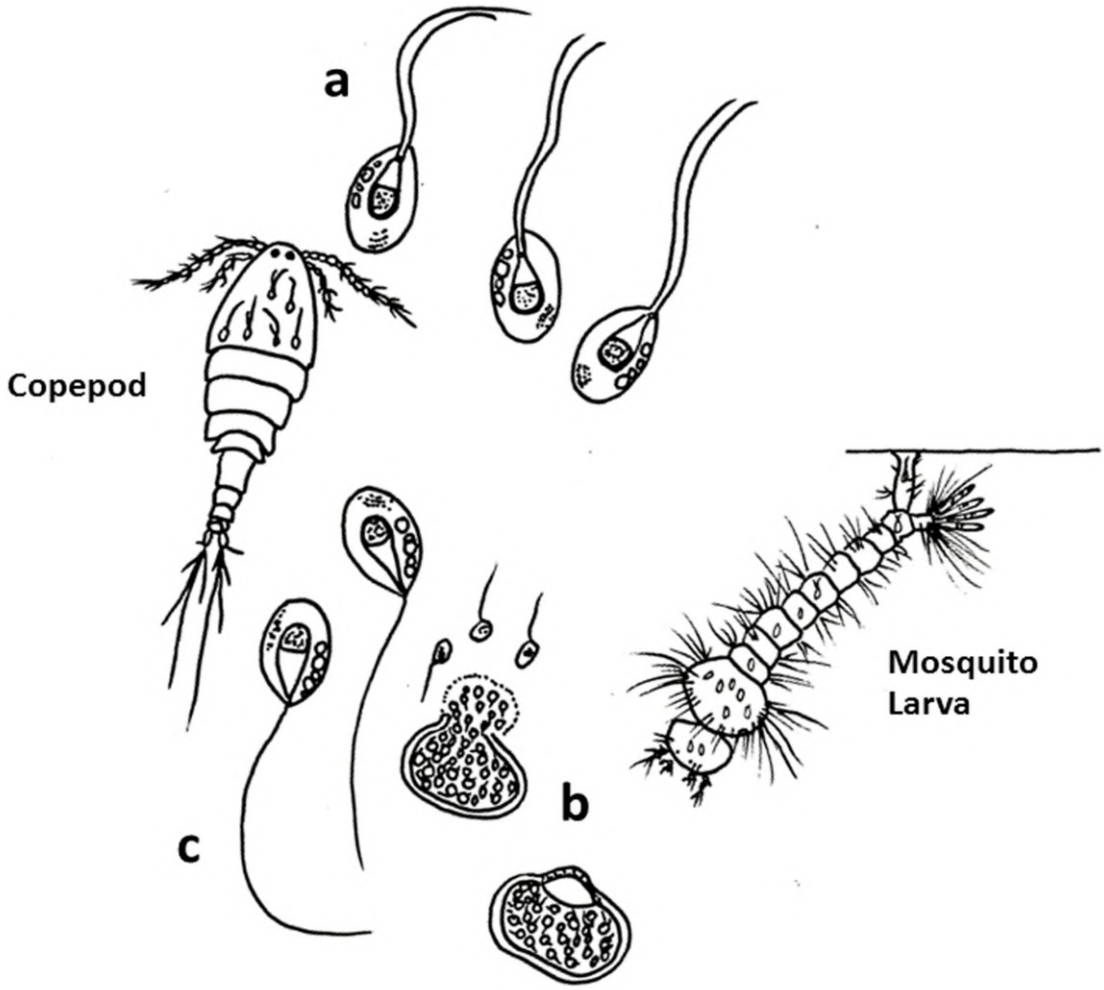


Figure 12 – *Coelomomyces stegomyiae*. a Zoospores in copepod. b Sporangium. c Zoospores in mosquito larva (Redrawn from Whisler et al. (1974) and Kalmakoff & Longworth (1980)).

Family type – *Physoderma* Wallr. 1833

Ecology & life modes – Plant parasite and saprophyte (Thirumalachar & Pavgi 1954, Farr et al. 1989, James et al. 2006b, Czeczuga et al. 2007a, Özaslan et al. 2015)

Notes – Sparrow (1952) introduced this family to accommodate *Physoderma*. However, Sparrow (1942) used *Physodermataceae* without a proper description, thus invalid (Art. 32.1(c), Art. 36.1). Phylogenetic analyses of rRNA gene (18S rRNA, 5.8S and 28S sequence data) of James et al. (2006b) accommodated this family in *Blastocladiomycota*.

Physoderma Wallr., Fl. crypt. Germ. (Norimbergae) 2: 192 (1833)
Index Fungorum Identifier 20415

Resting sporangia amphigenous, mostly hypophyllous and on leaf petioles, concentrated on leaves along the veins, scattered, covered by the unbroken epidermis, ellipsoid, ovoid, sometimes punctiform, 1–2 mm in diameter, chestnut brown. Resting spores chestnut brown, globoid, ovoid to ellipsoid, content granular with more refractive globules, (23.5)25.5–32 × 21.5–29 µm; with two distinct walls, the inner wall thin and hyaline, the outer wall chestnut brown, 1–2 µm thick, smooth.

Type species – *Physoderma maculare* Wallr., Fl. crypt. Germ. (Norimbergae) 2: 192 (1833)

Notes – *Physoderma* was introduced by Wallroth (1833) with *P. maculare* as the type species. Index Fungorum lists 112 species epithets however, Species Fungorum (2025) accepted

only 78 records. The species have been mainly reported as pathogens of a broad range of plants (e. g. You et al. 2021).

CALCARISPORIELLOMYCOTA Tedersoo et al.
Calcarisporiellomycetes Tedersoo et al.
Calcarisporiellales Tedersoo et al.
Calcarisporiellaceae Tedersoo, Sánchez-Ramírez, Kõljalg, Bahram, Döring, Schigel, T. May, M. Ryberg & Abarenkov, Fungal Diversity 90: 152 (2018)
Index Fungorum Identifier 554022

Thallus branched, with septate hyphae; vegetative hyphae hyaline, smooth, thin-walled; cultures with no distinctive smell; sporangiophores (if present) simple, hyaline, smooth, arising from undifferentiated hyphae; sporangia unispored, ellipsoid, with or without a small columella; spores uninucleate, hyaline, smooth, thin-walled, ovoid to ellipsoid, with a rounded base; chlamydospores (if present) born laterally on short hyphae, 1-celled, elongate to globose, thick-walled, spiny; sexual cycle not known; saprobic in soil, non-nematophagous (Jiang et al. 2011, Hirose et al. 2012).

Family type – *Calcarisporiella* de Hoog

Ecology & life modes – Thermophilic (Evans 1971), mesophilic (Hirose et al. 2012), saprobic in soil (Jiang et al. 2011, Hirose et al. 2012), cosmopolitan.

Notes – While proposing the higher-level classification of the fungi and a tool for evolutionary ecological analyses, Tedersoo et al. (2018) elevated the taxa from lower taxonomic levels to phylum rank, *Calcarisporiellomycota,* by confirming the findings of Hirose et al. (2012). The type species of the phylum *Calcarisporiella* de Hoog was introduced under *Mucoromycotina*, as an independent clade separated from the other known orders of this subphylum based on SSU phylogeny (Hirose et al. 2012). The second member of the family *Echinochlamydosporium* was earlier classified under *Mortierellaceae*, *Mortierellales*, *Zygomycota*. However, *Echinochlamydosporium* was distant from all other genera in *Mortierellaceae* based on phylogenetic analysis of LSU and SSU (Jiang et al. 2011). Tedersoo et al. (2018) introduced a new phylum under *Mucoromyceta* to accommodate these two taxa *C. thermophila* and *E. variabile.*

Calcarisporiella de Hoog, Studies in Mycology 7:68. 1974
Index Fungorum Identifier 7464

Colonies growing moderately rapidly, appearing thinly floccose, white. Vegetative hyphae hyaline, smooth and thin-walled, delicate, very loose, often flexuous. Conidiogenous cells scattered or in small groups, arising from undifferentiated hyphae, consisting of a somewhat inflated basal part with a narrow neck and a small apical group of cylindrical conidium bearing denticles. Conidia are single celled, hyaline, smooth and thin-walled, ovoid to ellipsoidal with a rounded base. No sexual state was observed (de Hoog 1974).

Descriptions are based on colonies growing on potato carrot agar at 30ºC.

Type species – *Calcarisporiella thermophila* (H.C. Evans) de Hoog

Other genus in *Calcarisporiellaceae*
Echinochlamydosporium X.Z. Jiang, H.Y. Yu, M.C. Xiang, X.Y. Liu & Xing Z. Liu, Fungal Diversity 46(1): 46 (2011); Index Fungorum Identifier 511829;
Index Fungorum (2025) and Species Fungorum (2025) accepted one species; DNA sequences are unavailable.

Type species – *Echinochlamydosporium variabile* X.Z. Jiang, H.Y. Yu, M.C. Xiang, X.Y. Liu & Xing Z. Liu (2011); Fig. 13

Notes – Jiang et al. (2011) introduced this genus from dead juveniles of *Heterodera glycines* in the soil of soybean land, China.

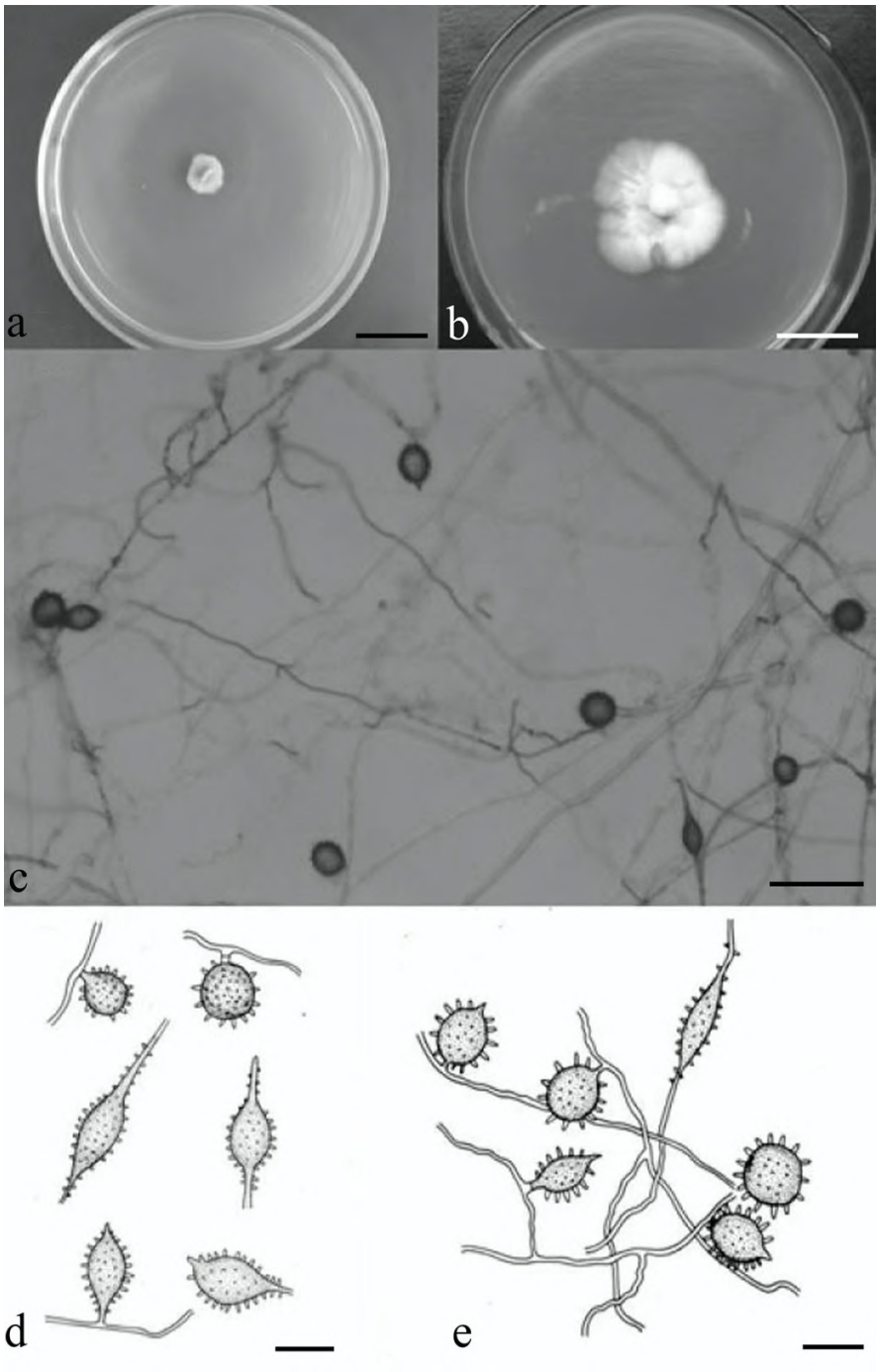


Figure 13 – *Echinochlamydosporium variabile.* a, b Colony on PDA. c-e Hyphae bearing different forms of chlamydospores and sporangia. Scale bars a, b = 10 cm, c-e = 10 μm.

CHYTRIDIOMYCOTA Doweld (= ***Caulochytriomycota*** Doweld)
Caulochytriomycetes Doweld
Caulochytriales Doweld
Caulochytriaceae Subram., Curr. Sci. 43: 723 (1974)
Index Fungorum Identifier 80561

Thallus eucarpic with endogenous development; monocentric; parasitic, penetrating the host by a haustorium. Zoosporangia inoperculate, with one to several papillae; sessile or hollow-stalked aerial. Zoospores are posteriorly uniflagellate. Planonts from sporangia of haploid thallus functioning as zoospores and perpetuating the haploid phase, or fusing in pairs to produce a diploid zygote (Subramanian 1974, Karling 1977, Doweld 2014b).

Family type – *Caulochytrium* Voos & L.S. Olive, Mycologia 60: 731 (1968)

Ecology & life modes – Parasitize hyphal fungi in association with plant tissues (Voos & Olive 1968, Olive 1980, 1983).

Notes – *Caulochytriaceae* was established by Subramanian (1974) to include the single genus *Caulochytrium*, and Voos & Olive (1968) accommodated it in *Chytridiales*. Subsequently, Hibbett et al. (2007) did not regard *Caulochytrium* in any higher-level taxa. Considering especially the morphological distinctiveness of this genus, as the production of both sessile zoosporangia, as well as aerial sporangiocarps, Doweld (2014b) erected *Caulochytriomycota*/*Caulochytriomycetes*/*Caulochytriales* to accommodate *Caulochytriaceae*. However, *Caulochytriomycota* is regarded as a synonym of *Chytridiomycota* (Wijayawardene et al. 2024).

Caulochytrium Voos & L.S. Olive, Mycologia 60: 731 (1968)
Index Fungorum Identifier 20109

Thallus eucarpic parasiting the host by a peg-like or knob-like haustorium, monocentric, rhizoids absent or present. Inoperculate zoosporangia with one to several papillae discharging one to many zoospores; sessile or hollow-stalked aerial. Zoospores are posteriorly uniflagellate. Planonts from sporangia of a haploid thallus function as zoospores and perpetuating the haploid phase or fuse in pairs to produce a diploid zygote.

Type species – *Caulochytrium gloeosporii* Voos & L.S. Olive, Mycologia 60: 731 (1968)

Notes – *Caulochytrium* is characterized by the production of both sessile zoosporangia and aerial sporangiocarps. The genus comprised two species *C. gloeosporii*, the type species, which is an obligate parasite of *Colletotrichum gloesporioides*, and isolated in Florida (Voos & Olive 1968). *Caulochytrium protostelioides*, an obligate parasite of *Cladosporium cladosporioides* and *Sordaria fimicola*, isolated from the British West Indies and North Carolina (Olive 1980, 1983). Cultures are available on ATCC (American Type Culture Collection) and sequences on GenBank.

Chytridiomycetes Caval.-Sm.
Chytridiales Cohn
Asterophlyctaceae Doweld, Index Fungorum 91: 1 (2014), emend Letcher & M.J. Powell (Turland et al. 2018, Art. 47).
Index Fungorum Identifier 550401

Thallus eucarpic, monocentric. Zoosporangium inoperculate with a spherical apophysis and branched rhizoids, irregularly stellate, angular, lobed, spherical to sub-spherical, sometimes possessing tapering, peg-like projections; zoosporangium formed either endogenously from the zoospore cyst or exogenously from a swelling of the germ tube. Zoospores are posteriorly uniflagellate, with a single lipid globule and multiple vacuoles. Resting spores borne like the zoosporangium, thick-walled, stellate or spherical, asexually formed or sexually formed after conjugation of thalli by means of rhizoidal anastomosis; upon germination, functioning as a prosporangium (Sparrow 1960, Letcher et al. 2018).

Family type – *Asterophlyctis* H.E. Petersen, Journal de Botanique (Paris) 17: 218 (1903)

Ecology & life modes – *Asterophlyctaceae* species are usually baited with insect exuviae and chitin bait from the aquatic and terrestrial ecosystem (Sparrow 1960, Karling 1977, Milanez et al. 2007, Letcher et al. 2018).

Notes – *Asterophlyctaceae* was introduced by Doweld (2014n) and emended by Letcher et al. (2018) based on DNA sequence data and zoospore ultrastructure of the species within *Asterophlyctis* and *Wheelerophlyctis*. Letcher et al. (2018) described a new species, *A. michiganensis*, as well as the new genus *Wheelerophlyctis*, with two species. Based on the molecular phylogenetic placements and zoospore ultrastructure of these two genera, they hypothesised that *Asterophlyctis* and *Wheelerophlyctis* represent a bridge between *Chytriomycetaceae* and *Chytridiaceae*.

Asterophlyctis H.E. Petersen, Journal de Botanique (Paris) 17: 218 (1903).
Index Fungorum Identifier 20062

Thallus eucarpic, monocentric, epibiotic. Zoosporangium inoperculate, angular to stellate, with a rhizoidal system composed of an apophysis with fine rhizoids. Thallus developed endogenously or exogenously from the encysted zoospore. Resting spores formed asexually or sexually by conjugation of thalli (Sparrow 1960, Letcher et al. 2018).

Type species – *Asterophlyctis sarcoptoides* H.E. Petersen, Journal de Botanique (Paris) 17: 218 (1903), emend Letcher & M.J. Powell; Fig. 14

Notes – *Asterophlyctis* comprises two species, typified with *A. sarcoptoides* (Petersen 1903, Letcher et al. 2018) and *A. michiganensis* (Letcher et al. 2018). *Asterophlyctis* was regarded as a synonym of *Diplophlyctis* by Dogma (1974). However, based on morphology, zoospore ultrastructure and molecular data, this synonymy was rejected (Letcher et al. 2018). This genus has been reported in Asia, Europe, North and South America and Oceania (Sparrow 1960, Milanez et al. 2007, Letcher et al. 2018). Cultures are available on the Alabama Chytrid Culture Collection (UACCC) and CZEUM (Collection of Zoosporic Eufungi at the University of Michigan).

Other genus in *Asterophlyctaceae*

Wheelerophlyctis Letcher & M.J. Powell, Fungal Biology 122(11): 1116 (2018)

Index Fungorum Identifier 826904; Index Fungorum (2025) and Species Fungorum (2025) accepted two species; DNA sequences are available.

Type specie –***:*** *Wheelerophlyctis interior* Letcher & M.J. Powell 2018

Notes – Both species are reported as saprobes only known from the USA (Letcher et al. 2018). Cultures are available on the Alabama Chytrid Culture Collection (UACCC).

Chytridiaceae Nowak., Akad. umiejetnosci Krakowie. Wydzíat mat.-przyród.: 174, 191 (1878), emend Vélez et al. (2011) (= *Phlyctochytriaceae* Doweld)

Index Fungorum Identifier 816372

Thallus eucarpic, monocentric. Zoosporangium endogenous or exogenous to the zoospore cyst, inoperculate or operculate, apophysate or non-apophysate. Zoospores are posteriorly uniflagellate and are produced into the zoosporangium. Resting spores are endogenous or exogenous. Members of the *Chytridiaceae* have a Group II-type zoospore (Vélez et al. 2011, Powell & Letcher 2014a).

Family type – *Chytridium* A. Braun, Betracht. Erschein. Verjüng. Natur., Ed. 2 (Leipzig): 198 (1851)

Ecology & life modes – Members of this family are common in aquatic and terrestrial ecosystems, acting as saprobic, with many facultative and obligate parasites of algae (Powell & Letcher 2014a, b).

Notes – *Chytridiaceae* is composed of seven genera based on morphological, ultrastructural and molecular studies (Letcher et al. 2012, 2014a, b, Vélez et al. 2011, Powell et al. 2018a, Letcher & Powell 2018a, b, Jesus et al. 2021). The ultrastructural and molecular studies of Vélez et al. (2011), with members of *Chytridiales*, especially with a purified culture of *Chytridium olla* (type species) isolated from Argentina, were fundamental for the definition of the limits of the *Chytridiales*/*Chytridiaceae* (Powell & Letcher 2014a). *Chytridiaceae* was emended by Vélez et al. (2011) and considered as a monophyletic family in *Chytridiales*.

Chytridium A. Braun, Betracht. Erschein. Verjüng. Natur., Ed. 2 (Leipzig): 198. 1851

Index Fungorum Identifier 20128

Thallus eucarpic, monocentric, epi- and endobiotic, the epibiotic part forming the rudiment of the zoosporangium, the endobiotic part producing the vegetative system and resting spore. Zoosporangium epibiotic, sessile, operculate, formed from all or part of the zoospore cyst, apophysate or non-apophysate, smooth or ornamented. Zoospores are posteriorly uniflagellate and are produced in the zoosporangium, usually with a single globule. Resting spores are endobiotic, thick-walled, and sexually or asexually formed (Sparrow 1960, Karling 1977).

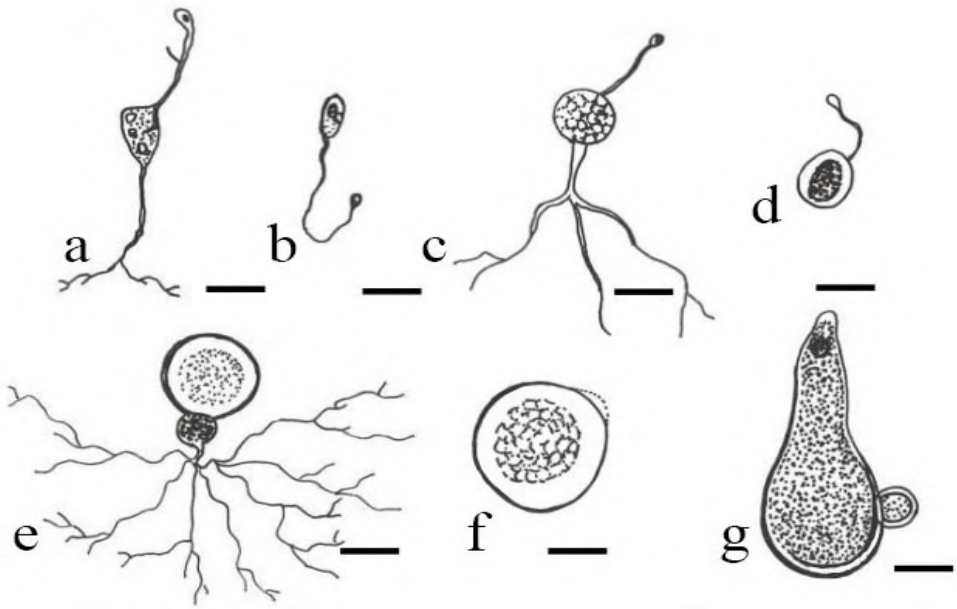


Figure 14 – *Asterophlyctis sarcoptoides*, strain WJD 209. a. Longitudinal section, with nucleus within ribosomal aggregation, multiple vacuoles, multiple mitochondria, a posterior flagellum with a narrow flagellar plug and a kinetosome-associated structure, a shield adjacent to and anterior to the kinetosome. b. Transverse section with nucleus within ribosomal aggregation, multiple vacuoles, multiple mitochondria, and a paracrystalline inclusion (PCI). c. LS of PCI. d. TS of PCI. e. TS through kinetosome, adjacent to which is a lipid globule, to which is appressed a fenestrated MLC cisterna (FC). f. LS of fenestrated cisterna appressed to the lipid globule; a cell coat (CC) surrounds the body of the zoospore. g. LS; A microbody (MB) is appressed to the lipid globule; flagellar props (Pr) connect kinetosome to plasma membrane. Scale bar in a, b = 1.0 µm; c, d = 0.5 µm; e–g = 0.25 µm (Letcher et al. 2018).

Type species – *Chytridium olla* A. Braun, Betracht. Erschein. Verjüng. Natur., Ed. 2 (Leipzig): 198. 1851 emend Vélez et al. (2011)

Notes – *Chytridium* has over 140 epithets (Index Fungorum 2025), with most members parasites or saprobic on freshwater and marine algae worldwide (Sparrow 1960, Milanez et al. 2007, Vélez et al. 2011, Steciow et al. 2012). *Chytridium olla* is the type species of *Chytridiaceae*, and it was first isolated as a parasite on the oospore of *Oedogonium* by A. Braun in 1851 (Powell & Letcher 2014a). Cultures are available on ATCC (American Type Culture Collection), UACCC (University of Alabama Chytrid Culture Collection) and CZEUM (Collection of Zoosporic Eufungi at the University of Michigan), and sequences are available in GenBank.

Dinochytrium Leshem, Letcher & M.J. Powell, Mycologia 108(4): 735 (2016)

Index Fungorum Identifier 813312; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Dinochytrium kinnereticum* Lesham, Letcher & M.J. Powell 2016

Notes – The genus is monotypic and a facultative parasite on the dinoflagellate *Peridinium gatunense*, and saprobic, with occurrence in Israel (Leshem et al. 2016).

Irineochytrium Letcher, Longcore & M.J. Powell, in Letcher, Index Fungorum 175: 1 (2014)

= *Irineochytrium* Letcher, Longcore & M.J. Powell, in Letcher, Index Fungorum 151: 1 (2014) (Nom. inval., Art. 40.1 (Melbourne))

Index Fungorum Identifier 550670; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Irineochytrium annulatum* (Dogma) Letcher, Longcore & M.J. Powell 2014

Notes – This genus was reported as a saprobic taxon, with occurrences in North and South America, and Poland (Dogma 1969, Booth & Barrett 1976, Booth 1979, Letcher & Powell 2002, Letcher et al. 2014b). Cultures are available on UACCC (the University of Alabama Chytrid Culture Collection) and CZEUM (Collection of Zoosporic Eufungi at the University of Michigan), and sequences are available in GenBank.

Phlyctochytrium J. Schröt., in Engler & Prantl, Nat. Pflanzenfam., Teil. I (Leipzig) 1(1): 78 (1897); Fig. 33a-c

Index Fungorum Identifier 20409; Index Fungorum (2025) lists 73 epithets, and Species Fungorum (2025) accepts 49 species.

Type species – not indicated.

Notes – Members of the genus have been reported as parasites of freshwater and marine algae, eggs of microscopic animals, and saprobic, with worldwide distribution (Karling 1977). Cultures are available on CZEUM (Collection of Zoosporic Eufungi at the University of Michigan), and sequences on GenBank. *Phlyctochytrium hydrodictyi* has been isolated as an obligate parasite of the green alga *Hydrodictyon reticulatum* (Letcher et al. 2012a). The genus is well-established and accommodated in *Chytridiaceae* (Letcher & Powell 2005b, Vélez et al. 2011, Letcher et al. 2012a, 2018, Leshem et al. 2016, Powell et al. 2018a, Jesus et al. 2021).

Polyphlyctis Karling, Sydowia 20: 86 (1968) [1966]

Index Fungorum Identifier 20437; Index Fungorum (2025) lists three species, and Species Fungorum (2025) accepts three species.

Type species – *Polyphlyctis unispina* (R.A. Paterson) Karling 1968

Notes – Members of the genus have been reported as saprophytic, with occurrences in Europe and North America (Letcher & Powell 2018a). Cultures are available on CZEUM (Collection of Zoosporic Eufungi at the University of Michigan) and UACCC (the University of Alabama Chytrid Culture Collection), and sequences are available in GenBank.

Zopfochytrium M.J. Powell, Longcore & Letcher, Fungal Biology 122(11): 1045 (2018)

Index Fungorum Identifier 825642; Index Fungorum (2025) lists one species, and Species Fungorum (2025) accepts one species.

Type species – *Zopfochytrium polystomum* (Zopf) M.J. Powell, Longcore & Letcher 2018

Notes – The genus has been reported from Europe and North America (Powell et al. 2018a). Cultures are available on CZEUM (Collection of Zoosporic Eufungi at the University of Michigan) and UACCC (the University of Alabama Chytrid Culture Collection), and sequences are available in GenBank.

Chytriomycetaceae Letcher, Mycologia 103(1): 127 (2011)

Index Fungorum Identifier 512387

Thallus eucarpic, monocentric or polycentric, sporangium endogenous or exogenous to the zoospore cyst. With operculate or inoperculate zoosporangium; rhizoids endobiotic or interbiotic. Resting spores are endogenous or exogenous. The spherical zoospore has a single or two lipid globules. Zoospore ultrastructure belonging to group I-type (Barr 1980, Picard et al. 2009), with a simple or fenestrated MLC cisterna and with or without a microtubular root and allied structures (Vélez et al. 2011, Jesus et al. 2021).

Ecology & life modes – More common in aquatic habitats than soil, degrade a wide array of substrates. Saprobic in exuviae of mayflies, on chitin, keratin, and cellulose, parasitic in a wide variety of algae species, dinoflagellates, chytrids, heliozoan, *Pythium*, *Aphanomyces* and plants (Sparrow 1937, Karling 1977, Longcore 1992a, Letcher & Powell 2002, Vélez et al. 2013a, Davis et al. 2015, Seto & Degawa 2018a, Powell et al. 2019a, Jesus et al. 2021).

Family type – *Chytriomyces* Karling, Am. J. Bot. 32(7): 363 (1945)

Notes – The family was proposed by Vélez et al (2011); it is composed of 15 genera, including the chytrid species with a Group I-type zoospore (Barr 1980, Picard et al. 2009). Considering the structures of zoospores and molecular analyses, the LSU combined dataset of partial SSU, partial LSU and ITS5.8S-ITS2 rDNA sequences. However, *Chytriomycetaceae* does not have a clear phylogenetic position, as many representatives are obligate parasites that have not yet been sequenced (Vélez et al. 2011, Seto et al. 2020b). The most complete and recent systematic studies related to the family were by Seto et al. (2018b) and Jesus et al. (2021), using North American isolates and a few South American strains (Vélez et al. 2011, 2013, Davis et al. 2015, Letcher et al. 2018, Powell et al. 2018a, 2019a, Jesus et al. 2021).

Chytriomyces Karling, Am. J. Bot. 32(7): 363 (1945)
Index Fungorum Identifier 20125

Thallus epibiotic; zoosporangium with one rhizoidal axis (rarely more than one), apical or subapical operculum present. Zoospore with a single lipid globule (rarely many). Zoospore ultrastructure described by Longcore (1992a). Resting spore epibiotic or endobiotic, spherical, ovoid, or angular, thick-walled, smooth, reticulate, tuberculate or ornamented, hyaline or yellowish.

Type species – *Chytriomyces hyalinus* Karling, Am. J. Bot. 32: 363 (1945); Figs. 15 & 33d
Index Fungorum Identifier 285191

Notes – The characteristics of the genus were succinctly described by Karling (1945b) to accommodate *C. hyalinus* and *C. aureus*. Since then, new species have been described, substantially changing the original description. Letcher & Powell (2002) redescribed the genus, including all described species and designated the lectotype. *Chytriomyces* has 28 species recorded having a cosmopolitan distribution (Letcher & Powell 2002, Davis et al. 2019a, Jerônimo & Pires-Zottarelli 2019, Species Fungorum 2025), being reported as saprobes and/or parasites (see Letcher & Powell 2002). Most of the cultures of *Chytriomyces* are maintained in CZEUM (Collection of Zoosporic Eufungi at the University of Michigan) and *the* American Type Culture Collection (ATCC). Only three species have sequences available for access; however, GenBank has 4,106 sequences, mostly at the genus level.

Other genera in *Chytriomycetaceae*

Avachytrium Vélez & Letcher, Mycologia 105(5): 1257 (2013)
Index Fungorum Identifier 801481; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species– *Avachytrium platense* Vélez & Letcher 2013

Notes – The genus was reported as saprobic from pollen grains in Argentina (Vélez et al. 2013b). Culture was deposited at the Culture Collection of the Facultad de Ciencias Exactas y Naturales, University of Buenos Aires, ARG 053 and GenBank sequences JX905509 and JX905536. This species was also reported in Brazil (Jesus & Pires-Zottarelli 2020).

Entophlyctis A. Fisch., in Winter, Rabenh. Krypt.-Fl., Edn 2 (Leipzig) 1(4): 114 (1892); Fig. 33e & f
Index Fungorum Identifier 20222; listed 34 epithets, but Species Fungorum (2025) accepted 21 species.

Lectotype species – *Entophlyctis cienkowskiana* (Zopf) A. Fisch. 1892

Notes – Members of the genus are mainly reported as saprobic and parasitic on *Chlamydomonas* species and show cosmopolitan distribution. Cultures and sequences of ex-type are unavailable. However, there are cultures of other species maintained in CBS (CBS-KNAW Fungal Biodiversity Centre), ATCC (American Type Culture Collection) and CZEUM (Collection of Zoosporic Eufungi at the University of Michigan).

Fayochytriomyces W.J. Davis, Letcher, Longcore & M.J. Powell, Mycologia 107(2): 435 (2015)

Index Fungorum Identifier 810999; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Fayochytriomyces spinosus* (Fay) W.J. Davis, Letcher, Longcore & M.J. Powell 2015; Fig. 33g

Notes – The genus is monotypic and reported as saprobic, isolated on cellulose, New Jersey (Davis et al. 2015). The culture of epitype is maintained at CZEUM (Collection of Zoosporic Eufungi at the University of Michigan), UACCC WJD186. Distribution is cosmopolitan.

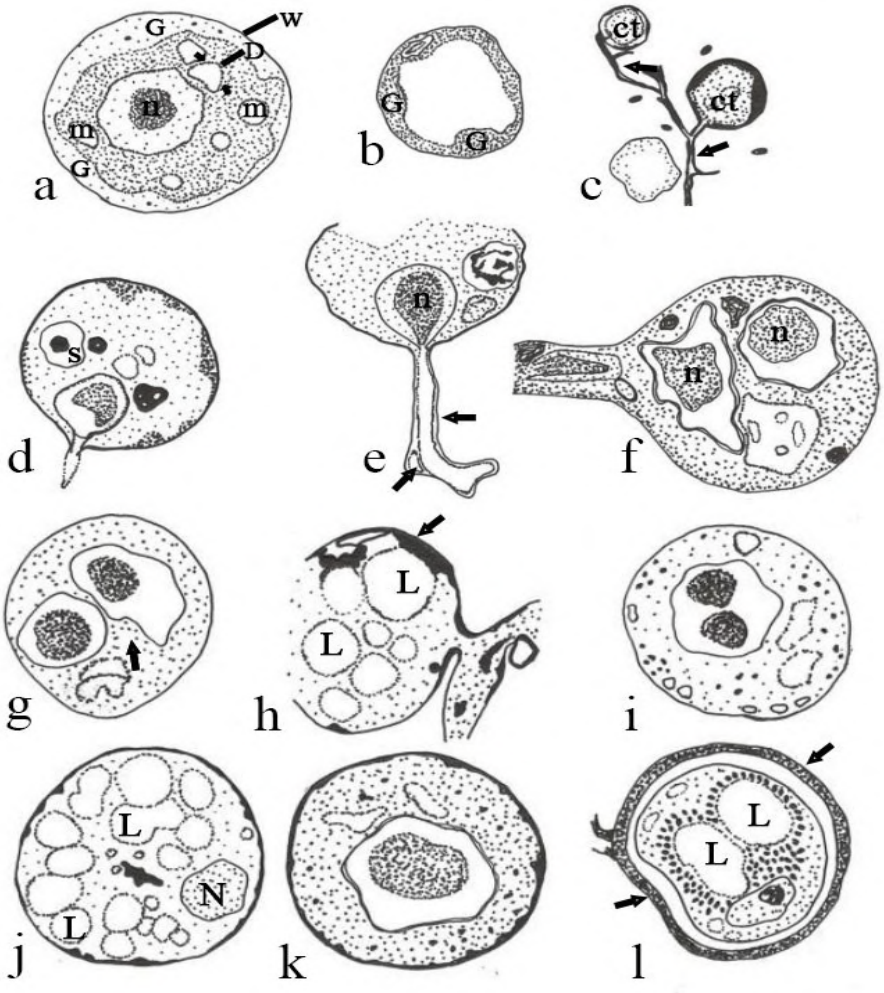


Figure 15 – a-c Contributing thalli, *C. hyalinus*. a Six-hour-old, uninucleate contributing thallus illustrating peripheral zone of glycogen-like particles (g), nucleus, nucleolus (n), mitochondria (m), dictyosomes (d), two centrioles (arrows) in L-section, and cell wall (w). b Empty contributing thallus with a remaining zone of glycogen-like particles (g). c Contributing thalli (ct) and part of connecting rhizoidal system (arrows). d-f Nuclear and cytoplasmic migration, *C. hyalinus*. d Intact centriole (arrow) and nucleus entering rhizoidal system near junction of contributing thallus body and rhizoid. Note enlarging cytoplasmic free space (s) of body of contributing thallus. e Nucleus passing into rhizoidal system; nuclear envelope (arrows), nucleolus (n). f Fusion body with two irregularly shaped pre-karyogamous nuclei, nucleoli (n) and mitochondria (m). g-l Pre-and post-karyogamy and developing resting body, *C. hyalinus*. g Nucleoplasmic bridges (arrow). h Post-karyogamous nucleus prior to nucleolar coalescence. i Post-karyogamous nucleus containing the elongated product of nucleolar coalescence. j Resting body (24 hr) and the associated rhizoidal system. Note the numerous lipid globules (L) and aggregations of glycogen-like particles (arrows). k Uninucleate (N) resting body containing lipid globules (L) and aggregations of glycogen-like particles. l Uninucleate (N) resting body (47 days old) with lipid globules (L). Note a thickened cell wall (arrows) (redrawn from Miller & Dylewski 1981).

Obelidium Nowak., in Cohn, Beitr. Biol. Pfl. 2: 86 (1877) [1876]
Index Fungorum Identifier 20375; Index Fungorum (2025) and Species Fungorum (2025) accepted three species.

Type species – *Obelidium mucronatum* Nowak. 1877

Notes – Members of the genus are saprobic on chitin (Nowakowski 1876, Sparrow 1937, Willoughby 1961). Ex-type cultures are unavailable; however, three cultures are maintained at CZEUM (Collection of Zoosporic Eufungi at the University of Michigan). Distribution is cosmopolitan.

Odontochytrium Vélez & Letcher, Mycologia 105(5): 1259 (2013)
Index Fungorum Identifier 801483; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Odontochytrium milleri* Vélez & Letcher 2013

Notes – The type species was reported as a saprobe and isolated from pollen grains, Argentina (Vélez et al. 2013b). Cultures were deposited at the Culture Collection of the Facultad de Ciencias Exactas y Naturales, University of Buenos Aires, ARG 095.

Pendulichytrium K. Seto & Degawa, Mycoscience 59(1): 62 (2017)
Index Fungorum Identifier 821132; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Pendulichytrium sphaericum* K. Seto & Degawa 2017

Notes – This genus was reported as a parasite on the diatom *Aulacoseira granulata*, Japan (Seto & Degawa 2018b). The ex-type culture is maintained at the Department of Environmental Science, Faculty of Science, Toho University.

Phlyctorhiza A.M. Hanson, Am. J. Bot. 33: 732 (1946)
Index Fungorum Identifier 20410; Index Fungorum (2025) has three epithets, but Species Fungorum (2025) has accepted one species.

Type species – *Phlyctorhiza endogena* A.M. Hanson 1946

Notes – The genus/species was initially accommodated in *Entophlyctaceae* because it has a similar appearance to *Rhizophlyctis* (Hanson 1946). Doweld (2014e) introduced *Phlyctorhizaceae* to accommodate this genus. However, other important studies did not accept this placement and regarded it as a member of *Chytriomycetaceae* (based on the phylogeny and ultrastructure of zoospores), along with *Obelidium*, *Siphonaria* and *Podochytrium* (James et al. 2006b, Vélez et al. 2011, Powell et al. 2018a, Jesus et al. 2021).

Physocladia Sparrow, Mycologia 24(3): 285 (1932)
Index Fungorum Identifier 20414; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Physocladia obscura* (Sparrow) Sparrow 1932

Podochytrium Pfitzer, Verh. naturh. Ver. preuss. Rheinl. Westphalens 27(Sitzungsber): 62 (1870)
Index Fungorum Identifier 20434; Index Fungorum (2025) and Species Fungorum (2025) accepted seven species.

Type species – *Podochytrium clavatum* Pfitzer 1870

Notes – Members of the genus are reported as saprobic on chitin and parasites of diatoms (Sparrow 1933a, 1951, Sparrow & Peterson 1955, Willoughby 1961, 1963, Pfitzer 1870, Longcore 1992b). The ex-type culture is maintained at CZEUM (Collection of Zoosporic Eufungi at the University of Michigan). The distribution of the species is cosmopolitan.

Rhopalophlyctis Karling, Am. J. Bot. 32: 363 (1945)
Index Fungorum Identifier 20491; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Rhopalophlyctis sarcoptoides* Karling 1945

Notes – The type species was reported as saprobic on insect exuviae in Brazil (Karling 1945b).

Rhizidium A. Braun, Monatsber. Königl. Preuss. Akad. Wiss. Berlin: 591 (1856)
Index Fungorum Identifier 20478; Index Fungorum (2025) 55 epithets, but Species Fungorum (2025) accepted 18 species.

Type species – *Rhizidium mycophilum* A. Braun 1856

Notes – Members of the genus were reported as saprobic on chitin and cellulose and/or parasites on diatoms and green algae (Sparrow 1960, Karling 1977, Picard et al. 2009, Jesus et al. 2021). Distribution is cosmopolitan.

Rodmanochytrium M.J. Powell & Letcher, Phytologia 101(3): 176 (2019)
Index Fungorum Identifier 830008; Index Fungorum (2025) and Species Fungorum (2025) accepted two species.

Type species – *Rodmanochytrium pyriforme* M.J. Powell & Letcher 2019

Notes – Members of the genus were reported as saprobes on chitin (Powell et al. 2019a). Ex-type culture is maintained in CZEUM (Collection of Zoosporic Eufungi at the University of Michigan). Distribution is cosmopolitan.

Rhizoclosmatium H.E. Petersen, J. Bot., Paris 17: 216 (1903)
Index Fungorum Identifier 20480; Index Fungorum (2025) and Species Fungorum (2025) accepted 8 species.

Type species – *Rhizoclosmatium globosum* H.E. Petersen 1909

Notes – The species are reported as saprobes on chitin and cellulose (Petersen 1903, Powell et al. 2019b). Distribution is cosmopolitan.

Siphonaria H.E. Petersen, J. Bot., Paris 17: 220 (1903)
Index Fungorum Identifier 20523; Index Fungorum (2025) and Species Fungorum (2025) accepted four species.

Type species – *Siphonaria variabilis* H.E. Petersen 1909

Notes – Members of the genus are reported as saprobic on chitin (Petersen 1903, Jesus et. al. 2021). Cultures are maintained at CZEUM (Collection of Zoosporic Eufungi at the University of Michigan), UACCC (University of Alabama Chytrid Culture Collection). However, ex-type cultures are unavailable. Reported from the American continents and Great Britain.

Pseudorhizidiaceae Doweld, Index Fungorum 82:1 (2014)
Index Fungorum Identifier 550390

Thallus eucarpic, monocentric, endogenous, interbiotic. Zoosporangia with multiple inoperculate discharge pores, oval to spherical, with a single rhizoidal axis and finely divided tips. Zoospores are posteriorly uniflagellate, with solitary to multiple lipid globules. Resting spores spherical, epibiotic (Doweld 2014c).

Family type – *Pseudorhizidium* M.J. Powell, Letcher & Longcore, Mycologia 105: 501 (2013)

Ecology & life modes – *Pseudorhizidiaceae* comprises two genera, *Pseudorhizidium* (Powell et al. 2013, Doweld 2014c), and *Delfinachytrium* (Vélez et al. 2013b). These two saprophytic genera were isolated from aquatic and terrestrial ecosystems on pollen grains.

Notes – *Pseudorhizidiaceae* was proposed by Doweld (2014c) to include the genus *Pseudorhizidium*. The single species, *P. endosporangium*, described by Karling (1968) as *Rhizidium endosporangium*, was considered as *incertae sedis* by Powell et al. (2013) and Vélez et al. (2013b), who described the sister genus *Delfinachytrium*. Seto & Degawa (2018b) and Jesus et al. (2021) considered the clade composed of these two genera as *incertae sedis*.

Pseudorhizidium MJ Powell, Letcher & Longcore, Mycologia 105: 501. 2013
Index Fungorum Identifier 801458
Thallus eucarpic, monocentric, endogenous, exhibiting interbiotic tendencies when grown with pollen in water cultures. Zoosporangia inoperculate with multiple discharge pores, oval to spherical, with a single main rhizoidal axis with finely divided tips. Zoospores are posteriorly uniflagellate, typically containing one large lipid globule, sometimes multiple lipid globules. Resting spores are spherical and epibiotic (Powell et al. 2013).

Type species – *Pseudorhizidium endosporangiatum* (Karling) MJ Powell, Letcher & Longcore, Mycologia 105: 501 (2013)

Notes – *Pseudorhizidium* was described by Powell et al. (2013) based on its thallus morphology, molecular phylogenetic placement and unique zoospore ultrastructure. *Pseudorhizidium endosporangium*, the type species, was described by Karling (1968) as *Rhizidium endosporangium.* This genus/species has occurrences in Oceania and the USA (Powell et al. 2013). Cultures are available on the University of Alabama Cryoculture Collection and CZEUM (Collection of Zoosporic Eufungi at the University of Michigan), and sequences are available on GenBank.

Other genus in *Pseudorhizidiaceae*
Delfinachytrium Vélez & Letcher, Mycologia 105(5): 1261 (2013)
Index Fungorum Identifier 801577; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Delfinachytrium mesopotamicum* Vélez & Letcher 2013

Notes – The type species was reported as saprobic in Argentina (Vélez et al. 2013b). Cultures are available in the Culture Collection of the Facultad de Ciencias Exactas y Naturales, University of Buenos Aires, and CZEUM (Collection of Zoosporic Eufungi at the University of Michigan).

Scherffeliomycetaceae Doweld, Index Fungorum 122: 1. 2014
Index Fungorum Identifier 550469

Thallus eucarpic, monocentric, extramatrical, epi- and endobiotic, consisting of an extramatrical persistent cyst of the zoospore, the proximal part of the germ tube, an epibiotic expanded rudiment of the sporangium and an endobiotic vegetative system, which may be rhizoidal or haustorial, sometimes with an apophysis. Zoosporangia inoperculate. Zoospores are posteriorly uniflagellate, with a single orange lipid globule. Resting spore thick-walled, epibiotic (Doweld 2014a).

Family type – *Scherffeliomyces* Sparrow, Mycologia 26: 377. 1934

Ecology & life modes – *Scherffeliomyces*, the single genus of the family, was isolated as a parasite of freshwater green algae.

Note – Sparrow (1934) introduced *Scherffeliomyces* and accommodated it in *Phlyctidiaceae* (Sparrow 1960). Doweld (2014a) introduced the family *Scherffeliomycetaceae* to accommodate *Scherffeliomyces*. These species lack sequences, and the classification and molecular position can be considered uncertain in the *Chytridiales*.

Scherffeliomyces Sparrow, Mycologia 26: 377. 1934.
Index Fungorum Identifier 20508

Thallus eucarpic, monocentric, extramatrical, epi- and endobiotic, consisting of an extramatrical persistent cyst of the zoospore, the proximal part of the germ tube, an epibiotic expanded rudiment of the sporangium and an endobiotic vegetative system. Zoosporangia inoperculate. Zoospores are posteriorly uniflagellate, with a single lipid globule. Resting spore thick-walled, borne like the zoosporangium, epibiotic; germination not observed (Sparrow 1960).

Type species – *Scherffeliomyces parasitans* (Sparrow) Sparrow, Bot. J. Linn. Soc. 50: 446 (1936)

Notes – Sparrow (1933a) introduced the genus *Scherffelia* Sparrow (1933a), but it was illegitimate (non *Scherffelia* Pascher 1911 (Algae)). Thus, Sparrow (1936) established the new name, *Scherffeliomyces*, to replace *Scherffelia*. Studies are necessary to confirm the classification and molecular position of this genus/species in *Chytridiales*.

Nephridiophagales Doweld
Nephridiophagaceae R. Radek, Letcher, Wijayaw., P.M. Kirk & K.D. Hyde, Fungal Diversity 92: 45 (2018)
Index Fungorum Identifier 550099

Nephridiophagids multiply in the lumen of the Malpighian tubules of insects, but occasionally individuals may also occur in their epithelial cells (Ivanić 1937, Gibbs 1959, Woolever 1966, Radek & Herth 1999). Life stages comprise vegetative merogonial plasmodia and sporogenic plasmodia with endogenous spore formation and residual somatic nuclei. Flagellated forms have not been found. Nuclear division takes place via cryptomitosis (closed mitosis with an intranuclear spindle). Transmission is ensured by oral uptake of spores released with the host faeces.

Family type – *Nephridiophaga* Ivanić, Cellule 45: 291–324 (1937)

Life modes and distribution – No free-living representatives of nephridiophagids have been documented. Their typical habitats are the Malpighian tubules of insects. Most luminal plasmodia adhere to the microvilli of the tubule cells by tiny protrusions. During the vegetative multiplication cycle, multinucleate merogonial plasmodia divide into oligo- or uninucleate stages. Other plasmodia enter sporogony and form spores endogenously: sporogenic cytoplasm surrounding a generative nucleus is delimited by cisterns of the endoplasmic reticulum, and spore wall material is subsequently deposited between the resulting membranes (Radek & Herth 1999). The spore wall contains chitin (Radek et al. 2002). Residual somatic nuclei always remain in the cytoplasm of the mother plasmodium. During spore formation bi- or tetranuclear sporoblasts have been observed, which implies that sexual stages (formed by meiosis) exist (Ivanić 1937). Mature spores are mostly uninucleate and have a flattened oval form.

Notes – *Nephridiophaga* was introduced by Ivanić (1937) for the unicellular spore-forming parasite of the honeybee, *Nephridiophaga apis*. The parasite lives in the Malpighian tubules of its host and partially destroys the epithelial cells. The systematic position of *Nephridiophaga* and morphologically similar spore-forming protists of arthropods has long been discussed (see Radek & Herth 1999, Voigt et al. 2021). In the first report published by Lutz & Splendore (1903), the so-called ‘nephridiophagids’ detected in the American cockroach *Periplaneta americana* were misclassified as microsporidia and described as *Plistophora periplanetae*. The poor morphological characteristics of the nephridiophagids led to further contested affiliations, for instance with the haplosporidia (Woolever 1966, Purrini & Weiser 1990) or mycetozoa (Léger 1909). In 1970, Sprague created the family *Nephridiophagidae* within the class *Haplosporea*. Other genera of spore-formers were included in the family by several authors (Sprague 1970, Toguebaye et al. 1986, Lange 1993). Purrini & Weiser (1990) transferred all species of *Nephridiophaga* to *Coelosporidium* and even rejected the family name *Nephridiophagidae* in favour of the name *Coelosporidiidae*. Like in previous reports, the authors assumed that the spore-formers in the Malpighian tubules belong to the haplosporids and therefore referred to the first-named species, i.e., *Coelosporidium blattellae* (Crawley 1905a, b). However, *Coelosporidium chydoricola*, the type species of *Coelosporidium*, was from a cladocere (Mesnil & Marchoux 1897), and has been confirmed to be a member of the haplosporida, thus, the tubule parasites from insects do not belong to that group. Thus, the family name *Coelosporidiidae* and the genus name *Coelosporidium* must be rejected for members of the nephridiophagids. The systematic affiliation of the nephridiophagids to the fungi could only be clarified by molecular phylogenetic analyses of the SSU rRNA gene (Wylezich et al. 2004, Radek et al. 2017). Accepting the fungal nature of the group, Wijayawardene et al. (2018) introduced the new family *Nephridiophagaceae* as an early-branching fungal clade within the order *Nephridiophagales* Doweld. Recently, an extended molecular phylogenetic

analysis using long rDNA amplicons of several species revealed an affiliation of these parasites to the *Chytridiomycota* (Strassert et al. 2021). rDNA sequences are available for *Nephridiophaga* isolates from eight cockroach species and for nephridiophagids isolated from the European earwig and a mallow beetle (Radek et al. 2023).

Radek & Herth (1999) discussed the validity of genera included in the *Nephridiophagidae* and accepted four genera, *Coleospora*, *Nephridiophaga*, *Peltomyces*, and *Oryctospora* as true members. Most reports of these genera are from cockroaches (ten species) and beetles (six species). The only nephridiophagids from other insect orders are *N. apis* from the honey bee (Hymenoptera) and *Nephridiochytrium forficulae* (Radek et al. 2023) from the European earwig (Dermaptera).

Nephridiophaga Ivanić, Cellule 45, 291–324 (1937)
Index Fungorum Identifier 29112

The characteristics of *Nephridiophaga* correspond to the family description of *Nephridiophagaceae*. Mature spores are always uninucleate and have a flattened oval form with a central spore opening on one side. The spore sizes of the species vary between 4.5–8 × 2–4 µm.

Original type species – *Nephridiophaga apis* Ivanić, Cellule 45: 291–324 (1937).

New type species – *Nephridiophaga blattellae*, Radek et al., Taxon 71(2): 471–472 (2022); Fig. 16

Notes – Ivanić (1937) established the genus *Nephridiophaga* for a honey bee pathogen and introduced *N. apis* as the type species. Meanwhile, many further species of *Nephridiophaga* have been described, mainly from cockroaches. Their closer relationship to *N. apis*, however, remains enigmatic due to the lack of preserved specimens. Also, *N. apis* has never been isolated again. Only the published drawings by Ivanić (1937) survived. While new molecular data show that cockroach nephridiophagids are closely related to each other (Strassert et al. 2021), clearly supporting their affiliation to the same genus, the only existing sequences from non-cockroach nephridiophagids, i.e., from the European earwig pathogen and the mallow beetle pathogen, are in sister-group positions (Radek et al. 2023). Thus, it is highly probable that the nephridiophagid from the honey bee, which is likewise phylogenetically only distantly related to cockroaches, is also more loosely related to the *Nephridiophaga* species from cockroaches. To maintain stability in the naming of the majority of nephridiophagid species, *Nephridiophaga blattellae*, the best-investigated cockroach nephridiophagid, was chosen as a new conserved type (Voigt et al. 2021, Radek et al. 2022). The former type *Nephridiophaga apis* should therefore receive a new generic name. The same may be necessary for the *Nephridiophaga* species described from beetles, i.e., *N. meloidorum* (Purrini & Rhode 1988, Lange 1993), *N. ormieresi* (Toguebaye et al. 1986, Purrini & Weiser 1990), *N. tangae* (Purrini et al. 1988, Lange 1993), and *N. schalleri* (Purrini & Rhode 1988, Lange 1993). The following species infecting cockroaches are true members of the genus *Nephridiophaga*: *N. archimandrita* (Radek et al. 2011), *N. blaberi* (Fabel et al. 2000), *N. blattellae* (Crawley 1905a,b, Woolever 1966), *N. javanicae* (Strassert et al. 2021), *N. lucihormetica* (Radek et al. 2011), *N. maderae* (Radek et al. 2017), *N. periplanetae* (Lutz & Splendore 1903, Lange 1993), and *N. postici* (Strassert et al. 2021).

Nephridiophaga blattellae is the new conserved type which lives in the Malpighian tubules of the German cockroach *Blattella germanica* (Fig. 16). Recently, it was shown that infected hosts have an overall reduced fitness (Strassert et al. 2022). The animals had lower fat reserves, showed reduced mobility, produced less progeny, and the ability to detoxify pesticides decreased. The life cycle of *N. blattellae* is well known (Crawley 1905a, Woolever 1966, Radek & Herth 1999). Experimental oral infection of parasite-free hosts revealed intracellular plasmodia as the first detectable stages after 15–17 days (Woolever 1966). The author hypothesized that the sporoplasms hatch in the gut, pass through the gut wall into the hemocoel and then enter the tissue of Malpighian tubules, which lie upon and near the gut surface. Parasite-bearing tubule cells grow and protrude into the lumen before they break open and release numerous parasite cells. Further development of vegetative and sporogenic plasmodia takes place in the tubule lumen (Figs. 1–6). Sporogenic plasmodia mostly contain 10–30 spores and residual somatic nuclei (Figs. 3, 6). Native mature

spores are flattened oval (about 2.5 µm thick) and measure 5.5 (5.0–6.0) µm in length and 3.2 (2.5–3.5) µm in width (Radek & Herth 1999). A central spore opening through which the infectious sporoplasm hatches could be detected on a flat side of the spore (Radek et al. 2002). Cytochemical and fluorescence labelling indicate the presence of chitin, protein, and calcium as components of the spore wall (Radek et al. 2002).

Other genera in *Nephridiophagaceae*

Coleospora Gibbs, Parasitology 49: 552–558 (1959)

Index Fungorum Identifier 22092; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Coleospora binucleata* Gibbs

Notes – *Coleospora binucleata* infects the Malpighian tubules of the tenebrionid beetle *Gonocephalum arenarium* (Gibbs 1959). No further species of this genus have been described to date. Life cycle and morphology of the stages resemble those of *Nephridiophaga*. In addition to the typical development in the lumen of the tubules, intracellular plasmodia infecting the tubular epithelium are common. The numerous intracellular plasmodia form projections into the tubule lumen during growth before they are released. Big multinucleate plasmodia in the lumen start spore formation. Within the sporogenic plasmodia, gametes are formed and fuse to form binucleate cells. After the formation of a synkaryon, the resulting sporoblasts secrete a spore wall. When the wall is fairly well developed, the nucleus undergoes a further division. Thus, the mature spores possess two nuclei, each located about one-third from the ends. The elongated spores measure about 10.5 × 2.5 µm. In saline solutions, they possess two elevated marginal ridges and a central longitudinal depression and ends, which are slightly curved in opposite directions. During experimentally induced hatching of the sporoplasm, a central spore opening allows the emergence of an elongated, binucleate cell.

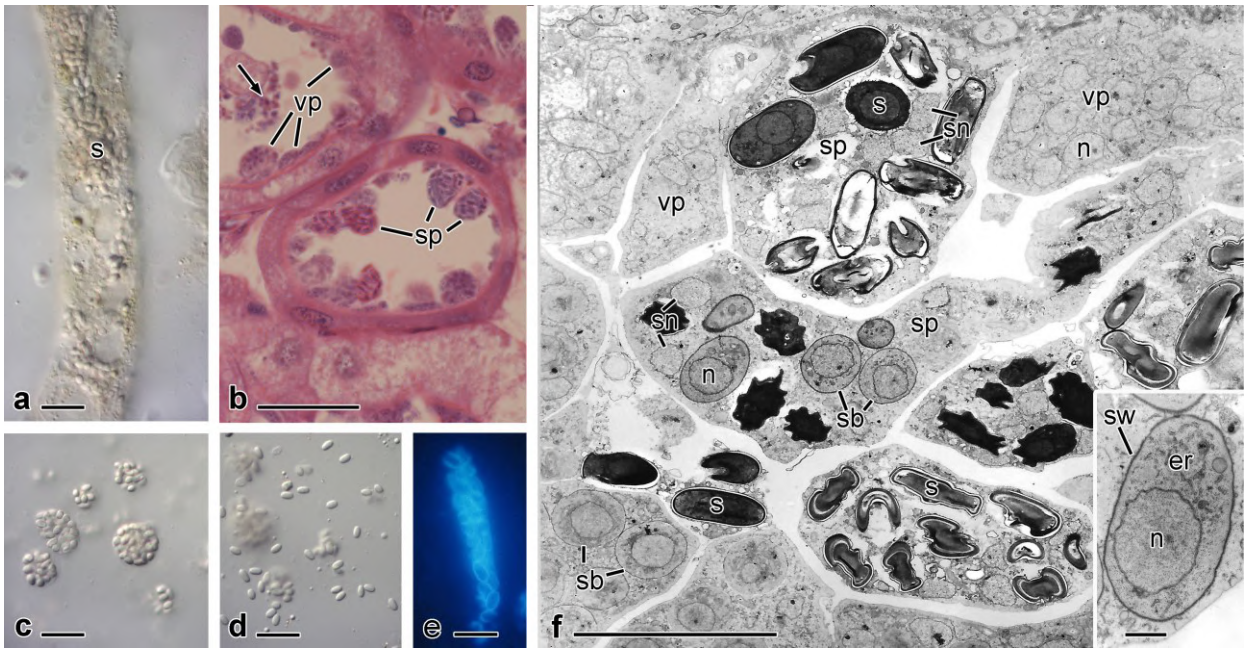


Figure 16 – *Nephridiophaga blattellae* from the German cockroach Blattella germanica. a Spores (s) in the lumen of a heavily infected Malpighian tubule. Differential interference contrast (DIC). b Paraffin section of infected Malpighian tubules stained with hemalaun eosin. Sporogenic plasmodia (sp) and vegetative plasmodia (vp) attach to the tubule epithelium. Arrow = uninucleate stages. c Released sporogenic plasmodia of different sizes. DIC. d Single spores. DIC. e Sporogenic plasmodium; spore-walls stained with fluorescent dye calcofluor. f Ultrathin section of an infected Malpighian tubule. Vegetative plasmodia (vp) with numerous nuclei (n), sporogenic plasmodia (sp) containing sporoblasts (sb), mature spores (s), and residual somatic nuclei (sn). Inset: Sporoblast

with thin spore-wall, nucleus and aggregation of endoplasmic reticulum (er). Transmission electron microscopy. Scale bars: a–d = 20 µm, e, f = 10 µm, f inset = 1 µm. © 2022 Renate Radek, all rights reserved.

Malpighivinco Radek & Strassert, MycoKeys 100: 255 (2023)
Index Fungorum Identifier 850002; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Malpighivinco podagricae* Radek & Strassert 2023, MycoKeys 100: 255 (2023)

Notes – This nephridiophagid has recently been described from the mallow beetle *Podagrica malvae* (Radek et al. 2023). A similar infection has already been found in a closely related host, *Podagrica fuscicornis*, and was originally classified as a haplosporidium (*Coelosporidium schalleri*) by Purrini & Rhode (1988). Lange (1993) later assigned it to the genus *Nephridiophaga* as *Nephridiophaga schalleri.* The new nephridiophagid from *P. malvae* has sporogenic plasmodia with considerably fewer and shorter spores than those from *P. fuscicornis*. Molecular data of the nephridiophagid from *P. malvae* revealed a branching in the phylogenetic tree as sister to all other nephridiophagids from cockroaches and the earwig, justifying the assignment to the new genus *Malpighivinco* (Radek et al. 2023). The name *Malpighivinco* refers to the Malpighian tubules as habitat, and the Latin word "vinco" (verb "vincere") for "I conquer", reflects that the pathogen infects the tubules. The species epithet *podagricae* refers to the mallow beetle host of the genus *Podagrica*. Probably, the nephridiophagid from *P. fuscicornis* belongs to the same genus and not to *Nephridiophaga*.

There are no obvious differences in morphology and life cycle from other nephridiophagid genera. In addition to oligo- and multinucleated vegetative plasmodia, sporogenic plasmodia are present, which internally form spores (7–36, mean 21.5 spores per plasmodium). The oval, flattened spores measure 4.2 (3.6–4.7) × 2.3 (2.1–2.5) µm and possess a central capped spore-opening at one side of the mature spores. Presently, *Malpighivinco* is a monotypic genus.

Nephridiochytrium Radek & Strassert, MycoKeys 100: 254 (2023)
Index Fungorum Identifier 850000; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Nephridiochytrium forficulae* Radek & Strassert 2023, MycoKeys 100: 254 (2023)

Notes – This pathogen was described by Léger (1909) as a species of *Peltomyces* from the European earwig *Forficulae auricularia*, and was named *Peltomyces forficulae* (MycoBank 147059). Later, this pathogen was investigated in more detail and renamed *Nephridiophaga forficulae* (Ormières & Manier 1973). In contrast to the only safely assigned species of the genus *Peltomyces* (*Peltomyces hyalinus*), the mature spore of the earwig pathogen contains only one nucleus. In a recent study, it was shown that the SSU rRNA gene sequence of the earwig nephridiophagid is more distantly related to the *Nephridiophaga* sequences from cockroaches and branches as a sister to them (Strassert et al. 2021). Based on these data and additional morphological studies, the earwig nephridiophagid was classified as a new genus, *Nephridiochytrium*, and renamed *Nephridiochytrium forficulae* (Radek et al. 2023). "Nephridio" refers to the site of infection, the nephridia (Malpighian tubules) and "chytrium" refers to the assignment to the *Chytridiomycota*.

The life cycle with the oligo- and multinucleated vegetative plasmodia and sporogenic generative plasmodia is similar to other genera of *Nephridiophagaceae*. A sporogenic plasmodium contains 13–37 (mean 19) flattened oval spores, which measure 6.3 (5.8–6.9) × 3.2 (2.9–3.5) µm. A central capped spore opening is present at one side of mature spores. *Nephridiochytrium* is a monotypic genus.

Oryctospora Purrini & Weiser, Zoologische Beiträge 33, 209–220 (1990).

Index Fungorum Identifier 92046; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Oryctospora alata* Purrini & Weiser 1990

Notes – *Oryctospora alata* was described to infect the Malpighian tubules of the rhinoceros beetle *Oryctes monoceros* (Purrini & Weiser 1990). Only adult beetles carried the infection, became lethargic, and died after 20–30 days. Their Malpighian tubules became partially hypertrophic.

Merogony and sporogony processes of *Oryctospora* are very similar to those of *Nephridiophaga*, but the mature spores are oval, measuring 7.0–7.5 × 3.0–3.5 µm, with up to 2.5 µm wide lateral protrusions (alae) on both sides. One to 13 uninucleate spores are formed within a sporogenic plasmodium. Currently, *Oryctospora* is a monotypic genus.

Peltomyces Léger, Comptes Rendues de l'Académie des Sciences [III] 149, 239–241 (1909).
Index Fungorum Identifier 12172; Index Fungorum (2025) listed three epithets, but Species Fungorum (2025) transferred two species to *Nephridiophaga.*

Type species – *Peltomyces hyalinus* Léger, Comptes Rendues de l'Académie des Sciences [III] 149, 239–241 (1909)

Notes – *Peltomyces hyalinus* infects the Malpighian tubules of the tenebrionid beetle *Olocrates abbreviatus.* The life cycles of *Peltomyces* and *Nepridiophaga* are similar, but there are some differences in spore formation (Léger 1909). The generative and somatic nuclei have a typical position in the sporogenic plasmodia. While the big generative nuclei accumulate in the centre of their mother cell, the small somatic nuclei move to the periphery. The generative nuclei seem to be able to undergo sexual processes with the formation of gamete nuclei and fusion to a synkaryon. The formation of a wall around the synkaryon and its surrounding cytoplasm leads to the production of spores. Mature spores have a cylindrical form with rounded ends (9 × 3 µm) and contain two nuclei since the original nucleus divides by mitosis. Occasionally, some gametes within the sporont do not copulate but form parthenogenetic spores directly that are only half the size of the sexual spores (Léger 1909).

Léger (1909) named a second species, *P. forficulae* (MycoBank 147059) from the European earwig *Forficulae auricularia*. Later, this pathogen was renamed as *Nephridiophaga forficulae* (Ormières & Manier 1973). The mature spore contains only one nucleus. In a recent study, it was shown that the SSU rRNA gene sequence of the earwig nephridiophagid is more distantly related to the *Nephridiphaga* sequences from cockroaches and branches as a sister to them (Strassert et al. 2021, Radek et al. 2023). Thus, the earwig nephridiophagid received the new genus name, *Nephridiochytrium.*

Polyphagales Doweld
Polyphagaceae F. Maekawa, J. Jap. Bot. 21: 119. 1948
Index Fungorum Identifier 816487

Thallus eucarpic, monocentric, interbiotic. Reproductive rudiment formed as an outgrowth from the body of the encysted zoospore, with radially oriented rhizoids. Zoospores posteriorly uniflagellate. Resting spores sexually formed in conjugation tube produced by 1 of 2 conjugating thalli (Sparrow 1960, Karling 1977, Doweld 2014d).

Family type – *Polyphagus* Nowak., in Cohn, Beitr. Biol. Pfl. 2(2): 203. (1877) [1876]

Ecology & life modes – This family is composed of two genera, *Polyphagus*, the type genus, and *Volvorax* (= *Endocoenobium)*, whose species were found as parasites of freshwater algae.

Notes – The phylogenetic analyses based on 18S rRNA sequences of *Polyphagus parasiticus* corroborated the erection of the *Polyphagales* by Doweld (2014d), an order that formed a clade sister to *Gromochytriales* and *Mesochytriales* (Karpov et al. 2016b). Posteriorly, phylogenetic analyses based on 18S and 28S rDNA sequences showed that *Endocoenobium eudorinae* (= *Volvorax ingoldii*) clustered together with *Polyphagus parasiticus*, which was further confirmed by Van der Wyngaert et al. (2018).

Polyphagus Nowak., Beitr. Biol. Pfl. 2(2): 203. (1877) [1876]
Index Fungorum Identifier 20436

Thallus eucarpic, monocentric, consisting of an expand central part, the rudiment of the prosporangium, with two or more rhizoids, much branched, strongly polyphagous, only the tips endobiotic. Zoosporangia inoperculate, formed as an outgrowth from the prosporangium. Zoospores posteriorly uniflagellate, completely formed into zoosporangium, with a single globule, discharged by one pore. Resting spore thick-walled, with a large globule, formed in conjugation tube produced by 1 of 2 conjugating thalli; upon germination functioning as a prosporangium (Sparrow 1960).

Type species – *Polyphagus euglenae* (Bail) Nowak., in Cohn, Beitr. Biol. Pfl. 2(2): 203. (1877) [1876]

Notes – *Polyphagus* comprises eleven epithets (Species Fungorum 2025). These species are parasitizing susceptible algae around the world. It was first placed into the *Chytridiales* based on morphology and ultrastructure data (Sparrow 1960, Karling 1977, Powell 1981). However, molecular studies included this genus in *Polyphagales* (Karpov et al. 2016b, Van der Wyngaert et al. 2018). Cultures are available on the Culture Collection of Parasitic Protista at the Zoological Institute RAS (CCPP ZIN RAS) and sequences on GenBank.

Other genus in *Polyphagaceae*
Volvorax Doweld, Index Fungorum 37: 1 (2013)
Index Fungorum Identifier 550301; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Volvorax ingoldii* Doweld 2013

Notes – Reported from the United Kingdom, Germany and Switzerland (Sparrow 1960, Van der Wyngaert et al. 2018). Cultures are not available, but sequences are available on GenBank.

Saccopodiales Doweld
Saccopodiaceae Jacz. & P.A. Jacz., Opredelitel' gribov. Sovershennyye griby (diploidnyye stadii). 3-ye izd. [Vyp. 1]. Fikomitsety: 46 (1931)
Index Fungorum Identifier 90715

Mycelium well developed, branched, extending inside substrate; sporangiophore simple, cylindrical, protruding from the substrate, bearing a cluster of spherical sporangia at apex; sporangia with a simple mouth at the apex from which zoospores emerge. Resting spore unknown.

Family type – *Saccopodium* Sorokin, Hedwigia 16: 88 (1877)

Ecology & life modes – Parasite of *Cladophora*.

Notes – *Saccopodiaceae* is a monotypic family in *Saccopodiales* (Doweld 2014j). It is necessary to do further sampling and carry out molecular analyses to confirm its classification and phylogenetic placement.

Saccopodium Sorokin, Hedwigia 16:88 (1877)
Index Fungorum Identifier 20498

Thallus tubular, without cross walls, branched, endobiotic with extrametrical unbranched sporangiophores; sporangia in clusters of from six to twelve at the tips of the extrametrical sporangiophores, spherical or pyriform, without a discharge tube; zoospores oblong, emerging through an opening in the sporangium, flagella not observed; resting spore not observed (Sparrow 1960).

Type species – *Saccopodium gracile* Sorokin, Hedwigia 16:88 (1877)

Note – *Saccopodium* is a monotypic genus characterized by clustered zoosporangia at the tips of sporangiophores. Sorokin (1877) could not observe a flagellum for this fungus. *Saccopodium*

was regarded as an imperfectly known genus of the *Cladochytriaceae* (Sparrow 1960) or a genus of doubtful affinity (Karling 1977).

Zygophlyctidales K. Seto
Zygophlyctidaceae K. Seto, Fungal Systematics and Evolution 5: 32 (2020)
Index Fungorum Identifier 831580

Thallus monocentric, eucarpic, endogenous; zoosporangium epibiotic, operculate; resting spore formed after fusion of male thallus and female thallus via conjugation tube (Seto et al. 2020b).

Family type – *Zygophlyctis* Doweld

Ecology & life modes – Diatom parasites

Notes – Seto et al. (2020b) introduced *Zygophlyctidales* to accommodate *Zygophlyctidaceae*, which includes three diatom parasites, *Zygophlyctis asterionellae*, *Z. melosirae*, and *Z. planktonica*. This phylogenetic group was known as "Novel Clade II (Jobard et al. 2012)" and composed of environmental sequences from freshwater environments. *Zygophlyctidales* belongs to *Chytridiomycetes* sensu Hibbett et al. (2007), but this order could be placed in an independent class in *Chytridiomycota* in the taxonomic system of Tedersoo et al. (2018).

Zygophlyctidaceae includes a single genus, *Zygophlyctis*.

Zygophlyctis Doweld, Index Fungorum 114: 1 (2014)
Index Fungorum Identifier 550450

Thallus monocentric, eucarpic, sporangium and resting spore developed by direct enlargement of the zoospore. Sporangium ampulliform to pyriform. Rhizoidal system endobiotic, of branched threads; operculum develops at the top of an apical papilla and dehiscence apical. Zoospores with dispersed or loosely aggregated ribosomes and a rumposome complex, possess some vesicle types (fibrillar vesicle lies adjacent to the fenestrated cisternae); nonfunctional centriole constructed of a ring of singlet microtubules or occasionally containing two or three triplet, and often completely disassociated from the kinetosome. Resting spores are globose, and spherical (Doweld 2014g, Seto et al. 2020b).

Type species – *Zygophlyctis planktonica* Doweld, Index Fungorum 114: 1 (2014)

Note – *Zygophlyctis* includes three species of diatom parasitic chytrids, which were formerly known as members of the genus *Zygorhizidium*. Doweld (2014g) pointed out that the descriptions of *Zygorhizidium planktonicum* (Canter & Lund 1953, Canter 1967) were invalid and gave a new description of the species. However, Doweld (2014g) described a new genus, *Zygophlyctis*, without molecular evidence. Subsequently, Seto et al. (2020b) revealed that *Z. planktonica* and two related species are distinguished from the type species of *Zygorhizium*, *Z. willei*, in zoospore ultrastructure and molecular phylogeny, which validates the genus establishment by Doweld (2014g).

Zygorhizidiales K. Seto
Zygorhizidiaceae Doweld, Index Fungorum 102: 1 (2014) emend. K. Seto, Fungal Systematics and Evolution 5: 30 (2020)
Index Fungorum Identifier 550424

Thallus monocentric, eucarpic, endogenous; zoosporangium epibiotic, operculate; resting spore formed after fusion of male and female thallus via conjugation tube (Seto et al. 2020b).

Family type – *Zygorhizidium* Löwenthal

Ecology & life modes – Parasites of green algae and chrysophycean algae

Notes – *Zygorhizidiaceae* was proposed by Doweld (2014i), based on the zoospore ultrastructural characteristics of *Z. affluens* observed by Beakes et al. (1988). However, molecular phylogenetic analysis of *Z. affluens* (Rad-Menéndez et al. 2018) revealed that it is related to *Lobulomycetales* (*Lobulomycetes*), which is separated from the type species of *Zygorhizidium*. Therefore, the description of *Zygorhizidiaceae* was emended based on morphological and ultrastructural characteristics of *Z. willei* (Seto et al. 2020b). Currently, *Zygorhizidiaceae* includes a single genus, *Zygorhizidium*.

Zygorhizidium Löwenthal, Archiv für Protistenkunde 5: 228 (1905)
Index Fungorum Identifier 20609

Thallus monocentric, eucarpic. Zoospore posteriorly uniflagellate. Zoosporangium operculate, epibiotic, sessile, formed from the enlarged body of the encysted zoospore. Rhizoidal system endobiotic, consisting usually of a subsporangial apophysis with or without an unbranched or branched broad rhizoid. Resting spore epibiotic, sessile, thick-walled, formed from the body of the receptive thallus after conjugation with a usually contributing smaller thallus by means of a conjugation tube produced by the smaller thallus (Sparrow 1960).

Type species – *Zygorhizidium willei* Löwenthal, Archiv für Protistenkunde 5: 228 (1905); Fig. 17

Notes – *Zygorhizidium* formerly belonged to the order *Chytridiales* (Sparrow 1960). However, it was placed in the new order *Zygorhizidiales* based on the molecular phylogeny and zoospore ultrastructure of the type species *Z. willei* (Seto et al. 2020b). *Zygorhizidiales* belongs to *Chytridiomycetes* sensu Hibbett et al. (2007). However, this order could be placed in an independent class in *Chytridiomycota* in the taxonomic system of Tedersoo et al. (2018).

Zygorhizidium comprises eleven species, including invalid species and excluding *Z. vaucheriae* whose affinity to the genus is unsure because of its anteriorly uniflagellate zoospores (Karling 1977). Three diatom parasitic species were transferred to *Zygophlyctis* in *Zygophlyctidales* (Seto et al. 2020b), and another diatom parasite, *Z. affluens*, should be excluded from *Zygorhizidium* (Rad-Menéndez et al. 2018). The remaining seven species include parasites of zygnematophycean green algae (two species), chrysophycean algae (two species), and chlorophycean green algae (three species). Currently, only the type species *Z. willei* has been accepted by molecular analysis.

Chytridiomycetes* families *incertae sedis
Amoebochytriaceae Doweld, Index Fungorum 58:1 (2014)
Index Fungorum Identifier 550356

Thallus polycentric, eucarpic, consisting of a branched rhizoidal system bearing intercalary swellings. Sporangia inoperculate, pyriform, basally apophysate with more or less prolonged discharge tubes, formed by enlargement of the body of the encysted zoospore or of the intercalary swellings of the rhizoids, cut off at maturity by cross walls from the vegetative system and often disarticulated. Zoospores are aflagellate, ovoid, with a large yellowish globule, escaping by forcing one of the gelatinized cross walls, movement strongly amoeboid; resting spores not observed. Saprophytic in the gelatinous matrix of colonies of *Chaetophora elegans* (Doweld 2014k).

Family type – *Amoebochytrium* Zopf

Ecology & life mode – on *Chaetophora*

Notes – *Amoebochytriaceae* was proposed by Doweld (2014k) based on morphological characteristics observed by Zopf (1884), but there is no evidence from molecular phylogeny.

Amoebochytrium Zopf, Nova Acta Acad. Leop.-Carol. 47: 181 (1885)
Index Fungorum Identifier 20023

Thallus polycentric, eucarpic, consisting of a branched rhizoidal system bearing on it intercalary swellings. Zoosporangia inoperculate, formed by enlargement of the body of the encysted zoospore or of the intercalary swellings of the rhizoids, cut off at maturity by cross walls from the vegetative system and often disarticulated. Zoospores without flagella, escaping by forcing one of the gelatinized cross walls, and amoeboid movement. Resting spore not observed (Zopf 1884, Sparrow 1960).

Type species – *Amoebochytrium rhizidioides* Zopf, Nova Acta Acad. Leop.-Carol. 47: 181 (1885)

Notes – The genus is monotypic and apparently restricted to Europe. Cultures or sequence data are lacking; thus, this genus needs a systematic revision to confirm its suprageneric placement.

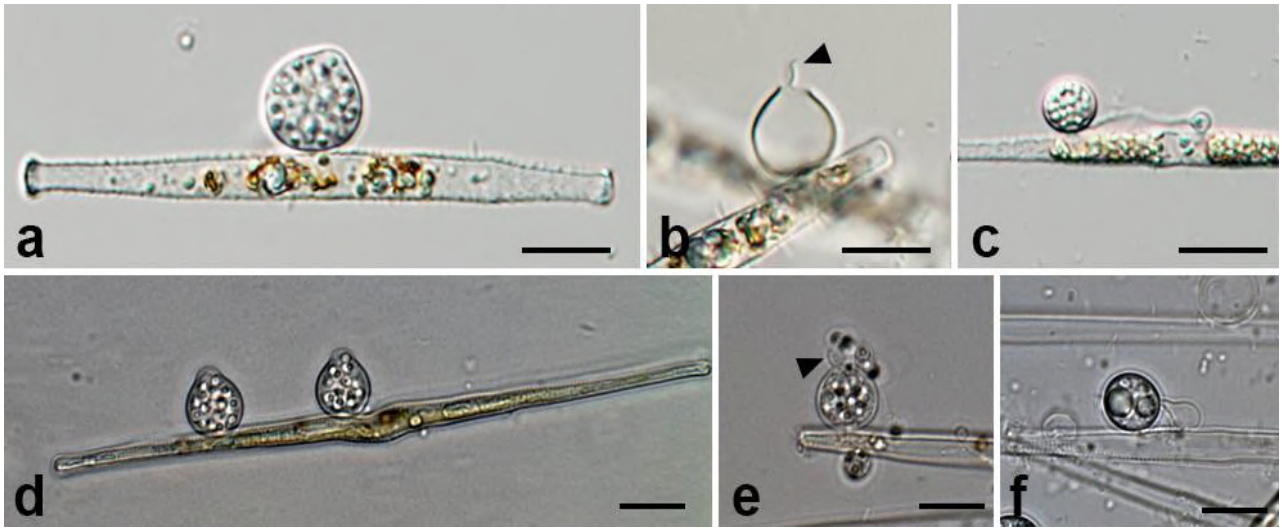


Figure 17 – Morphology of *Zygorhizidiales* and *Zygophlyctidales*. a-c *Zygorhizidium willei* (*Zygorhizidiales*) parasitic on *Gonatozygon brebissonii*. a Mature zoosporangium. b Empty zoosporangium with an operculum (arrowhead). c Resting spore and empty male thallus connected by a conjugation tube. d-f *Zygophlyctis planktonica* (*Zygophlyctidales*) on *Ulnaria* sp. d Mature zoosporangium. e Zoosporangium with an operculum (arrowhead) during zoospore discharge. f Resting spore and empty male thallus connected by a conjugation tube. Scale bars = 10 μm.

Sparrowiaceae Doweld, Index Fungorum 104:1 (2014)
Index Fungorum Identifier 550426

Thallus monocentric, eucarpic, epibiotic. Sporangia and resting bodies with a basal hemispherical protuberance derived from the zoospore cyst, rhizoids branched, endobiotic, sometimes digitate. Sporangia operculate; zoospores posteriorly uniflagellate, with a single lipid globule. Resting bodies are elongated, divided by a cross wall into an empty proximal portion and a distal thick-walled portion (resting spore).

Family type – *Sparrowia* Willoughby

Ecology & life modes – Parasite of oogonia of *Oomycetes*.

Notes – *Sparrowiaceae* was proposed by Doweld (2014l) based on morphological characteristics observed by Willoughby (1963), but there is no evidence from molecular phylogeny.

Sparrowia Willoughby, Nova Hedwigia 5:336 (1963)
Index Fungorum Identifier 20531

Thallus monocentric, eucarpic, epibiotic. Sporangia and resting bodies with a basal hemispherical protuberance, the latter derived from the zoospore cyst, and with a delicate, branched endobiotic rhizoid. Sporangia with a single operculum. Zoospore with a single oil globule and posterior flagellum. Resting bodies are elongated, divided by a cross wall into an empty proximal portion and a distal portion (the resting spore), which is thick-walled and contains oil globules (Willoughby 1963).

Notes – *Sparrowia* comprises two species with a cosmopolitan distribution. DNA sequences are lacking, thus higher-level classification is uncertain.

Type species – *Sparrowia parasitica* Willoughby, Nova Hedwigia 5:337 (1963); Fig. 18

Sphaeromonadaceae Doweld, Index Fungorum 108: 1 (2014)
Index Fungorum Identifier 550435

Monocentric and uni- or multisporangiate; rhizoids bulbous; sporangiophores branched; zoospores spherical to ovoid, uniflagellate, occasionally biflagellate (extracted from Doweld 2014o)

Family type – *Sphaeromonas* E. Liebet.

Ecology & life modes – Stomach of a ruminant in Switzerland

Notes – Doweld (2014o) introduced this family to accommodate *Sphaeromonas.* The genus comprises three species (Species Fungorum 2025).

Sphaeromonas E. Liebet., Arch. Protistenk. 19: 25 (1910)
Index Fungorum Identifier 25137

Similar to the family description.

Notes – Similar to the notes under the family.

Type species – *Sphaeromonas* minima E. Liebet., Arch. Protistenk. 19: 31 (1910)

Tetrachytriaceae Doweld, Index Fungorum 39:1 (2013)
Index Fungorum Identifier 550321

Thallus polycentric, eucarpic, hyphoid. Sporangiophore axes are dichotomously branched, bearing 3 terminal, solitary, apically operculate zoosporangia (with apical umbo) and a single sterile recurved appendage (branch). Asexual reproduction by zoospores; zoospores spherical, posteriorly uniflagellate, with a vacuole, forming outside the sporangium in an evanescent vesicle, movement not amoeboid. Sexual reproduction by zygospores. Saprophytes on decaying wood and grass stems, insect cadavers (Coleoptera) (extracted from Doweld 2013a).

Family type – *Tetrachytrium* Sorokīn

Ecology & life modes – Saprobic on decaying wood, grass stems, and insect cadavers.

Notes – In the description of *Tetrachytriaceae*, Doweld (2013a) indicated *Tetrachytrium* as the type genus of the family and did not mention other genera. However, according to his description, *Zygochytrium* is also included in this family.

Tetrachytrium Sorokīn, Bot. Ztg. 32:311 (1874)
Index Fungorum Identifier 20567

Zoospore upon germination developing at one pole a cylindrical axis which forms distally a single short reflexed lateral sterile branch and three terminal ones, each of which bears a single operculate sporangium, developing at the opposite pole a lobed holdfast which anchors the plant to the substratum; the thallus polycentric, eucarpic, hypha-like; zoospores four, with a central vacuole, posteriorly uniflagellate, mature outside the sporangium in a delicate evanescent vesicle which envelops the extruded protoplasm after dehiscence of the operculum, conjugating in pairs to from a new sporangial plant; no resting stage formed (Sparrow 1960).

Type species – *Tetrachytrium triceps* Sorokīn, Bot. Ztg. 32: 315 (1874)

Tetrachytrium Sorokīn, Bot. Ztg. 32:311 (1874)
Index Fungorum Identifier 20567

Zoospore upon germination developing at one pole a cylindrical axis which forms distally a single short reflexed lateral sterile branch and three terminal ones, each of which bears a single operculate sporangium, developing at the opposite pole a lobed holdfast which anchors the plant to the substratum; the thallus polycentric, eucarpic, hypha-like; zoospores four, with a central vacuole, posteriorly uniflagellate, mature outside the sporangium in a delicate evanescent vesicle which envelops the extruded protoplasm after dehiscence of the operculum, conjugating in pairs to from a new sporangial plant; no resting stage formed (Sparrow 1960).

Type species – *Tetrachytrium triceps* Sorokīn, Bot. Ztg. 32: 315 (1874)

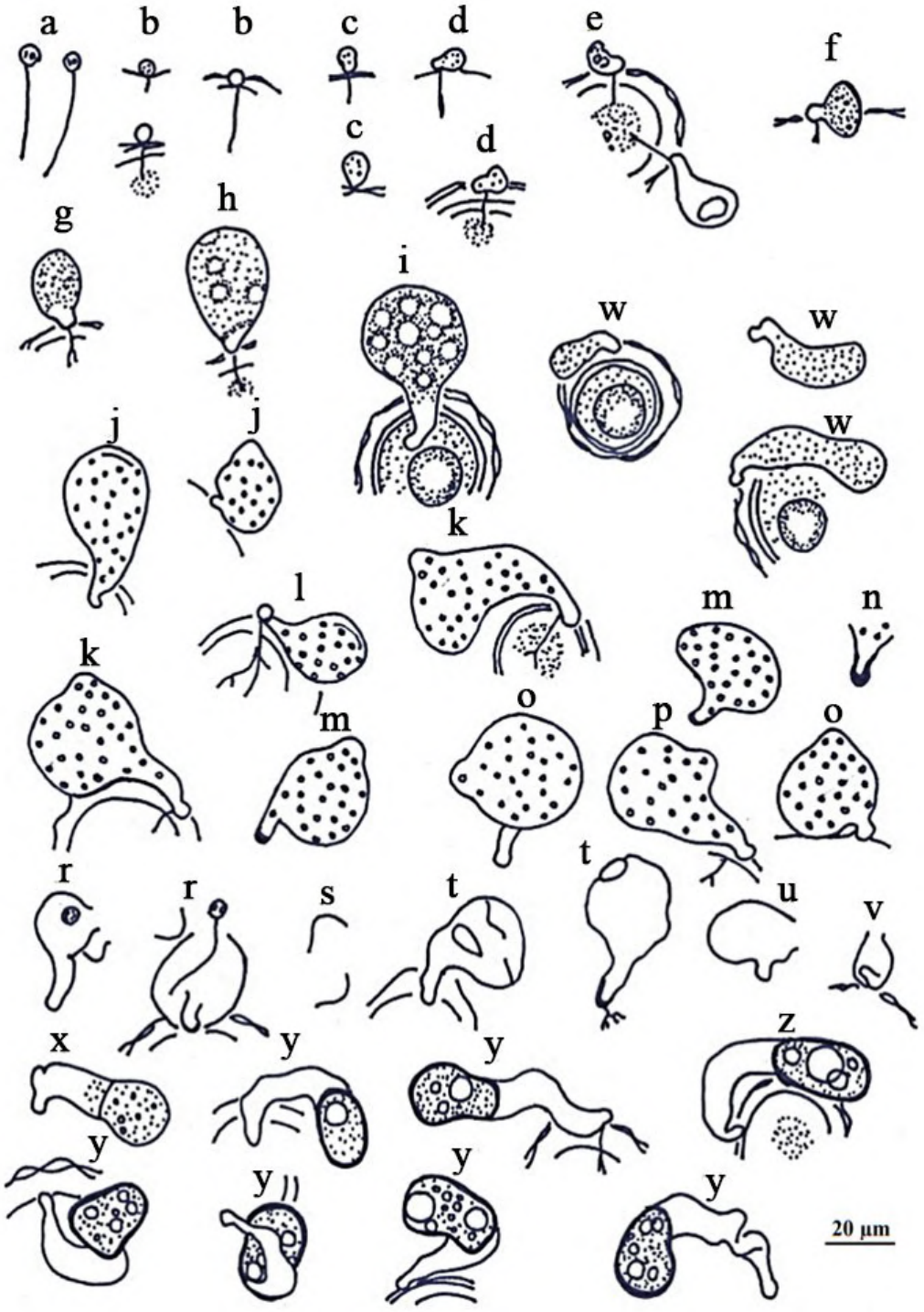


Figure 18 – *Sparrowia parasitica* a zoospore. b germinating zoospores. c later stages in growth with the sporangium developing vertically. d stages in growth with the sporangium developing laterally. e–g young thalli. h, i sporangia approaching maturity and showing central vacuolation; j, o mature sporangia showing opercula. k, p mature sporangia with the operculum in a lateral position. l a mature sporangium showing extensive development of the rhizoid. m mature sporangia with the basal cyst heavily thickened. n the base of a mature sporangium showing a heavily thickened cyst. g a globose mature sporangium. r dehiscing sporangia with opercula. s detached opercula observed. t dehisced sporangia with the basal cyst heavily thickened. u an oblong dehisced sporangium. v a small dehisced sporangium. w developing resting bodies. x a developing resting body with the resting spore just delimited by a cross wall. y mature resting bodies. z a mature resting body. All drawings at the same scale (Redrawn from Willoughby 1963).

Other genus in *Tetrachytriaceae*

Zygochytrium Sorokīn, Bot. Ztg. 32:308 (1874)

Index Fungorum Identifier 20605; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Zygochytrium aurantiacum* Sorokīn, Bot. Ztg. 32:308 (1874)

Notes – Both *Tetrachytrium* and *Zygochytrium* were described by Sorokin (1874), but they have not been rediscovered since. In the monographic works of chytrid fungi, these genera were regarded as genera of doubtful affinity (Sparrow 1960, Karling 1977).

Thalassochytriaceae Doweld, Index Fungorum 51:1 (2014)

Index Fungorum Identifier 550349

Thallus endobiotic, polycentric, septate hyphae form haustoria penetrating algal cells. Sporangia are elliptical, with a single discharge papillum. Zoospores are oval, tapering toward a single posterior flagellum, with five lipid globules, and ribosomes dispersed in the cytoplasm. Kinetosome is anteriorly located, associated with a helical structure. Nucleus with a heel-like protrusion toward the kinetosome. Flagellar axoneme traverse zoospores and exits the zoospore posteriorly. Lacking props, non-flagellated kinetosome, kinetosomal roots and rumposome. Parasitic in Rhodophyceae (Doweld 2014e).

Family type – *Thalassochytrium* Nyvall, M. Pedersén & Longcore

Ecology & life modes – Endoparasite of red algae.

Notes – *Thalassochytriaceae* was proposed by Doweld (2014m) based on the morphological and ultrastructural observations by Nyvall et al. (1999), but there are no molecular phylogeny studies.

Thalassochytrium Nyvall, M. Pedersén & Longcore, Journal of Phycology 35:182 (1999)

Index Fungorum Identifier 27961

Parasitic in *Gracilariopsis* sp. (*Rhodophyceae*). Thallus endobiotic and polycentric, septate hyphae form haustoria that penetrate algal cells. Sporangia orange, large (50–300 mm), elliptical, with one discharge papillum protruding from the algal cortex at maturity. Zoospores ooze out of the pore in a cluster and remain motionless for several minutes before dispersing by flagellar motion. Zoospores are oval, tapering toward a single posterior flagellum. About five orange lipid globules are in the anterior of the spore, and ribosomes are dispersed in the cytoplasm. Kinetosome is anteriorly located and associated with a helical structure. Nucleus with a heel-like protrusion toward the kinetosome. Flagellar axoneme traverse zoospores and exits the zoospore posteriorly. Lacking props, nonflagellated kinetosome, kinetosomal roots and rumposome (Nyvall et al. 1999).

Type species – *Thalassochytrium gracilariopsidis* Nyvall, M. Pedersén & Longcore, Journal of Phycology 35:182 (1999); Fig. 19

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

Cladochytriales Mozl.-Standr., Mycol. Res. 113(4): 502 (2009)

Cladochytriaceae J. Schrot. in Engler & Prantl, Nat. Pflanzenfam 1: 80 (1897)

Index Fungorum Identifier 80598

Thallus polycentric, consisting of rhizomycelium with septate intercalary swellings (turbinate cells), and inoperculate or operculate zoosporangia. Zoospore description as for *Cladochytriales* (Mozley-Standridge et al. 2009).

Ecology & life modes – The family is composed mainly saprophytic species, facultative parasites and a few reports of obligate parasites. Saprophytic species decompose decaying plant material, moribund algae, insect exuviae and other organic substrates in freshwater and terrestrial ecosystems (Sparrow 1960, Karling 1977, Mozley-Standridge et al. 2009).

Family type – *Cladochytrium* Nowak. in Cohn, Beitr. Biol. Pfl. 2: 92 (1877)

Notes – Two polycentric genera (*Cladochytrium* and *Karlingiella*) are included in *Cladochytriacea*. *Karlingiella* is a monotypic operculate genus, which includes only *K. elongata*, previously named *Nowakowskiella elongata* and placed in a new genus based on multigenic analysis of ribosomal data (Jerônimo et al. 2019). *Cladochytrium* is inoperculate and produces septate swellings or turbinate cells in the rhizomycellium. This genus comprises 51 species, and typified with *C. tenue* (Clements & Shear 1931). However, several taxa were transferred to the plant parasitic genus, *Physoderma*, and currently, 20 legitimate species are recognized in *Cladochytrium*. Among these, *Cladochytrium maydis* (*Physoderma maydis*) causes brown spot of maize, and *C. alfalfae* (*Physoderma alfalfae*) causes crown wart of alfalfa. *Physoderma* was placed in *Blastocladiomycota* by James et al. (2006b) through the analysis of ribosomal genes.

Sequences are available for only four species (*Cladochytrium replicatum*, *C. tenue*, *C. polystomum* and *Karlingiella elongata*), and the systematics of the family remains uncertain. Some species, such as *C. polystomum*, were transferred to *Zopfochytrium* within *Chytridiales*. The type species of *Cladochytrium* (*C. tenue*) forms a distinctive branch within *Chytridiales* genera *incertae sedis* (Powell et al. 2018a, Jesus et al. 2021, Amses et al. 2022). An important aspect of *Cladochytriaceae* phylogeny is the necessity of expanding the taxa sampling and culture isolation, especially for unsequenced strains, which will help us to better understand their systematics. Cultures are available on CZEUM (Collection of Zoosporic Eufungi at the University of Michigan) and sequences on GenBank.

Cladochytrium Nowak. in Cohn, Beitr. Biol. Pfl. 2: 92 (1877)
Index Fungorum Identifier 20132

Thallus polycentric, formed by a rhizomycellium with septate, turbinate cells and inoperculate zoosporangia. Zoospores are posteriorly uniflagellate and discharged through a pore. Resting spores are apparently asexually formed, borne like the sporangia on the thallus, with a thickened smooth or spiny wall (Nowakowskii 1877, Sparrow 1960).

Type species – *Cladochytrium tenue* Nowak. in Cohn, Beitr. Biol. Pfl. 2: 92 (1877)

Notes – The genus was proposed by Nowakowskii (1877) to accommodate two species, *C. tenue* and *C. elegans*, the latter transferred to *Nowakowskiella* by Engler & Prantl (1897), based on the absence of turbinate cells in rhizomycelium and the presence of an operculum in zoosporangium. The 20 species described in the genus are primarily inhabitants of decaying plant tissues such as those of *Acorus* and *Elodea* (Sparrow 1960). They have also been found in the gelatinous envelope of algae such as *Chaetophora*, *Spirogyra* and *Coleochaete* (Sparrow 1960). *Cladochytrium replicatum* is a well-documented species, which is characterized by the production of zoospores with an orange lipid globule. Jerônimo et al. (2019, 2022) observed at least five phylogenetically distinctive lineages named *C. replicatum*, indicating that these taxa represent a species-complex and its taxonomy should be reevaluated. *Cladochytrium* is distributed in South America (Nascimento et al. 2009, Steciow et al. 2012, Jesus et al. 2013, Jerônimo et al. 2015 and others), North America (Karling 1931, Berdan 1941, Karling 1949, Karling 1951, Sparrow 1960, Karling 1977, and others), Europe (Remy 1948, Richards 1956, Batko & Hassan 1986, Czeczuga et al. 2007a, and others), Asia (Singh & Pavgi 1971, Chen et al. 2000 and others) and Africa (Gaertner 1954, Hassan & Shoulkamy 1991 and others).

Other genus included

Karlingiella (Karling) G.H. Jerônimo, A.L. Jesus & Pires-Zottar., in Jerônimo, Jesus, Simmons, James & Pires-Zottarelli, Mycologia 111: 8 (2019)
Index Fungorum Identifier 829121

Type species – *Karlingiella elongata* (Karling) G.H. Jerônimo, Jesus & Pires-Zottarelli, Mycologia 111: 8 (2019); Fig. 33h

Notes – *Karlingiella* is a monotypic genus, including only *K. elongata*, which was originally described as *Nowakowskiella elongata* (Jerônimo et al. 2019). Through the analysis of ribosomal genes, Jerônimo et al. (2019) placed it in a new genus closely related to *Cladochytriaceae* rather

than *Nowakowskiellaceae*. *Nowakowskiella elongata* was originally found in Brazil by John Karling, and then another isolate from the same country was purified in culture and included in phylogenetic analysis (Jerônimo et al. 2019). There are reports of this chytrid in South America (Karling 1944, Jesus et al. 2013, Jerônimo et al. 2019 and others) and Africa (Hassan 1993).

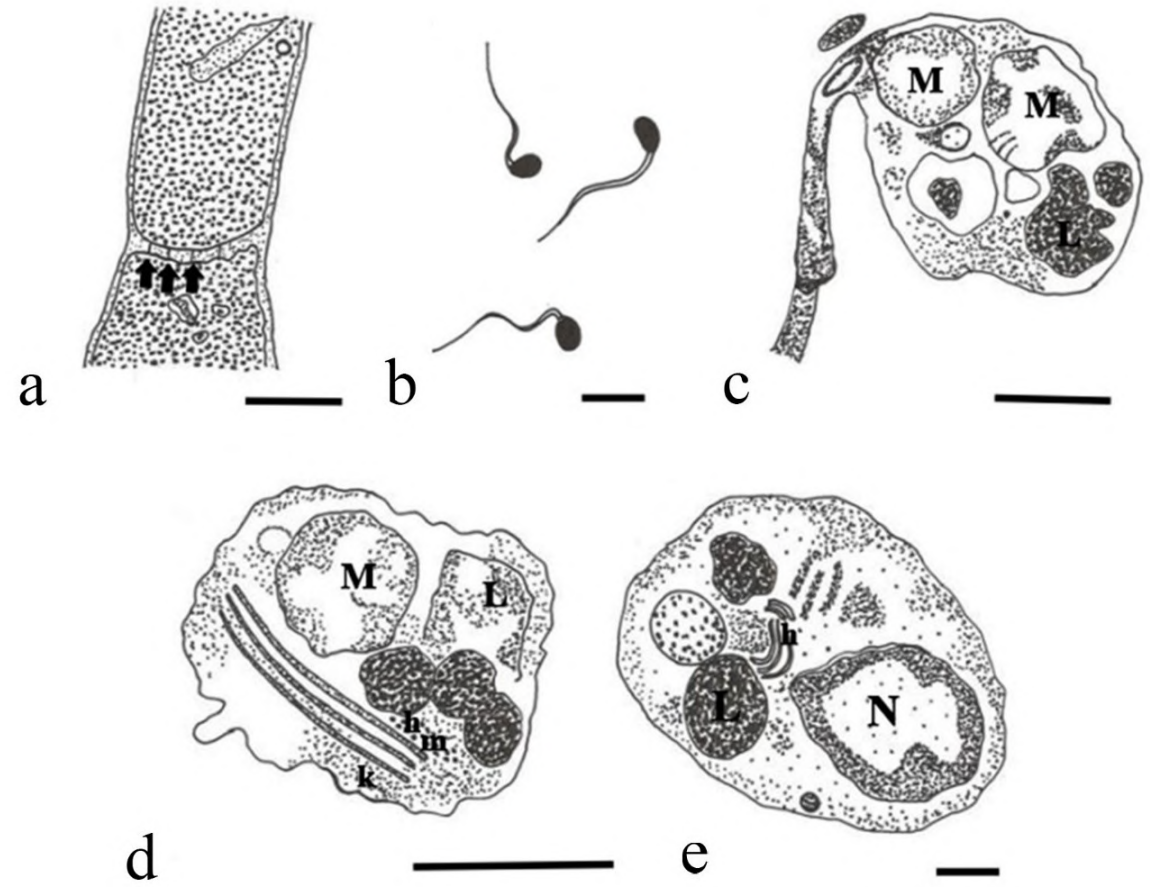


Figure 19 – *Thalassochytrium gracilariopsidis*; Ultrastructure of septum and zoospores and light microscopy of zoospores. a Longitudinal section of fungal hypha with transverse septum perforated by pores (arrowheads); b Light micrograph showing characteristic tapering shape of zoospores (Karnovsky-fixed); scale bar 5 10 mm. c Longitudinal section through zoospore showing mitochondria (M), axoneme (A), and electron-opaque lipid globules (L); scale bar 5 1 mm. d Longitudinal section through kinetosomal area showing close association of lipid globules (L), microbodies (m), electron-opaque helix (h), and kinetosome (K), e Oblique section of (encysted) zoospore with the nucleus (N) surrounded by rough endoplasmic reticulum and protruding toward the helix and kinetosomal area. Scale bars: a 5 μm; b 10 μm, c-e 1 μm (redrawn from Nyvall et al. 1999).

Endochytriaceae Sparrow ex D.J.S. Barr, Canadian Journal of Botany 58: 2390 (1980)
Index Fungorum Identifier 81677

Thallus monocentric with an exogenous development. Operculate zoosporangia and an exogenous resting spore. Grouping with *E. ramosum* in analyses of SSU and LSU rDNA sequences (Mozley-Standridge et al. 2009).

Ecology & life modes – The family is weakly parasitic in freshwater green algae or saprophytic in decaying plant tissues (Sparrow 1960).

Family type – *Endochytrium* Sparrow, American Journal of Botany 20: 71 (1933)

Notes – Sparrow (1933b) sequentially described *E. ramosum* and *E. oophilum*, without designated type. Sparrow questioned the authenticity of *E. oophilum* because he was not able to observe rhizoids (Mozley-Standridge et al. 2009). Index Fungorum (2025) considered *Endochytriceae* as an invalid family since a Latin description was missing. However, Mozley-Standridge et al. (2009) validated the family and designated *E. ramosum* as the type. At present, there are seven species (*E. cystarum*, *E. digitatum*, *E. multiguttulatum*, *E. oophilum*, *E. operculatum*, *E. pseudodistomum* and *E. ramosum*), which are morphologically characterized by the production of monocentric thallus, exogenous development and operculate zoosporangium.

Only the type species (*Endochytrium ramosum*) was included in the phylogenetic analysis. Jerônimo et al. (2022, 2024) included several other strains identified at the generic level in their phylogeny, but these were placed in new genera. However, there are still some taxa that remain uncertain and need to be reevaluated in future. Cultures are available on CZEUM (Collection of Zoosporic Eufungi at the University of Michigan) and sequences on GenBank.

Endochytrium Sparrow, Am. J. Bot. 20: 71 (1933)
Index Fungorum Identifier 20204

Thallus monocentric with an exogenous development. Zoosporangium produces a discharge tube with an operculum at the apex. Zoospores formed in the sporangium are posteriorly uniflagellate, with a single globule. Resting spore thick-walled, endobiotic, apparently asexually formed (Sparrow 1933b, 1960)

Type species – *Endochytrium ramosum* Sparrow, Am. J. Bot. 20: 72 (1933)

Notes – The species are weakly parasitic or saprophytic in freshwater green algae or saprophytic in decaying plant tissues. Sparrow (1960) based his species distinction mainly on the morphology of the resting spores, recognising four species (*E. ramosum*, *E. digitatum*, *E. operculatum* and *E. pseudodistomum*). According to Index Fungorum (2025), *E. oophilum* is the type species, information which is incorrect based on the explanation provided above. Currently, there are seven described species, but phylogenetic data are available only for *E. ramosum*. Jerônimo et al. (2022) questioned the monophyly of the genus since several strains identified as *Endochytrium* did not group with the type species (*E. ramosum* JEL402) in their phylogenetic analysis.

This genus was recorded in North America (Karling 1938, 1941a, 1977, Sparrow 1952, 1960, Dogma 1969), South America (Karling 1946, Jerônimo et al. 2020, and others), Central America (Shanor 1944, Sparrow 1952), Europe (Czeczuga et al. 2003b, Czeczuga et al. 2005 and others), and Africa (Hassan & Shoulkamy 1991, Hassan 1993, and others).

Nowakowskiellaceae Sparrow ex Mozl.-Standr., Mycol. Res. 113: 503 (2009)
Index Fungorum Identifier 512050

Thallus polycentric. Rhizomycellium extensive, producing irregular swellings and operculate zoosporangia. Zoospores are posteriorly uniflagellate with a single lipid globule. Resting spore borne like the sporangium, thick-walled (Sparrow 1960).

Ecology & life modes – Members of the family are saprobic in the decaying parts of higher plants and in the gelatinous sheath of *Chaetophora* (Sparrow 1960).

Family type – *Nowakowskiella* J. Schrot., in Engler & Prantl, Nat. Pflanzenfam 1: 82 (1897); Figs. 33i-k

Notes – *Nowakowskiella* was established by Engler & Prantl (1897) through the morphological analysis of the operculation and rhizomycelial swellings (absence of turbinate cells), which placed *Cladochytrium elegans*, described by Nowakowskii (1877), in the new genus, *Nowakowskiella*. Sparrow (1942) erected *Nowakowskiellaceae*, but replaced the name with *Megachytriaceae* (Sparrow 1943a) on the basis that any family names formed by using the older genus *Nowakowskiella* as a basis result in combinations which are too polysyllabic to be tenable (Sparrow 1943b). Considering that neither *Nowakowskiellaceae* nor *Megachytriaceae* were validly

published by Sparrow (1942, 1943). Mozley-Standridge et al. (2009) validated the family by providing a Latin description and designating a type.

Nowakowskiella has the most species sequenced in the order, with phylogenetic information for five species, including the type, *N. elegans*. Jerônimo et al. (2019) described a new species, *N. crenulata*, and transferred *N. elongata* to the new genus, *Karlingiella* based on the phylogeny of ribosomal genes and morphological development. These phylogenetic data support the monophyly of the family (Jerônimo et al. 2022). Cultures are available on CZEUM (Collection of Zoosporic Eufungi at the University of Michigan) and sequences on GenBank.

Nowakowskiella J. Schrot., in Engler & Prantl, Nat. Pflanzenfam 1: 82 (1897)
Index Fungorum Identifier 20372

Thallus polycentric. Rhizomycellium extensive, producing irregular swellings and operculate zoosporangia. Zoospores are posteriorly uniflagellate with a single lipid globule. Resting spore borne like the sporangium, thick-walled (Sparrow 1960).

Type species – *Nowakowskiella elegans* (Nowak.) J. Schrot., in Engler & Prantl, Nat. Pflanzenfam 1: 82 (1893)

Notes – *Nowakowskiella* is a polycentric genus, which produces operculate zoosporangia and, in general, non-septate swellings in rhizomycelium. However, in some species, the presence of turbinate cells was also observed (Sparrow 1960, Karling 1977). The genus contains 16 legitimate species. Correct species identification is highly dependent on the morphology of the resting spore since the zoosporangia are similar between different species and are often non-decisive. Phylogenetic analysis supports the monophyly of the family (Jerônimo et al. 2022). *Nowakowskiella* is one of the most common genera within *Cladochytriales*, which were reported in South America (Karling 1945a, Marano et al. 2007, Steciow et al. 2012, Jesus et al. 2013, Jerônimo et al. 2015, 2019 and others), North America (Karling 1944, 1977, and others), Europe (Batko & Hassan 1982, Czeczuga et al. 2006, 2007, and others), Africa (Hassan & Shoulkamy 1991, Hassan 1993) and Asia (Karling 1964a).

Septochytriaceae Mozl.-Standr., Mycol. Res. 113: 503 (2009)
Index Fungorum Identifier 512008

= *Catenochytridiaceae* Doweld, Index Fungorum 55: 1 (2014)

Thallus monocentric or polycentric with endogenous or exogenous development. Zoosporangium operculate, apophysate or non-apophysate, producing operculum or pores. Discharge tubes are observed in some genera. The rhizoidal system is extensive, smooth, constricted or catenulated. The rhizomycelium can present septate or non-septate filaments.

Family type – *Septochytrium* Berdan, Am. J. Bot. 26: 461 (1939)

Ecology & life modes – Saprophytic on various grasses, wheat, rye, oats, corn leaves and also on narcissus root tips (Sparrow 1960).

Notes – *Septochytriaceae* includes a variety of monocentric and polycentric strains which produce operculate zoosporangia. Wijayawardene et al. (2020, 2022) accepted only *Septochytrium.* In this study, we accept seven genera (*Allochytridium*, *Catenochytridium*, *Cylindrochytridium*, *Septochytrium*, *Nephrochytrium*, *Sparrowiella* and *Phytochytridium*), and *Septochytrium* was designated as the type by Mozley-Standridge et al. (2009). The reasons for these new inclusions are provided below under ‘other genera included’.

Jerônimo et al. (2022) expanded the circumscription of the family to include two new polycentric genera (*Sparrowiella* and *Phytochytridium*) and *Catenochytrium*. The family *Catenochytridiaceae* proposed by Doweld (2014p) is not accepted since the type genus (*Catenochytridium*) is polyphyletic (Simmons et al. 2021, Jerônimo et al. 2022) and molecular information for the type species (*C. carolinianum*) is not available. Cultures are available on CZEUM (Collection of Zoosporic Eufungi at the University of Michigan) and sequences on GenBank.

According to Jerônimo et al. (2022), *Catenochytrium* is a polyphyletic genus, and the absence of molecular information for the type species leaves the systematics of the genus unresolved. Cultures are available on CZEUM (Collection of Zoosporic Eufungi at the University of Michigan) and sequences on GenBank.

Septochytrium Berdan, Am. J. Bot. 26: 461 (1939)
Index Fungorum Identifier 20517

Thallus predominantly polycentric, consisting of elongate, septate, and constricted filaments, intercalary swellings, and finely branched rhizoids. Zoosporangia are variously shaped, operculate, terminal and intercalary. Zoospores uniflagellate. Resting spores are terminal or intercalary, formed in the same position as the sporangia or from the intercalary swellings (Berdan 1939).

Type species – *Septochytrium variabile* Berdan, Am. J. Bot. 26: 461 (1939); Fig. 33m

Notes – *Septochytrium* is one of the most enigmatic genera within *Cladochytriales*. It can produce a monocentric or polycentric thallus, which is not common among members of *Chytridiomycota*. Berdan (1942) mentioned that many variations occur in the development of *Septochytrium,* and it is very difficult to describe any one type as definitely representing the normal. There are five legitimate species (*S. macroporosum*, *S. marilandicum*, *S. plurilobulum*, *S. variabile* and *S. willoughbyi*), and *S. variabile* was designated as the type by Berdan (1939).

Septochytrium species have been reported from North America (Karling 1942, 1949, 1951, 1977, Johanson 1943, Sparrow 1960), South America (Dogma 1973, Rocha & Pires-Zottarelli 2002, Steciow et al. 2012, Nascimento & Pires-Zottarelli 2009), Europe (Czeczuga et al. 2007b), Asia (Chen 2008) and Africa (Hassan & Shoulkamy 1991).

Other genera included in *Septochytriaceae*

Allochytridium D.J.S. Barr & Desauln, Mycologia 79: 195 (1987)
Index Fungorum Identifier 91163; Index Fungorum (2025) lists four epithets and Species Fungorum (2025) accepts only three species.

Type species – *Allochytridium expandens* Salkin, Am. J. Bot. 57: 652 (1970)

Notes – *Allochytridium* was described by Salkin (1970) with the type-species *A. expandens*. This genus was compared to *Karlingia* or *Karlingiomyces* by the first author. However, differences in zoospore germination were the criteria used to propose the new genus. Barr (1986) detailed the development, morphology, and zoospore ultrastructure of *A. expandens*. In this study, the author mentioned morphological similarities with other cladochytrialean members such as *Catenochytridium*, *Nephrochytrium* and *Cylindochytridium*. However, analysis of the zoospore ultrastructure revealed that *A. expandens* was probably related to the polycentric members of *Cladochytrium* and *Nowakowskiella*, especially considering the similarity of the flagellar apparatus. Species belonging to *Allochytridium* have reported from North America (Sparrow 1960, Salkin 1970, Karling 1977, Barr & Desaulniers 1987, and others) and Asia (Chen & Chien 1995).

Catenochytridium Berdan, Am. J. Bot. 26: 460 (1939); Figs. 20 & 33l
Index Fungorum Identifier 20106; Index Fungorum (2025) lists eight epithets, and Species Fungorum (2025) accepts only seven species.

Type species – *Catenochytridium carolinianum* Berdan, Am. J. Bot. 26: 461 (1939)

Notes – *Catenochytrium* is a polyphyletic genus which forms distinctive branches within *Septochytriaceae* (Jerônimo et al. 2022, 2024). There are six described species (*C. carolinianum, C. hemicysti, C. kevorkianni, C. laterale, C. marinum, C. oahuense*), which are morphologically characterized by the production of operculate zoosporangium and catenulated rhizoids. The type-species, *C. carolinianum*, was not grown in pure cultures or sequenced, leaving the systematics of the genus uncertain. There are records of *Catenochytridium* in South America (Steciow et al. 2012, Jesus et al. 2013, Jerônimo & Pires-Zottarelli 2020), North America (Berdan 1939, Sparrow 1960, 1965, Karling 1941, 1977, Barr et al. 1987), Central America (Sparrow 1952), and Asia (Kobayashi & Ookubo 1953, Chen & Chien 1995).

Cylindrochytridium Karling, Bull. Torrey Bot. Club 68: 382 (1941)
Index Fungorum Identifier 20152; Index Fungorum (2025) and Species Fungorum (2025) accepted two species.

Type species – *Cylindrochytridium johnstonii* Karling, Bull. Torrey Bot. Club 68: 382 (1941)

Notes – *Cylindrochytridium* has only two described species (*C. johnstonii* and *C. endobioticum*), with *C. johnstonii* being the type species (Karling 1941b). It is morphologically characterised by the production of a monocentric thallus and operculate zoosporangium with a typical empty basal region. This genus was transferred from *Chytridiales* based on the phylogeny of ribosomal genes (Steiger et al. 2011). The genus was recorded in South America (Steciow et al. 2012, Jerônimo & Pires-Zottarelli 2020, and others), North America (Whiffen 1941, Sparrow 1960, Karling 1941b, Karling 1977, and others), Central America (Shanor 1944), and Europe (Willoughby 1964, Czeczuga et al. 2007b, and others).

Dogmamyces G.H. Jerônimo, C.L.A. Pires-Zottar., T.Y. James & J.E. Longcore, Mycol. Prog. 23: 1 (2023)
Index Fungorum Identifier 848810; Index Fungorum (2025) and Species Fungorum (2025) accept one species.

Type species – *Dogmamyces elongatus* G.H. Jerônimo, C.L.A. Pires-Zottar., T.Y. James & J.E. Longcore, Mycol. Prog. 23: 1 (2024)

Notes – *Dogmamyces* is morphologically distinct from the other monocentric genera in *Septochytriaceae* since it has an endogenous development. A multigenic analysis by Jerônimo et al. (2024) also supported the genus and placed it as a sister group of *Phytochytrium*. The genus was recorded exclusively in South America (Jerônimo et al. 2024).

Nephrochytrium Karling, Am. J. Bot. 25: 211 (1938)
Index Fungorum Identifier 20367; Index Fungorum (2025) lists eight epithets, and Species Fungorum (2025) accepts three species.

Type species – *Nephrochytrium appendiculatum* Karling Am. J. Bot. 25: 211 (1938)

Notes – *Nephrochytrium* contains four valid species *viz.*, *N. appendiculatum*, *N. aurantium*, *N. bipes*, and *N. stellatum*. *Nephrochytrium* species are morphologically characterised by the production of operculate zoosporangia, usually somewhat kidney-shaped, and they are saprophytic on grass leaves and in cells of *Chara* and *Nitella* (Karling 1938, Sparrow 1960). Phylogenetic analysis in Mozley-Standridge et al. (2009) and Jerônimo et al. (2022) placed *Nephrochytrium* within *Septochytriaceae*, and closely related to *Allochytridium.* This genus was recorded in South America (Karling 1944 and others), North America (Couch 1938, Karling 1941, Whiffen 1941, Sparrow & Barr 1955), Europe (Czeczuga et al. 1988, Willoughby 1961, Czeczuga et al. 2005) and Africa (Hassan 1993).

Phytochytrium Longcore & G.H. Jerônimo, Mycol. Prog. 21: 5 (2022); Index Fungorum (2025) and Species Fungorum (2025) accept one species
Index Fungorum Identifier 841930; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Phytochytrium stagnum* Longcore & G.H. Jerônimo, in Jerônimo, Simmons, Amses, Seto, James, Pires-Zottarelli & Longcore, Mycol. Prog. 21: 6 (2022)

Notes – *Phytochytrium* is a polycentric genus, which produces rhizomycelium without swellings and sometimes in a bead-like shape. The operculate zoosporangia are formed perpendicular to the rhizomycelium axis. According to Jerônimo et al. (2022), this monotypic genus is sister to monocentric strains with endobiotic thalli and operculate zoosporangia (JEL050 and JEL931) within *Septochytriaceae*. This genus has only been reported from Maine, USA (Jerônimo et al. 2022).

Sparrowiella Longcore & G.H. Jerônimo, Mycol. Prog. 21: 6 (2022)
Index Fungorum Identifier 841931

Type species – *Sparrowiella insolita* Longcore & G.H. Jerônimo, Mycol. Prog. 21: 7 (2022)

Notes – *Sparrowiella* is a polycentric genus which produces rhizomycelium without swellings and is sometimes bead-like. Similar to *Phytochytrium*, this genus also produces operculate zoosporangia perpendicularly attached to the rhizomycelium axis. However, the presence of apophysis and the size of zoosporangia and discharge tube can be used as morphological characters to differentiate these two genera.

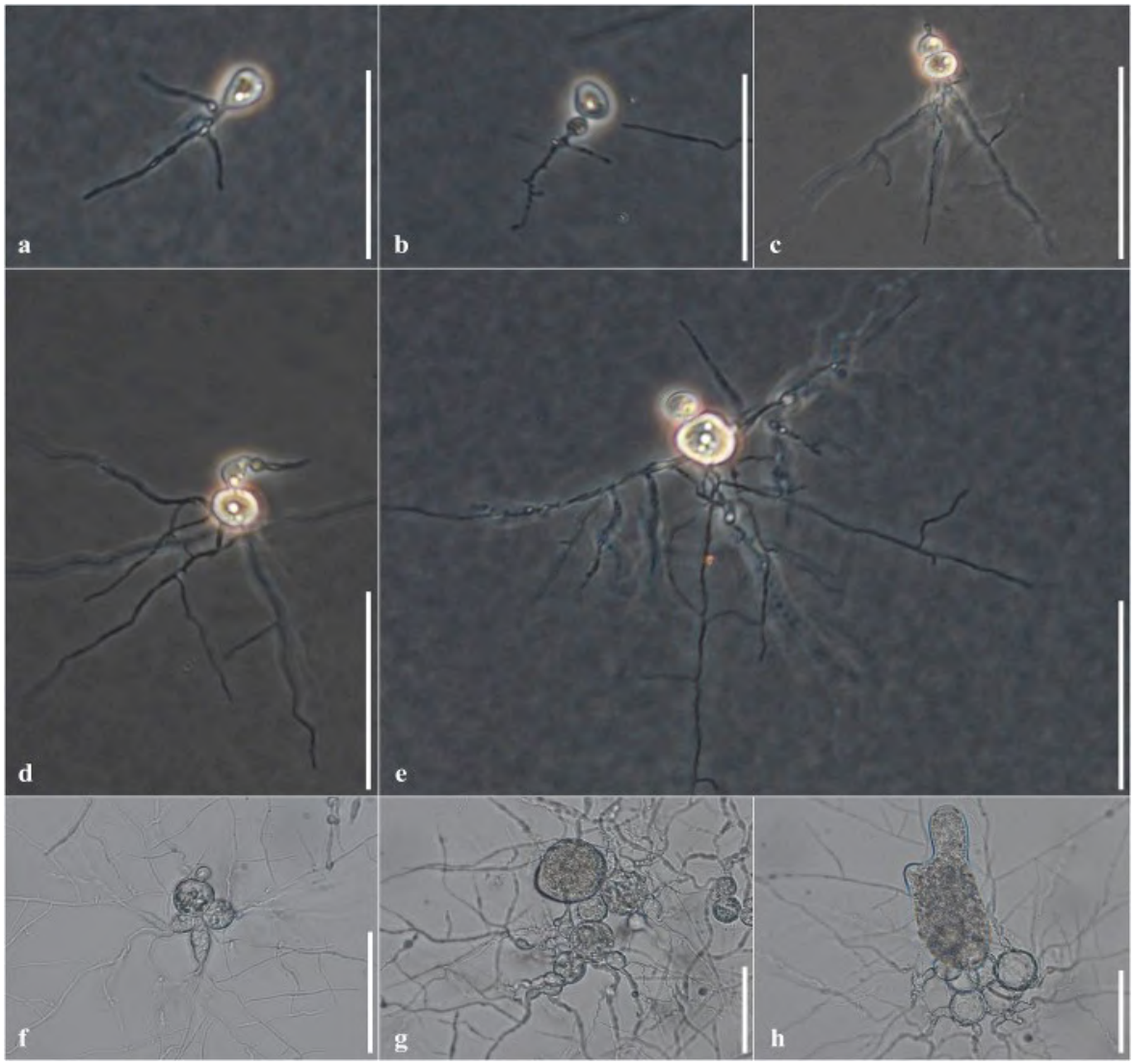


Figure 20 – Development of *Catenochytridium* sp. JEL024. a-e. Exogenous development in immature thallus. f. Early stages of apophisis development. g. Young zoosporangium and catenulate apophisis. h. Mature zoosporangium and catenulate aphophisis. Scale bars: 10 µm.

Lobulomycetes Tedersoo et al.
Lobulomycetales D.R. Simmons
Lobulomycetaceae D.R. Simmons, Mycol. Res. 113: 453 (2009)
Index Fungorum Identifier 511805

= *Alogomycetaceae*-Doweld, Index Fungorum 76: 1 (2014)

Thallus monocentric, eucarpic, with endogenous development. Rhizoids isodiametric, 0.5–1.5 mm wide (Simmons et al. 2009)

Family type – *Lobulomyces* D.R. Simmons, Mycol. Res. 113: 454 (2009)

Ecology & life modes – *Lobulomycetaceae* comprises aquatic (Longcore 1992, Doweld 2014b, Van den Wyngaert et al. 2018) and terrestrial genera (Simmons et al. 2009, 2012, Seto & Degawa 2015), reported as algal parasites or saprobes (Longcore 1992, Doweld 2014b, Van den Wyngaert et al. 2018) or growing on pollen baits (Longcore 1992, Simmons et al. 2009, 2012, Seto & Degawa 2015). Though most terrestrial species are from soils or tree canopy debris, *Alogomyces* was isolated from horse manure (Simmons et al. 2012).

Notes – Doweld (2014q) introduced *Alogomycetaceae* to include *Alogomyces*, yet the author did not justify this new taxon, other than a recapitulation of the ultrastructural and thallus characters of *Alogomyces tanneri*, previously detailed in the generic and species descriptions (Simmons et al. 2012). *Alogomyces* was originally described as a member of *Lobulomycetaceae* based on molecular and morphological evidence, which was consistent with the description of the family (Simmons et al. 2009). Though the horse manure habitat of *Alogomyces* is exceptional in this order, Doweld (2014q) did not mention this aspect of the taxon in the description of *Alogomycetaceae*, and we do not agree that it is indicative of a new family. Additionally, acceptance of *Alogomycetaceae* would make *Lobulomycetaceae* paraphyletic, as *Alogomyces* and *Maunachytrium* are monophyletic within the *Lobulomycetales* (Simmons et al. 2012, Seto & Degawa 2015). Rather than transfer *Maunachytrium* to an unjustified family, we choose to neglect the recommendation of Doweld (2014q), and instead include all genera in the molecularly and morphologically justified family *Lobulomycetaceae*.

Lobulomyces D.R. Simmons, Mycol. Res. 113: 454 (2009)
Index Fungorum Identifier 511806

Zoospore with dense fibrillar connection between kinetosome and nonflagellated centriole; flagellar plug extensions anterior and posterior; one lipid globule (Simmons et al. 2009).

Type species – *Lobulomyces angularis* (Longcore) D.R. Simmons, Mycol. Res. 113: 454 (2009)

Notes – *Lobulomyces angularis* was introduced to accommodate *Chytriomyces angularis* Longcore. At the time of the latter's description, the zoospore was noted for being dissimilar to the *Chytriomyces* zoospore type in its lack of many ultrastructural characters, but novel generic placement was considered otherwise unjustified. Molecular phylogenetics in James et al. (2000) showed that the species was not monophyletic with other *Chytriomyces*, or the *Chytridiales*, leading to the species serving as a type of *Lobulomyces*. Cultures are available from CZEUM (Collection of Zoosporic Eufungi at the University of Michigan), and sequences are available in GenBank.

Other genera in *Lobulomycetaceae*

Algochytrops Doweld, Index Fungorum 123: 1 (2014)
Index Fungorum Identifier 550472; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Algochytrops polysiphoniae* (Cohn) Doweld 2014

Notes – Parasite on *Pylaiella littoralis* marine alga in Scotland (Cohn et al. 2006 as *Chytridium polysiphoniae*). Sequences are available in GenBank.

Algomyces Van den Wyngaert, K. Rojas & K. Seto, J. Eukary. Microbiol. 65(6): 877 (2018)
Index Fungorum Identifier 825142; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Algomyces stechlinensis* Van den Wyngaert, K. Rojas & K. Seto 2018

Notes – Parasite on colonial green algae in Germany (Van den Wyngaert et al. 2018). Sequences are available in GenBank.

Alogomyces D.R. Simmons & Letcher, Mycologia 104(1): 158 (2012)
Index Fungorum Identifier 519672; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Alogomyces tanneri* D.R. Simmons & Letcher 2012

Notes – Saprobic, from horse manure from the USA (Simmons et al. 2012). Culture is available from CZEUM (Collection of Zoosporic Eufungi at the University of Michigan) and sequences are available in GenBank.

Clydaea D.R. Simmons, Mycol. Res. 113(4): 455 (2009)
Index Fungorum Identifier 512109; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Clydaea vesicula* D.R. Simmons 2009

Notes – Saprobic, from soils in the USA (Simmons et al. 2009). Cultures are available from CZEUM (Collection of Zoosporic Eufungi at the University of Michigan), and sequences are available in GenBank.

Cyclopsomyces K. Seto & Degawa, Mycologia 107(3): 637 (2015)
Index Fungorum Identifier 810512; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Cyclopsomyces plurioperculatus* K. Seto & Degawa 2015

Notes – From soil in Japan (Seto & Degawa 2015). Sequences are available in GenBank.

Maunachytrium D.R. Simmons, Mycol. Res. 113(4): 456 (2009)
Index Fungorum Identifier 512111; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Maunachytrium keaense* D.R. Simmons 2009

Notes – From alpine soil in Hawaii, USA (Simmons et al. 2009). Sequences are available in GenBank.

Mesochytriomycetes Tedersoo et al.
Gromochytriales Karpov & Aleoshin
Gromochytriaceae Karpov & Aleoshin, Persoonia 32: 124 (2014)
Index Fungorum Identifier: 805306

Zoospores with posterior ribosomal aggregation are not bounded by endoplasmic reticulum. Microbody-lipid complex pressed to the nucleus and containing a single microbody enveloping a large anterior lipid globule with an anteriorly oriented fenestrated cisterna (rumposome). Several mitochondria are separated from MLC. Small dense bodies are present in the peripheral cytoplasm. Kinetosome and centriole are embedded in the posterior side of the ribosomal core. The flagellar transition zone contains a spiral fibre or a cylinder. Centriole at an angle of c. 30° to kinetosome; the bottom of kinetosome is connected by a broad fibrillar bridge to the centriole. Anterior and posterior microtubular roots and a short straight spur associated with the kinetosome. Simple thallus with inoperculate, monocentric, epibiotic sporangium having endogenous development and a single slightly branching rhizoidal axis (Karpov et al. 2014b).

Family type – *Gromochytrium* Karpov & Aleoshin, Persoonia 32: 124 (2014)

Ecology & life modes – The family contains two genera, both of which are obligate parasites of *Tribonema gayanum* algae from aquatic locations in the Leningrad district, Russia (Karpov et al. 2014b, 2019b).

Notes – Karpov et al. (2014b) introduced this family with *Gromochytrium* as the type genus. The family comprises two genera. Further sampling in the same region or similar habitats may yield additional taxa.

Gromochytrium Karpov & Aleoshin, Persoonia 32: 124 (2014)

Index Fungorum Identifier: 805307

Mature inoperculate epibiotic sporangium long ovoid (18 × 10 μm) without papillae. Zoospores are released through apical pores. Delicate, weakly branched rhizoidal system with short

rhizoids emerging from a slender main axis. Zoospores 2 µm diam. with a single lipid globule (Karpov et al. 2014b).

Type species – *Gromochytrium mamkaevae* Karpov & Aleoshin, Persoonia 32: 124 (2014); Fig. 21d, e

Other genera included in *Gromochytriaceae*

Apiochytrium Karpov & D. Moreira, Journal of Eukaryotic Microbiology. 66(4): 590 (2019)
Index Fungorum Identifier: 827963; Index Fungorum (2023) and Species Fungorum (2023) accepted one species.

Type species – *Apiochytrium granulosporum* Karpov & D. Moreira 2019; Fig. 21a-c

Mesochytriales, Mesochytriaceae

Mesochytriaceae Doweld, Index Fungorum 45: 1 (2013)
Index Fungorum Identifier: 550330

Zoosporangium sessile, partially penetrating the host cell by a haustorium, pyriform, thin-walled, smooth, with a single apical discharge papilla. Inoperculate. Rhizoids are delicate, branched, and arise near the sporangial base. Zoospores are spherical, posteriorly uniflagellate, a single lipid globule and ribosomes dispersed through the cytoplasm. Flagellar kinetosome short with developed props and non-flagellated centriole proximal to the fenestrated cisterna; flagellar transition zone simple, without a transverse transitional plate, but with a spiral fiber; non-flagellated centriole shorter than the kinetosome, lies at a sharp angle (approx. 30Â°), with a veil; kinetosome connected to the non-flagellated centriole with a broad, dense fibrillar bridge. Resting spores endobiotic, spherical, thick-walled (3-layered), laevigate. Obligate parasite of the green alga *Chlorococcum minutum* (Doweld 2013b).

Family type – *Mesochytrium* B.V. Gromov, Mamkaeva & Pljusch (1 species), Nova Hedwigia 71: 159 (2000)

Ecology & life modes – The single species in the family is an obligate parasite of *Chlorococcum minutum* green algae from the Leningrad district, Russia (Gromov et al. 2000).

Mesochytrium B.V. Gromov, Mamkaeva & Pljusch (1 species), Nova Hedwigia 71: 159 (2000)
Index Fungorum Identifier: 28580

Zoosporangium sessile, partly penetrating the host cell, pyriform, 14 × 7.5 µm, wall colourless, thin, smooth, with one apical discharge papilla. Delicate branched rhizoids arise near the sporangial base. Zoospores spherical, 2.5 µm diam., with one refractive globule and a 14 µm long posterior flagellum. Resting spores are endobiotic, spherical, smooth- and thick-walled. Parasite of the alga *Chlorococcum minutum* (Gromov et al. 2000).

Type species – *Mesochytrium penetrans* B.V. Gromov, Mamkaeva & Pljusch, Nova Hedwigia 71(1-2): 159 (2000); Fig. 22

Notes – *Mesochytrium* was introduced by Gromov et al. (2000) as a member of *Chytridiales*, and the ex-type culture was molecularly and ultrastructurally characterised by Karpov et al. (2010). Karpov et al. (2010) suggested that the marginal support for the placement of *Mesochytrium* as sister to *Lobulomycetes* was not sufficient for higher taxa descriptions until more representatives of the lineage could be evaluated. However, Doweld (2013b) ignored this recommendation and described *Mesochytriales* and *Mesochytriaceae* based solely on the evidence generated by Karpov et al. (2010). We believe that additional sampling and molecular studies would resolve the classification and taxonomic status of this taxon.

Polychytriomycetes Tedersoo et al.
Polychytriales Longcore & D.R. Simmons
Polychytriaceae Doweld, Index Fungorum 89: 1 (2014)
(= ? *Arkayaceae* Doweld)
Index Fungorum Identifier 550399

Thalli are polycentric, tubular, with broad rhizomycelial hyphae that lack intercalary swellings. Zoospores posteriorly uniflagellate, with a plug or none, microtubule roots 1–3, extend to the microbody-lipid globule complex, lipid globules multiple, surrounded by microbody, rumposomes lacking; ribosomes aggregated, spherical mitochondria and nucleus lie exterior to ribosomal mass, non-flagellated centriole with a veil or none, attached to the kinetosome (Doweld 2014r, s).

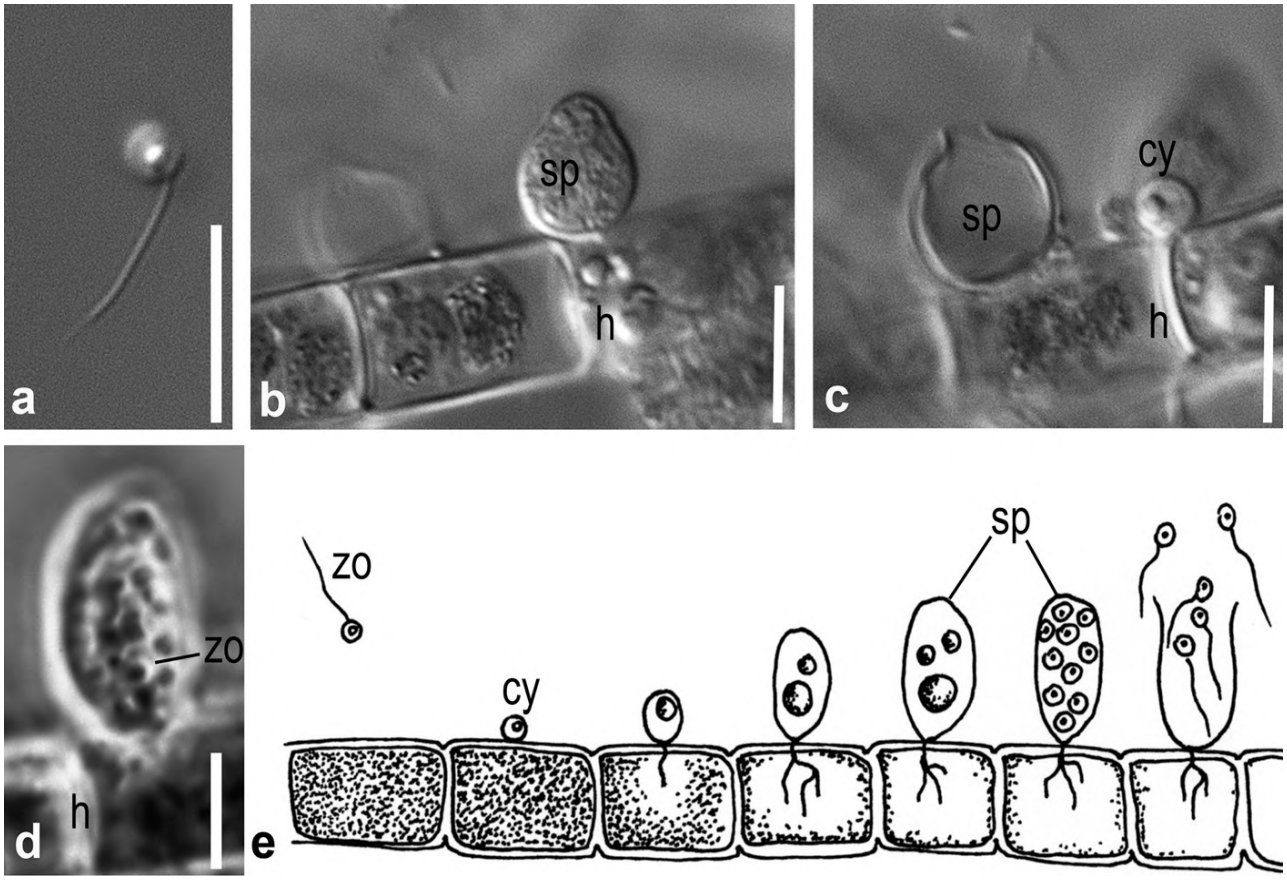


Figure 21 – Light microscopic images of the life cycle stages of *Apiochytrium granulosporum* (a-c) and *Gromochytrium mamkaevae* (d, and drawing e) on the host *Tribonema gayanum* (after: Karpov et al. 2014b, modified). a zoospore. b premature sporangium with papillum. c empty sporangium after zoospore releasing. d mature sporangium with zoospores. e consecutive stages of *G. mamkaevae* life cycle. Abbreviations: cy = cyst; h = host, sp = sporangium; zo = zoospores. Scale bars: a-d = 10 μm.

Family type – *Polychytrium* Ajello, in Ajello, Mycologia 34: 442 (1942)

Ecology & life modes – *Polychytriaceae sensu lato* (discussed below) contains monocentric and polycentric fungi from soil and aquatic substrates, often isolated from chitin baits. Molecularly verified taxa have mainly been observed and described from North America, though one isolate of an undescribed *Arkaya* originated from Australia (Longcore & Simmons 2012).

Notes – At the time of its inception, the *Polychytriales* contained five *incertae sedis* genera (Longcore & Simmons 2012). Doweld (2014r, s) described the families *Arkayaceae* and *Polychytriaceae* to accommodate the monocentric and polycentric genera, respectively. However, acceptance of either of these families without amendment would result in a paraphyly of the resulting taxa, as neither monocentricity nor polycentricity is monophyletic within the *Polychytriales* (Longcore & Simmons 2012). Further study and sampling are necessary to determine the division or consolidation of families within the order. Hence, we reject *Polychytriaceae sensu* Doweld and list all monocentric and polycentric genera in *Polychytriaceae sensu lato*, as Longcore & Simmons (2012) reported the type of the order to be *Polychytrium*. We

are aware that previous outlines by Wijayawardene et al. (2018, 2020, 2022) accepted *Arkayaceae*, however, in this study, we tentatively regard it as a synonym of *Polychytriaceae*.

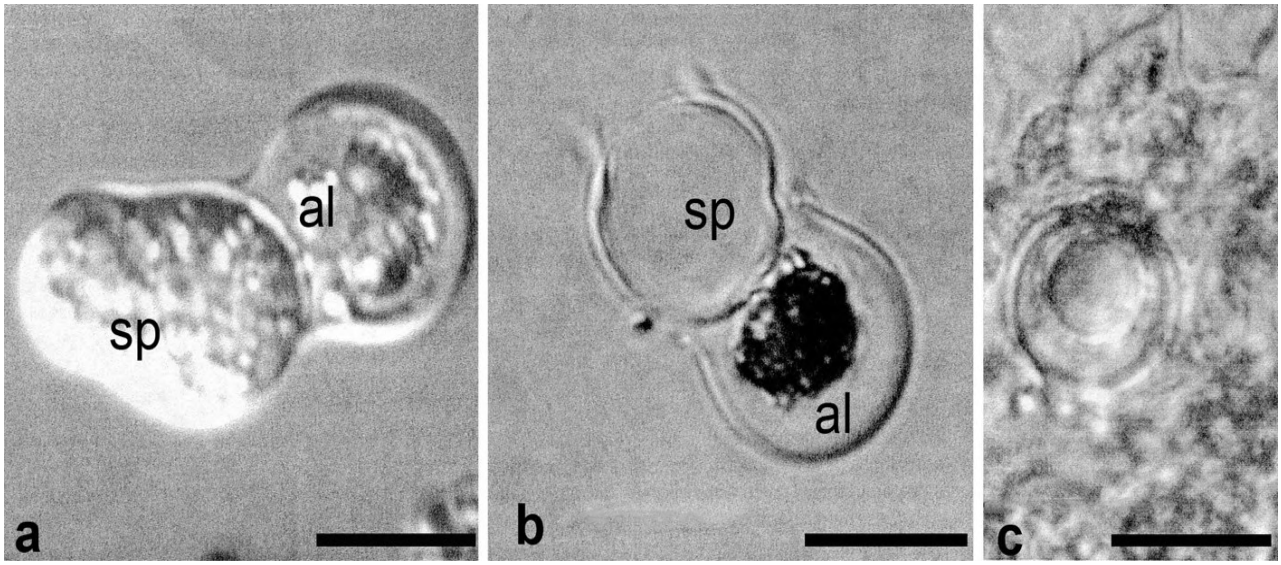


Figure 22 – Light microscopic images of the life cycle stages of *Mesochytrium penetrans* (strain X-46) on green alga *Chlorococcum minutum* (after: Gromov et al. 2000, modified). a mature sporangium penetrating alga. b empty sporangium on the alga. c resting spore inside the alga. Scale bars: a-c = 10 μm.

Polychytrium Ajello, Mycologia 34: 442 (1942); Fig. 33n & o
Index Fungorum Identifier 20435

Rhizomycelium intra- and extramatrical, extensive, coarse, branched, occasionally septate with rhizoids, conspicuous spindle organs or swellings lacking. Zoosporangia non-operculate, terminal and intercalary, variously shaped, spherical, clavate, or pyriform. Zoospores are posteriorly uniflagellate, emerging fully formed in a globular mass and remaining quiescent for a few moments before swimming away (Ajello 1942).

Type species – *Polychytrium aggregatum* Ajello, Mycologia 34: 442 (1942)

Notes – This distinctive polycentric fungus grows on chitinous or pollen baits, observed occurring primarily in North America, though Ajello (1948) categorized its physiology from an isolate from Brazil. Cultures are available from CZEUM (Collection of Zoosporic Eufungi at the University of Michigan), and sequences are available in GenBank.

Other genera in *Polychytriaceae sensu lato*

Arkaya Longcore & D.R. Simmons, Mycologia 104(1): 285 (2012)
Index Fungorum Identifier 561588; Index Fungorum (2025) and Species Fungorum (2025) accepted two species.

Type species – *Arkaya lepida* Longcore & D.R. Simmons 2012

Notes – Monocentric, saprobic from various soil and aquatic samples from USA and Australia (Longcore & Simmons 2012). Culture is available from CZEUM (Collection of Zoosporic Eufungi at the University of Michigan), and sequences are available in GenBank.

Karlingiomyces Sparrow, Aquatic *Phycomycetes*, Edn 2 (Ann Arbor) 15: 559 (1960)
Index Fungorum Identifier 20285; Index Fungorum (2025) and Species Fungorum (2025) accepted six species.

Type species – *Karlingiomyces asterocystis* (Karling) Sparrow 1960

Notes – Monocentric, saprobic on chitin and cellulose baits, though the affinity of cellulosic species is questionable (Longcore & Simmons 2012). Sequences are available in GenBank.

Lacustromyces Longcore, Canadian Journal of Botany 71(3): 415 (1993)
Index Fungorum Identifier 8308; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Lacustromyces hiemalis* Longcore 1993

Notes – Polycentric, saprobic on chitin baits added to aquatic samples from adjacent ponds in Maine, USA (Longcore 1993). Culture is available from CZEUM (Collection of Zoosporic Eufungi at the University of Michigan) and sequences are available in GenBank.

Neokarlingia Longcore & D.R. Simmons, Mycologia 104(1): 281 (2012)
Index Fungorum Identifier 561586; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Neokarlingia chitinophila* (Karling) Longcore & D.R. Simmons 2012

Notes – Monocentric, saprobic on chitin baits added to a soil sample from Louisiana, USA (Longcore & Simmons 2012). Culture is available from CZEUM (Collection of Zoosporic Eufungi at the University of Michigan) and sequences are available in GenBank.

Rhizophlyctidomycetes Tedersoo et al.
Rhizophlyctidales Letcher
Arizonaphlyctidaceae Letcher, Mycol. Res. 112: 1045 (2008)
Index Fungorum Identifier 511796

In zoospore ribosomes are aggregated in the cytoplasm; ribosomal aggregation is partially surrounded by endoplasmic reticulum; multiple lipid globules. Nucleus with no nuclear extension and not proximal to the kinetosome; microbody lobes or multiple microbodies are abundant and associated with the nucleus and mitochondria (Letcher et al. 2008a).

Family type – *Arizonaphlyctis* Letcher, Mycol. Res. 112: 1045 (2008)

Ecology & life modes – This family is known from a single species isolated from a cellulose bait added to a soil sample from the bed of a dried stream in Arizona, USA (Letcher et al. 2008a). Letcher et al. (2008a) suggested that additional taxa may be found in similar habitats.

Notes – Letcher et al. (2008a) introduced this family based on molecular phylogenetic analyses and ultrastructural characteristics. However, morphologically, the genera in *Rhizophlyctidales* are difficult to separate.

Arizonaphlyctis Letcher, Mycol. Res. 112: 1045 (2008)
Index Fungorum Identifier 511799

In zoospore ribosomes aggregated; nucleus without a nuclear extension; striated fibrillar rhizoplast absent (Letcher et al. 2008a).

Type species – *Arizonaphlyctis lemmonensis* Letcher, Mycol. Res. 112: 1045 (2008);

Notes – Letcher et al. (2008a) introduced this monotypic genus and thought that more taxa would be found in similar, high-altitude desert regions. Sequences are available in GenBank.

Borealophlyctidaceae Letcher, Mycol. Res. 112(9): 1045 (2008)
Index Fungorum Identifier 511797

In zoospore ribosomes are aggregated in the cytoplasm; ribosomal aggregation is partially surrounded by endoplasmic reticulum; usually a single lipid globule; nucleus with a nuclear extension proximal to the kinetosome; microbody lobes or numerous microbodies abundant and associated with the anterior portion of the nucleus and lipid globule (Letcher et al. 2008a).

Family type – *Borealophlyctis* Letcher, in Letcher, Powell, Barr, Churchill, Wakefield & Picard, Mycol. Res. 112: 1045 (2008)

Ecology & life modes – This family was initially based on two isolates from pollen baiting of forest soil samples originating from British Columbia and Ontario, Canada (Letcher et al.

2008a). An additional species was described from the Ontario isolate and other strains from baits of flooded forest and agricultural soils in Alabama, USA (Davis et al. 2016a).

Notes – As in other families of *Rhizophlyctidales*, Letcher et al. (2008a) relied on molecular phylogenetic analyses and ultrastructural character suites to delimit this family. The family comprises only one genus.

Borealophlyctis Letcher, Mycol. Res. 112: 1045 (2008)
Index Fungorum Identifier 511800

In zoospore ribosomes aggregated; nucleus with a nuclear extension proximal to the kinetosome; striated fibrillar rhizoplast absent (Letcher et al. 2008a).

Type species – *Borealophlyctis paxensis* Letcher, Mycol. Res. 112: 1045 (2008); Fig. 23

Notes – The genus contains two species, which Davis et al. (2016a) argue are distinguishable by light microscopy of the thallus. However, the elimination of morphologically similar members of the *Rhizophlyctidales* would first require molecular or ultrastructural comparisons, making species determination without these lines of evidence extremely difficult. Cultures are available from CZEUM (Collection of Zoosporic Eufungi at the University of Michigan), and sequences are available in GenBank.

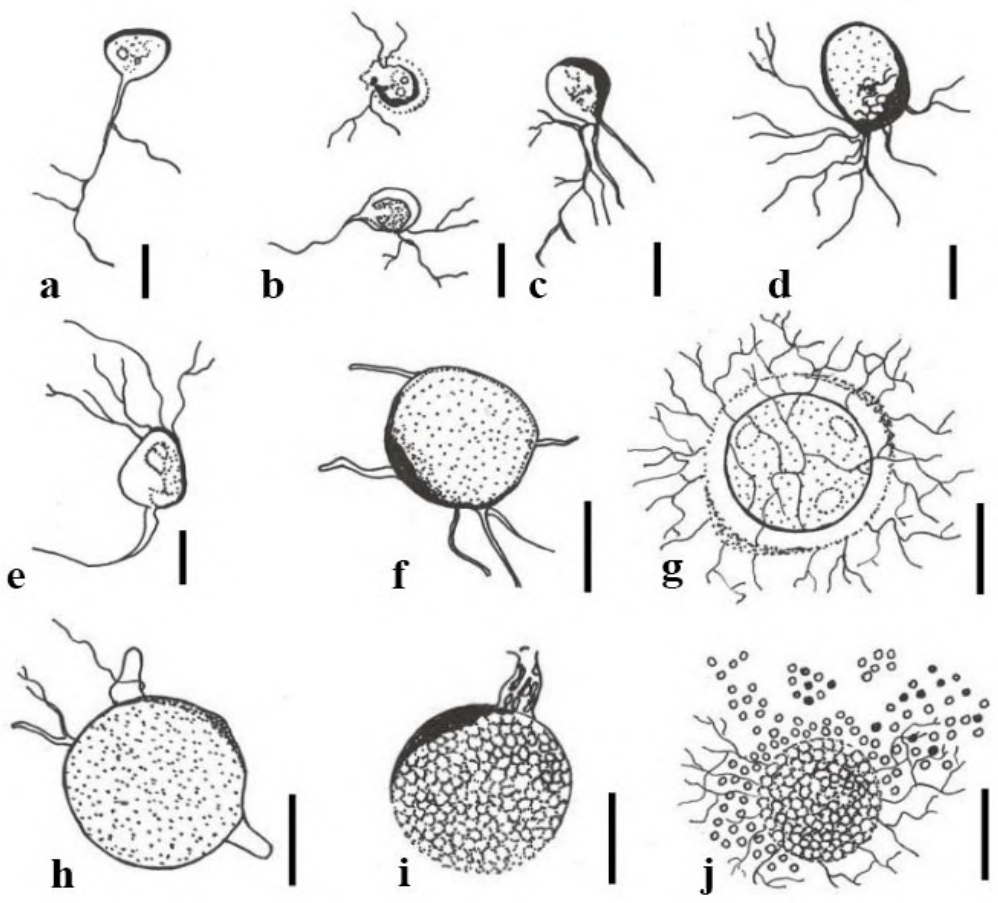


Figure 23 – Morphology of *Borealophlyctis paxensis* (type), isolate BR 368 on agar. a, c Germlings with a single rhizoidal axis. b, d, e Germlings with multiple rhizoidal axes. f, h Developing thalli. i Zoospores being released through a discharge tube. j Zoospores discharged as a loose mass. Scale bars a–e 10 µm, f–j 25 µm (Redrawn from Letcher et al. 2008a).

Rhizophlyctidaceae H.E. Petersen [as 'Rhizophlyctaceae'], Bot. Tidsskr. 29: 357 (1909)
Index Fungorum Identifier 81344

In zoospore ribosomes are dispersed in the cytoplasm; endoplasmic reticulum is scattered in the cytoplasm; lipid globules are numerous; the nucleus is helmet-shaped and associated directly with the kinetosome and non-flagellated centriole by an extensive striated fibrillar rhizoplast; microbody lobes or multiple microbodies are abundant around the rhizoplast (Letcher et al. 2008a).

Family type – *Rhizophlyctis* A. Fisch., in Winter, Rabenh. Krypt.-Fl., Edn 2 (Leipzig) 1(4): 114 (1892)

Ecology & life modes – *Rhizophlyctis rosea*, the type species, is one of the most commonly observed cellulosic members of the *Chytridiomycota* from soils (Letcher et al. 2008a), with a seemingly worldwide distribution.

Notes – Petersen (1909) introduced this family to accommodate *Rhizophlyctis*, which was previously a member of the *Spizellomycetales*, based on zoosporic ultrastructure (Barr 1980). However, molecular phylogenetics (James et al. 2000, 2006b) showed *Rhizophlyctis* to be in a distinct clade from the remaining taxa of *Spizellomycetales* and illustrated the need for taxonomic reclassifications.

Rhizophlyctis A. Fisch., Rabenh. Krypt.-Fl., Edn 2 (Leipzig) 1(4): 114 (1892)
Index Fungorum Identifier 20483

Thallus monocentric, eucarpic, ordinarily polyphagous, consisting of a reproductive rudiment of the encysted zoospore and several branched or unbranched rhizoidal axes, only the ultimate tips of which are endobiotic; sporangium inoperculate, with one or more discharge papillae. Zoospores formed within the sporangium, posteriorly uniflagellate, usually with a single globule, generally discharged in a compact group embedded in a gelatinous matrix from which they eventually escape. Resting spore thick-walled, borne like the sporangium on the thallus, upon germination functioning as a prosporangium (Sparrow 1960).

Type species – *Rhizophlyctis rosea* (de Bary & Woronin) A. Fisch., Rabenh. Krypt.-Fl., Edn 2 (Leipzig) 1(4): 122 (1892); Fig. 33p

Notes – The genus contains 31 species (Sparrow 1960, Karling 1977, Longcore 1996), though *R. rosea* is the most extensively examined, both physiologically and ultrastructurally (see Letcher et al. 2008a). Letcher et al. (2008a) split three additional genera into monotypic families based on differences in ultrastructural character suites, which were corroborated by molecular phylogenetics. Cultures are available from CZEUM (Collection of Zoosporic Eufungi at the University of Michigan), and sequences are available in GenBank.

Sonoraphlyctidaceae Letcher, Mycol. Res. 112: 1038 (2008)
Index Fungorum Identifier 511795

In zoospore ribosomes are dispersed in the cytoplasm; lipid globules are numerous. Nucleus with a nuclear extension, and associated directly with the kinetosome and non-flagellated centriole by two short, striated fibrillar rhizoplasts; microbody lobes or multiple microbodies are abundant and associated with the rhizoplasts and the anterior portion of the nucleus (Letcher et al. 2008a).

Family type – *Sonoraphlyctis* Letcher, Mycol. Res. 112: 1039 (2008)

Ecology & life modes – This family contains a single species represented by four isolates found in arid soils from North America and Australia, baited with cellulosic substrates (Letcher et al. 2008a). Letcher et al. (2008a) suggested that broader sampling of desert climates using cellulose baits would yield additional taxa.

Notes – This family is not morphologically distinct from other taxa in the *Rhizophlyctidales*, but was separated by molecular and ultrastructural comparisons.

Sonoraphlyctis Letcher, Mycol. Res. 112: 1039 (2008)
Index Fungorum Identifier 511798

In zoospore ribosomes are dispersed in the cytoplasm. Nucleus with a short posterior nuclear extension; a compact (0.35 mm long) striated fibrillar rhizoplast between the nucleus and kinetosome (Letcher et al. 2008a).

Type species – *Sonoraphlyctis ranzonii* Letcher, in Letcher, Powell, Barr, Churchill, Wakefield & Picard, Mycol. Res. 112: 1039 (2008); Fig. 24

Notes – This species is based on four cellulolytic isolates from North American and Australian arid soils (Letcher et al. 2008a). The North American isolates are genetically monophyletic, but the Australian isolates show some dissimilarity from the others and each other. Letcher et al. (2008a) credit this divergence to a likely long history of continental isolation, though the authors only described the single species to contain all four isolates. Cultures are available from CZEUM (Collection of Zoosporic Eufungi at the University of Michigan), and sequences are available in GenBank.

Rhizophydiomycetes Tedersoo et al.
Rhizophydiales Letcher et al.
Alphamycetaceae Letcher, Mycol. Res. 112: 771 (2008)
Index Fungorum Identifier 511771

Sporangium spherical with a single discharge pore; rhizoids branched. Zoospore contains a single lipid globule partially covered with a fenestrated cisterna. The kinetosome and nonflagellated centriole are parallel and connected by a band of fibrillar material situated diagonally between the two structures. Kinetosome-associated structure (KAS) is absent. Microbody is simple. Mitochondrion is single, a portion of which is anterior to the kinetosome. Moderately and uniformly electron-dense, thin-membraned vesicles occur in the cytoplasm adjacent to the kinetosome. From aquatic habitats, saprophytic on pollen (Letcher et al. 2008a).

Family type – *Alphamyces* Letcher, Mycol. Res. 112: 772 (2008)

Ecology & life modes – The family is composed of three genera isolated from pollen baits, two of which, *Alphamyces* and *Betamyces*, were isolated from aquatic and soil samples in Central and South America (Letcher et al. 2008a, 2012). However, *Gammamyces* was isolated from rainforest soils in New South Wales, Australia (Letcher et al. 2012).

Notes – Though initially described to accommodate the single species *A. chaetifer* (Letcher et al. 2008a), two additional genera were included in the family based on zoosporic ultrastructure and molecular phylogenetics.

Alphamyces Letcher, Mycol. Res. 112: 772 (2008)
Index Fungorum Identifier 511785

Sporangium spherical with a single discharge pore, the upper two-thirds of the sporangial wall covered with long, slender, branched or unbranched hairs up to 30–50 mm in length. Rhizoids branched. Zoospore contains a single, rather small lipid globule partially covered with a fenestrated cisterna. Mitochondrion is single, a portion of which lies above and proximal to the kinetosome. Moderately electron-dense walled vesicles occur in the cytoplasm adjacent to the kinetosome (Letcher et al. 2008c).

Type species – *Alphamyces chaetifer* (Sparrow) Letcher, Mycol. Res. 112: 772 (2008)

Notes – *Alphamyces chaetifer* is the most distinctive fungus in the family. *Betamyces* and *Gammamyces* possess spherical zoosporangia, common for multiple families of *Rhizophydiales*. However, *A. chaetifer* has a zoosporangium with multiple, slender, long, sometimes branching, hair-like structures emerging over its entirety. The species was formerly within *Rhizophydium* but was placed in *Alphamyces* when *Rhizophydium* was reassessed (Letcher et al. 2008c). Letcher et al. (2008c) argued that additional species may be necessary to reflect phylogenetic dissimilarity in investigated isolates. Cultures are available from CZEUM (Collection of Zoosporic Eufungi at the University of Michigan), and sequences are available in GenBank.

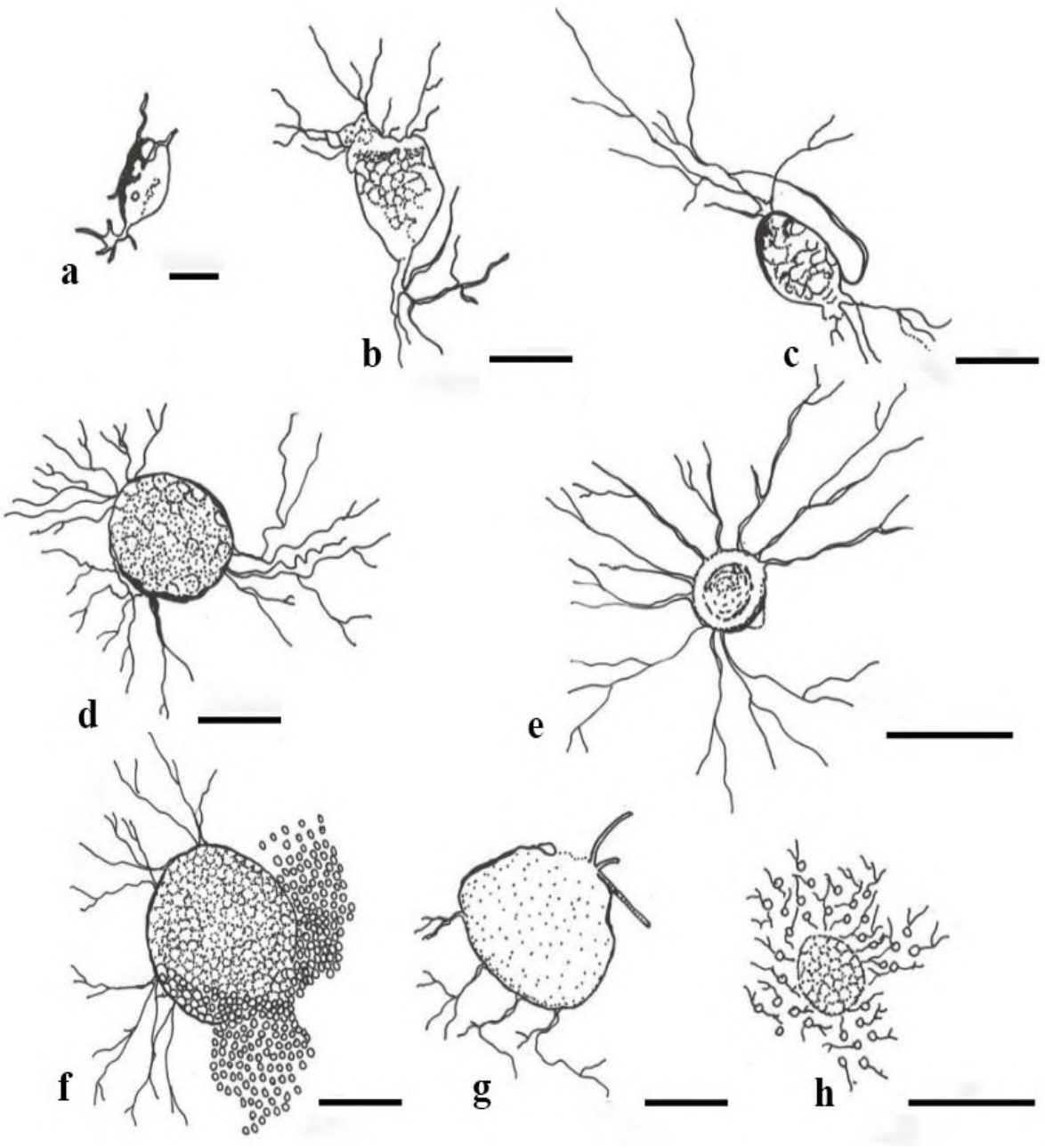


Figure 24 – Morphology of *Sonoraphlyctis ranzonii* (type), isolate BR 060 on agar. a Germling. b–e Developing thalli. f Zoospore discharge. g Empty sporangium with discharge pores adjacent to origins of rhizoidal axes. h Germinated zoospores in vicinity of parent sporangium. Scale bars a 10 µm, b–d, f–g 25 µm, e, h 50 µm (Redrawn from Letcher et al. 2008a).

Other genera in *Alphamycetaceae*

Betamyces Letcher, in Letcher, Vélez, Schultz & Powell, Nova Hedwigia 94(1-2): 19 (2012)
Index Fungorum Identifier 561196; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Betamyces americae-meridionalis* Letcher, Vélez, M. Schultz & M.J. Powell 2012

Notes – On pollen bait from aquatic and soil samples from Argentina and Costa Rica (Letcher et al. 2012b). Cultures are available from CZEUM (Collection of Zoosporic Eufungi at the University of Michigan), and sequences are available in GenBank.

Gammamyces Letcher, in Letcher, Vélez, Schultz & Powell, Nova Hedwigia 94(1-2): 21 (2012)
Index Fungorum Identifier 561198; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Gammamyces ourimbahensis* Letcher 2012

Notes – On pollen baits added to soil from subtropical rainforest in New South Wales, Australia. Culture is available from CZEUM (Collection of Zoosporic Eufungi at the University of Michigan) and sequences are available in GenBank.

Angulomycetaceae Letcher, Mycol. Res. 112: 775 (2008)
Index Fungorum Identifier 511774

Sporangium spherical with few to numerous discharge papillae. Rhizoids are branched, extensive, and compact. Zoospore contains a single lipid globule partially covered with a simple cisterna. Kinetosome and non-flagellated centriole are parallel and connected by fibrillar material with a zone of convergence approximately 0.01–0.025mm in width, centrally located between the two structures. Kinetosome-associated structure (KAS) is absent. Microbody is lobed with a portion anterior to the kinetosome (Letcher et al. 2008c).

Family type – *Angulomyces* Letcher, in Letcher, Vélez, Barrantes, Powell, Churchill & Wakefield, Mycol. Res. 112: 776 (2008)

Ecology & life modes – Cultures identified in this family have been isolated from pollen baits of aquatic samples from streams and lakes in Argentina and the USA (Letcher et al. 2008c, Simmons et al. 2020) and soils in Malaysia (Letcher et al. 2008c) and Thailand (Hurdeal et al. 2023).

Notes – The family was described by Letcher et al. (2008c) to accommodate *Angulomyces*. The family comprises only one genus.

Angulomyces Letcher, in Letcher, Vélez, Barrantes, Powell, Churchill & Wakefield, Mycol. Res. 112: 776 (2008)
Index Fungorum Identifier 511779

Sporangia are spherical with multiple discharge pores. Rhizoids branched. In the zoospore, a KAS is absent. The microbody is lobed, a portion of which is anterior to the kinetosome. Mitochondria are numerous. Thick-membraned vesicles with electron-opaque, reticulated contents occur in the peripheral cytoplasm (Letcher et al. 2008c).

Type species – *Angulomyces argentinensis* Letcher, Mycol. Res. 112: 776 (2008); Fig. 25

Notes – Though a single species was initially described, the authors believed that the genus would have additional taxa (Letcher et al. 2008c). A subsequent study by Hurdeal et al. (2023) discovered a new species from soil in Thailand. Cultures are available from CZEUM (Collection of Zoosporic Eufungi at the University of Michigan), and sequences are available in GenBank.

Aquamycetaceae Letcher, Mycol. Res. 112: 774 (2008)
Index Fungorum Identifier 511773

Sporangium spherical with few or many discharge pores; rhizoids branched. Zoospore contains a single lipid globule partially covered with a fenestrated cisterna. The kinetosome and non-flagellated centriole are parallel and connected by fibrillar material with a zone of convergence approximately 0.075 mm in width, centrally located between the two structures. Kinetosome-associated structure (KAS) is absent. A microtubular root is present. Mitochondria are single or few, with a portion anterior to the kinetosome. Microbody lobes around a portion of a mitochondrion. The zone of convergence in the fibrillar bridge that connects the kinetosome to the non-flagellated centriole is ~0.075 mm wide (Letcher et al. 2008c).

Family type – *Aquamyces* Letcher, in Letcher, Vélez, Barrantes, Powell, Churchill & Wakefield, Mycol. Res. 112: 775 (2008)

Ecology & life modes – This family has been collected from pollen baits in exclusively aquatic samples, in Canada, the USA, and Argentina (Letcher et al. 2008c, Simmons et al. 2020).

Notes – The family was introduced to accommodate *Aquamyces*, a monotypic genus (Letcher et al. 2008c).

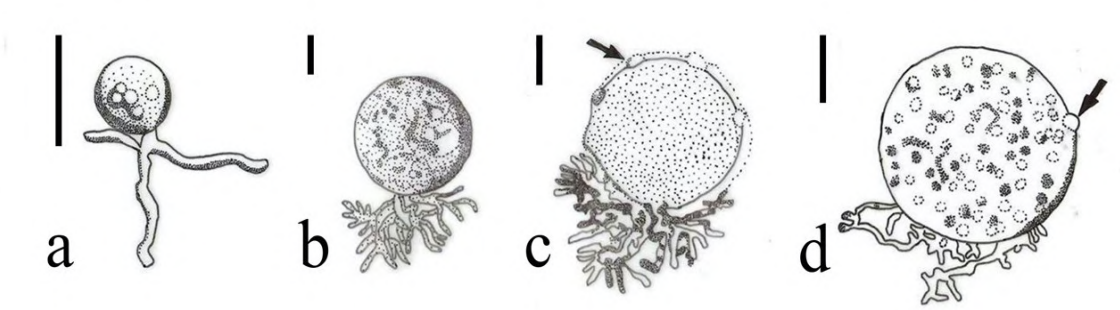


Figure 25 – *Angulomyces argentinensis.* a Germling. b Immature thallus. c Thallus with multiple discharge papillae. d Mature thallus with cleaved zoospores. Scale bars 10 µm (Redrawn from Letcher et al. 2008c).

Aquamyces Letcher, Mycol. Res. 112: 775 (2008)
Index Fungorum Identifier 511778

Sporangium spherical with one to several raised discharge pores or short discharge tubes. Rhizoids branched and compact on agar. Zoospore contains a single lipid globule partially covered with a fenestrated cisterna. Kinetosome-associated structure (KAS) is absent. Mitochondrions are usually one or a few, with a portion anterior to the kinetosome. Microbody lobed around a portion of the mitochondrion adjacent to the lipid globule (Letcher et al. 2008c).

Type species – *Aquamyces chlorogonii* (Serbinow) Letcher, in Letcher, Vélez, Barrantes, Powell, Churchill & Wakefield, Mycol. Res. 112: 775 (2008); Fig. 26

Basionym – *Phlyctidium chlorogonii* Serbinow 1907

Synonym – *Rhizophydium chlorogonii* (Serbinow) Jacz. & P.A. Jacz 1931

Notes – The genus consists of one species. Letcher et al. (2008c) assigned an Argentinian isolate as the epitype of this species and stated that molecular dissimilarity of isolates in hand could be used to describe additional taxa, though limited materials now remain of the genus (Simmons et al. 2020). Culture is available from CZEUM (Collection of Zoosporic Eufungi at the University of Michigan), and sequences are available in GenBank.

Batrachochytriaceae Doweld, Index Fungorum 44: 1 (2013)
Index Fungorum Identifier 550329

Reported from amphibians. Thalli monocentric or colonial, with one to several rhizoidal axes; rhizoids thread-like; each segment of the colonial thallus forms a zoosporangium. Zoosporangia with one or more inoperculate discharge papillae. Zoospores are posteriorly uniflagellate, subspherical, with aggregated ribosomes and numerous lipid globules organized into two clumps, associated with a sheet of microbody and nested in the periphery of the ribosomal mass. Kinetosomal root consisting of a group of microtubules extending parallel to the kinetosome into ribosomal core. Kinetosome is attached to a non-flagellated centriole with overlapping fibers. Rumposome and transition zone plug lacking (Doweld 2013c).

Family type – *Batrachochytrium* Longcore, Pessier & Nichols, Mycologia 91: 220 (1999)

Ecology & life modes – *Batrachochytrium dendrobatidis* (or *Bd*), and its sister species *B. salamandrivorans* (or *Bsal*), pathogens of a wide range of aquatic amphibians worldwide (e.g., Byrne et al. 2019).

Notes – At the time of its description, *Batrachochytrium* was not placed in any family of the *Chytridiomycota*, though the authors argue that it was morphologically similar, both by zoosporic ultrastructure and thallus characters, to a few genera, including *Rhizophydium* (Longcore et al. 1999). However, the genus was placed in *Rhizophydiales* (Letcher et al. 2008b, Longcore et al. 2011), but no family was assigned. Hence, Doweld (2013c) introduced *Batrachochytriaceae*. *Homolaphlyctis*, *Polyrhizophydium* are sisters to *Batrachochytriaceae* (Ames et al. 2022, Simmons et al. 2020, 2021), but only *Batrachochytrium* is recognised in the family.

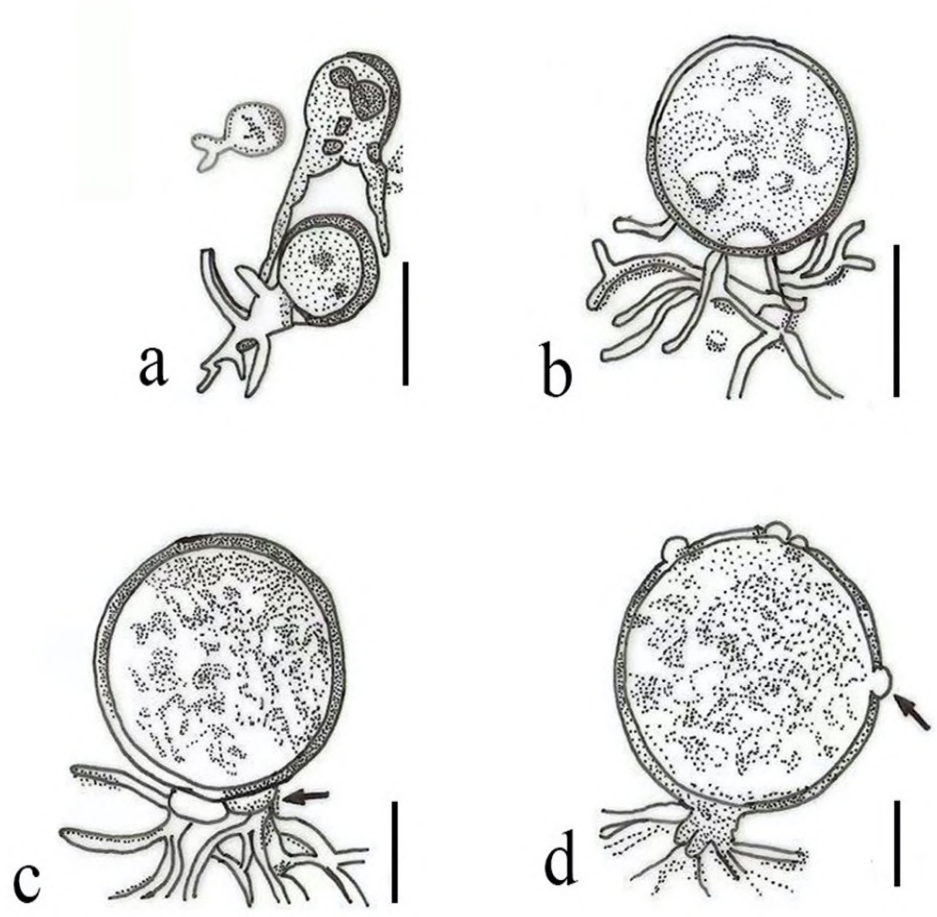


Figure 26 – *Aquamyces chlorogonii*. a Germling and early thallus development. b Immature thallus. c Mature thallus with apophysis. d Mature thallus with multiple discharge papillae. Scale bars 10 µm (redrawn from Letcher et al. 2008c).

Batrachochytrium Longcore, Pessier & Nichols (2), Mycologia 91: 220 (1999)
Index Fungorum Identifier 27960

Thalli are monocentric or colonial. One to several rhizoidal axes; rhizoids are thread-like. Each segment of the colonial thallus forms a zoosporangium. Zoosporangia with one or more inoperculate discharge papillae; swimming zoospores spherical or slightly ovate. Ribosomes aggregated. Numerous lipid globules are associated with a sheet of microbody and are nested in the periphery of ribosomal mass. Kinetosomal root consisting of a group of microtubules; arising near triplets 9-1 and extending parallel to the kinetosome into the ribosomal core. Kinetosome is attached to the non-flagellated centriole with overlapping fibres. Lacking rumposome and transition zone plug (Longcore et al 1999).

Type species – *Batrachochytrium dendrobatidis* Longcore, Pessier & Nichols, Mycologia 91: 220 (1999); Fig. 27

Notes – *Batrachochytrium* is extensively studied by herpetologists and mycologists worldwide (Byrne et al. 2019). Cultures are available from CZEUM (Collection of Zoosporic Eufungi at the University of Michigan), and sequences are available in GenBank (see Longcore et al. 1999).

Collimycetaceae Seto & Degawa, Protist 169: 514 (2018)
Index Fungorum Identifier 823272

Thallus monocentric, eucarpic, endogenous. Zoosporangium with several inoperculate discharge pores. Zoospore with microbody-lipid globule complex, including a single lipid globule partially covered by a fenestrated cisterna and microbody; kinetosome-associated structure elongated, dome-shaped in longitudinal section of kinetosome, appressed to kinetosome, near fibrillar bridge in transverse section of kinetosome. Monophyletic within *Rhizophydiales* (Seto & Degawa 2018a).

Family type – *Collimyces* Seto & Degawa, Protist 169: 514 (2018)

Ecology & life modes – This family contains a single species, *Collimyces mutans*, which is an obligate parasite of the green alga *Microglena* found in a pond in Chiba Prefecture, Japan.

Notes – This lineage proved distinct in a molecular phylogeny generated by Seto & Degawa (2018a), but its relation to other families in *Rhizophydiales* could not be determined due to its unsupported placement.

Collimyces Seto & Degawa, Protist 169: 514 (2018)
Index Fungorum Identifier 823273

Parasitic fungus of the green algal genus *Microglena*. Thallus monocentric, eucarpic, endogenous. Zoosporangium with several inoperculate discharge pores. Rhizoids branched at the base, extending in a fan-like shape. Zoospore with alignment of a nucleus, ribosomal aggregation, a single mitochondrion, microbody-lipid globule complex at anterior half to two-thirds of cell; microbody-lipid globule complex including a single lipid globule partially covered by a fenestrated cisterna and microbody, associated with a mitochondrion; kinetosome and nonflagellated centriole parallel, connected by fibrillar bridge with a wide (up to 75 nm) zone of convergence; kinetosome-associated structure elongated, dome-shaped in longitudinal section of kinetosome, appressed to kinetosome, near fibrillar bridge in transverse section of kinetosome; microtubular root composed of stacked microtubules, extending from kinetosome to fenestrated cisterna (Seto & Degawa 2018a).

Type species – *Collimyces mutans* Seto & Degawa, Protist 169: 514 (2018)

Notes – Seto & Degawa (2018a) noted that this was yet another instance of obligate algal parasitism in *Rhizophydiales* in disparate lineages, indicative of the diversity of parasitic fungi in this order. Sequences are available in GenBank.

Coralloidiomycetaceae Doweld, Index Fungorum 94: 1 (2014)
Index Fungorum Identifier 550405

Thallus monocentric, eucarpic, sporangia sessile to occasionally interbiotic with multiple lobes. Zoospores are posteriorly uniflagellate, with a single lipid globule partially covered with a conspicuous fenestrated cisterna and microbody with laminated lobes that extend into and partially around the ribosomal core; the kinetosome-associated structure is a solid shield, from which a microtubular root of four microtubules extends to the fenestrated cisterna. Saprophytic (Doweld 2014a).

Family type – *Coralloidiomyces* Letcher, Mycologia 100: 328 (2008)

Ecology & life modes – The family contains one species, *Coralloidiomyces digitatus*, known from a single pollen bait of a marshland mud sample near Lake Muster, Chubut Province, Argentina (Letcher et al 2008b).

Notes – Letcher et al. (2008b) maintained the genus in *incertae sedis* since the phylogenetic support is poor. However, Doweld (2014t) introduced *Coralloidiomycetaceae* to accommodate the genus. Currently, the family comprises one genus.

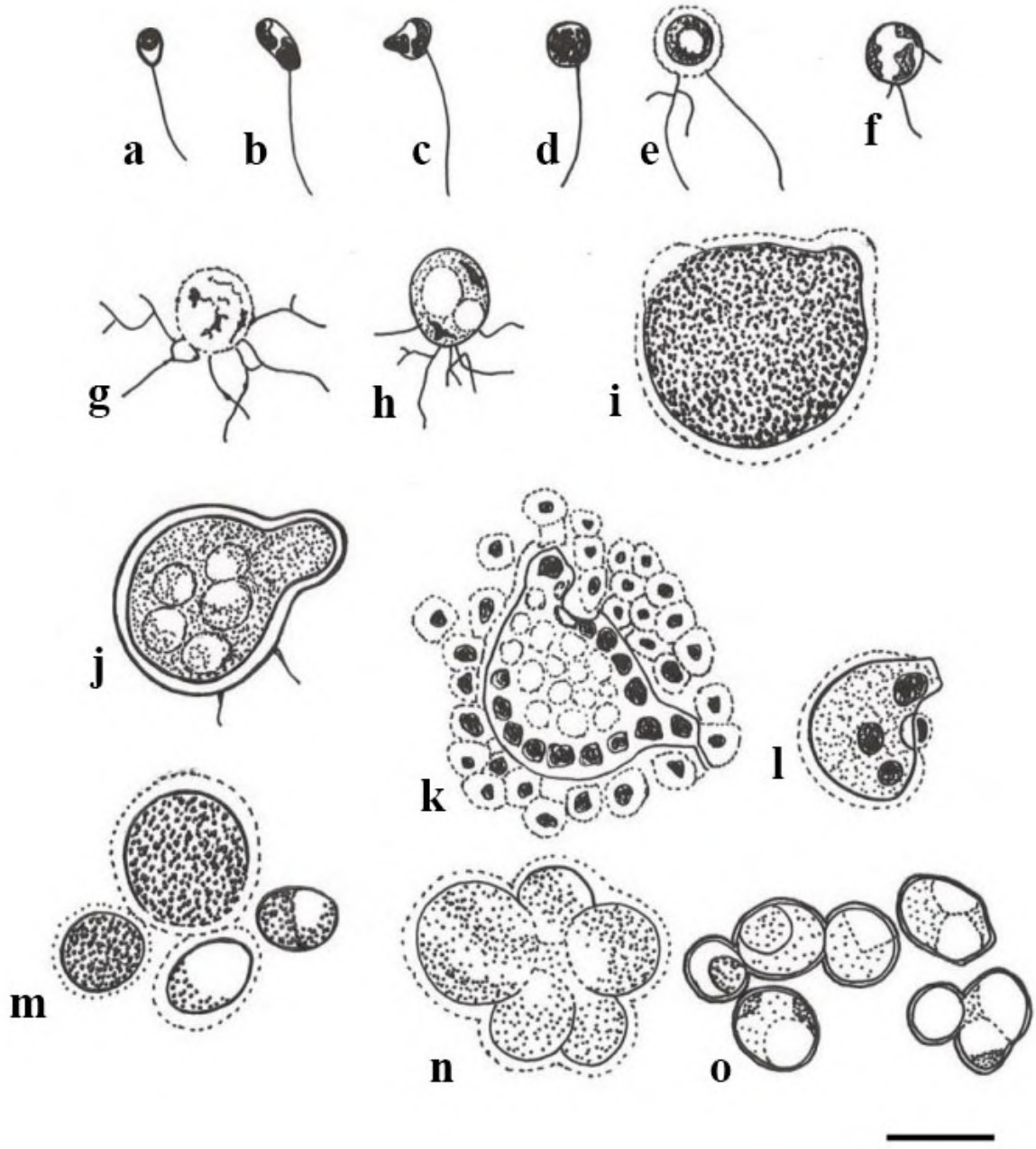


Figure 27 – *Batrachochytrium dendrobatidis*. a shape of motile zoospore. b elongate amoeboid zoospore. c fine cytoplasmic extension (arrow) from surface of zoospore. d zoospore flattened on agar surface under cover slip; black dots are probably lipids and microbody and grey shadowy area is the aggregation of ribosomes. e germling with rhizoids from single area of thallus. f germling with 3 rhizoidal axes. g, h thread-like rhizoids on developing sporangia. i large zoosporangium with 2 discharge papillae (arrows). j wall of tip of papilla has begun to deliquesce. k zoospores discharging through 2 papillae (arrows). l nearly empty zoosporangium showing slight thickening of wall at tip of papilla. m group of thalli; one thallus with internal septation (arrow). n colonial thallus with several walls (arrows). o appearance of isolate L-197 in skin of blue-and-yellow dart frog. Colonial thallus (arrow) and monocentric zoosporangium (arrowhead) in epidermis of host that was experimentally infected. Scale bar = 10 μm (redrawn from Longcore et al. 1999).

Coralloidiomyces Letcher, Mycologia 100: 328 (2008)
Index Fungorum Identifier 506748

Saprophytic. Thallus monocentric, eucarpic, with sessile or occasionally interbiotic sporangia having multiple lobes. Zoospore with a single lipid globule partially covered with a conspicuous fenestrated cisterna and a microbody with laminated lobes that extend into and partially around the ribosomal core. KAS acts as a solid shield, from which a microtubular root composed of four microtubules extends to the fenestrated cisterna (Letcher et al. 2008b).

Type species – *Coralloidiomyces digitatus* Letcher, Mycologia 100(2): 330 (2008); Fig. 28

Notes – The genus and species etymologies describe the coral-like irregularity and finger-like projections of the zoosporangium, respectively, that are indicative of this ornate genus, making it easily recognizable in an order mainly composed of taxa with spherical zoosporangia. Culture is available from CZEUM (Collection of Zoosporic Eufungi at the University of Michigan), and sequences are available in GenBank.

Dinomycetaceae Karpov & Guillou, Protist 165: 230 (2014)
Index Fungorum Identifier: 807620

Zoospore has a centriole not parallel to kinetosome with bilaminated spur, ribosomal core crossed by endoplasmic reticulum (Lepelletier et al. 2014), and a paracristalline inclusion is present (Fernández-Valero et al. 2024).

Family type – *Dinomyces* Karpov & Guillou, Protist 165: 241 (2014); Fig. 29

Ecology & life modes – The family contains two genera and four species: *Dinomyces arenysensis, D. gilberthii, Paradinomyces triforaminorum* and *P. evelyniae* observed as parasites on marine dinoflagellates from the Mediterranean Sea near Spain. The species can grow on agar, but only in the presence of a host, with the authors concluding the species to be obligately biotrophic (Lepelletier et al. 2014, Reñé et al. 2022, Fernández-Valero et al. 2024). *Paradinomyces triforaminorum* was detected during a high-biomass bloom of the dinoflagellate *Kryptoperidinium foliaceum*. Laboratory experiments suggest this species is highly specific and demonstrate the impact it can have on HAB development. *Dinomyces gilberthii* was detected in several Mediterranean habitats, including harbours and beaches, and was particularly prevalent during summer dinoflagellate blooms. Its widespread occurrence in coastal ecosystems suggested a high level of adaptability to this environment. *Paradinomyces evelyniae* had a more restricted distribution in the coastal-marine environment, occurring in harbour sediments and only occasionally in the water column during winter and early spring. *Paradinomyces evelyniae* has previously been detected in the Baltic Sea, suggesting that its distribution encompasses contrasting coastal environments, although its presence is rare. These chytrids co-occurred with other parasites belonging to *Perkinsea* (Alveolata), highlighting that parasitic interactions are common during HABs in brackish and marine systems, and these multiple parasites compete for similar hosts.

Notes – Lepelletier et al. (2014) investigated five obligate biotrophic isolates to determine their phylogenetic placement, resulting in a new family in *Rhizophydiales*. The zoosporic ultrastructure of one isolate was examined and found to have features common to *Rhizophydiales* taxa. Zoospores of *D. gilberthii, P. triforaminorum* and *P. evelyniae* are similar to those of *D. arenysensis*, and all of them contain a paracristalline inclusion, an additional character of the family *Dinomycetaceae* (Fernández-Valero et al. 2024).

Dinomyces Karpov & Guillou, Protist 165: 241 (2014)
Index Fungorum Identifier: 807621

Parasitoid of marine dinoflagellates with a simple thallus with an inoperculate, monocentric, epibiotic sporangium having endogenous development, with an apophysum and a branching rhizoidal axis. Zoospore with central ribosomal aggregation separating nucleus from microbody-lipid-complex, which contains a single microbody enveloping a large lateral lipid globule with fenestrated cisterna. One mitochondrion is associated with MLC. Small dense bodies are present in the peripheral cytoplasm. Kinetid is adjacent to the ribosomal core. The flagellar transition zone

contains a spiral fibre. Centriole at angles from 80 to 45° to the kinetosome; both are connected by a broad fibrillar bridge. Lateral root composed of five microtubules passes from kinetosome to rumposome (fenestrated cisterna) (Lepelletier et al. 2014).

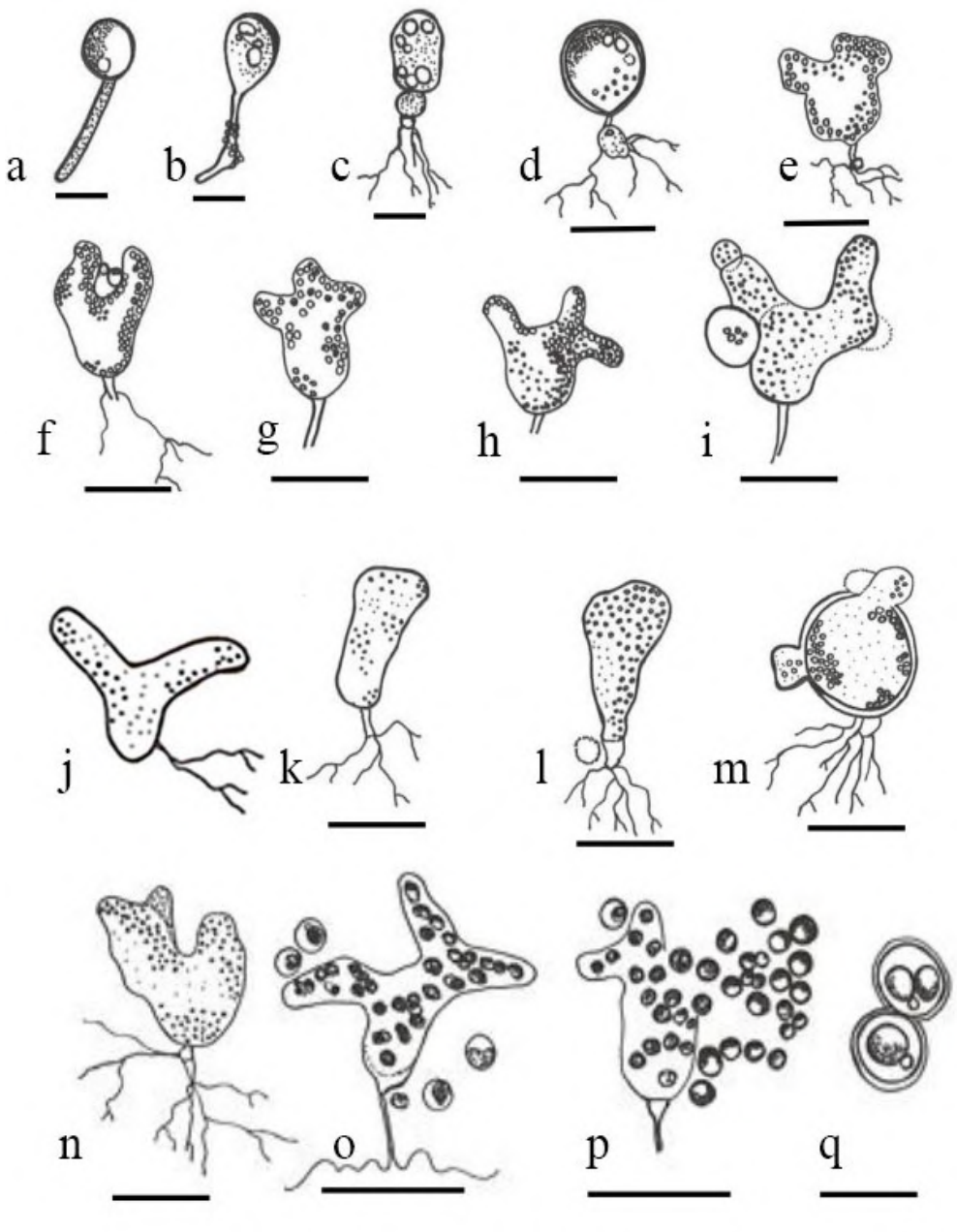


Figure 28 – *Coralloidiomyces digitatus* on dSS agar. a, b Germlings. c, d Rhizoidal axis with a subsporangial apophysis. e–n Illustrations of variable sporangial morphology. o Mature sporangium with cleaved zoospores, prior to discharge. p Mature sporangium discharging zoospores. q Two resting spores. Scale bars in a-c = 5 μm, d–f = 10 μm, g–n, q = 15 μm, o, p = 20 μm (redrawn from Letcher et al. 2008b).

Type species – *Dinomyces arenysensis* Karpov & Guillou, Protist 165: 241 (2014); Fig. 32 (a-d)

Notes – Lepelletier et al. (2014) argue that *D. arenysensis*, like similar parasites of freshwater algae, could influence population dynamics of hosts, which can produce levels of toxins that are

lethal to vertebrates during algal blooms, with the fungus potentially serving as a biocontrol of these toxic blooms. Fernández-Valero et al. (2024) introduced the second species, *Dinomyces gilberthii* Karpov, Fernández-Valero & Reñé of the genus. According to this study, zoospores contain a paracristalline inclusion, which has been found in all four species of this family (Fig. 29a). Sequences are available in GenBank.

Other genera in *Dinomycetaceae*

Paradinomyces Reñé & Karpov, in Reñé, Alacid, Vishnyakov, Seto, Paloheimo, Tcvetkova, Kagami, Kremp, Garcés & Karpov, Harmful Algae 120 (no. 102352): 6 (2022)
Index Fungorum Identifier: 846461; Index Fungorum (2023) and Species Fungorum (2023) accepted two species.

Type species – *Paradinomyces triforaminorum* Reñé & Karpov 2022; Fig. 29e-j

Notes – Observed as a parasite of the marine dinoflagellate *Kryptoperidinium foliaceum* during a bloom in the northern Baltic Sea near Finland (Reñé et al. 2022). Sequences are available in GenBank. Fernández-Valero et al. (2024) introduced a new species, *Paradinomyces evelyniae* Karpov et al., from the marine environment.

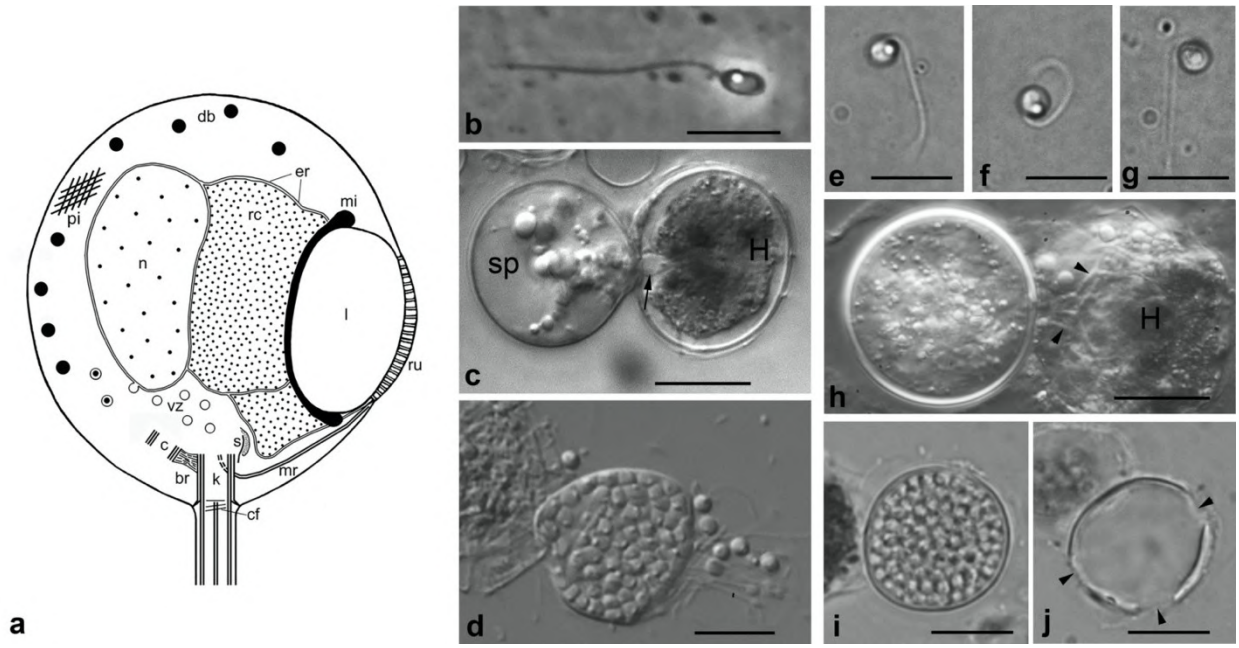


Figure 29 – Main characters of zoospore structure of *Dinomyces arenysensis*. a light microscopic image of the life-cycle stages of *D. arenysensis*. b-d *Paradinomyces triforaminorum*. a zoospore drawing (mitochondrion not shown), b, e-g released zoospore. c, h immature sporangia (sp) attached to the host (h). d, i mature sporangia with zoospores. j empty sporangium with three discharge pores (arrowheads). Abbreviations: br-bridge, connecting kinetosome (k) with centriole (c), cf-coiled fiber in flagellar transition zone, db-dense bodies, mr- root of 5 microtubules, connecting kinetosome with rumposome (ru) on the lipid globule (l) surface, mi-microbody, n-nucleus, pi-paracristalline inclusion, rc-ribosomal core surrounded by endoplasmic reticulum (er), s-spur, vz-vesiculated zone. Scale bars b,e-g = 5 μm, c,d,h-j = 10 μm.

Ericiomycetaceae Karpov & Reñé, Mycol. Prog. 20: 106 (2021)
Index Fungorum Identifier: 836465

Parasitic brackish-water chytrid. Sporangium formed as a lateral outgrowth from the encysted zoospore. Zoospore has a kinetosome with an anterior microtubular root associated with a short basal fibrillar plate, a ribosomal core ramified and crossed by endoplasmic reticulum (Karpov et al. 2021).

Family type – *Ericiomyces* Karpov & Reñé, Mycol. Prog. 20: 106 (2021)

Ecology & life modes – This family accommodates a single species, *Ericiomyces syringoforeus*, a parasite observed on marine dinoflagellate *Kryptoperidinium foliaceum* in the northern Baltic Sea near Finland (Karpov et al. 2021).

Notes – Karpov et al. (2021) showed molecular and ultrastructural evidence for the placement of this family in the *Rhizophydiales*, though the lineage was highly divergent in the molecular phylogeny.

Ericiomyces Karpov & Reñé, Mycol. Prog. 20: 106 (2021)
Index Fungorum Identifier: 836466

Parasitoid of brackish-water dinoflagellates with a simple thallus with a monocentric, epibiotic sporangium having endogenous development, with a haustorium. Sporangium covered with spines has a smooth papilla. Zoospore with central ribosomal aggregation around the nucleus. Posterior microbody-lipid-complex contains a lobed microbody enveloping a large lipid globule. Mitochondria are located around the ribosomal core. Kinetid is adjacent to the MLC. The centriole is connected to the kinetosome by oblique fibrils without a zone of convergence. The anterior root composed of six microtubules, passes from the kinetosome along the microbody. Cyst contains a syringe-like structure, and uses a special funnel-shaped structure for penetration into the host (Karpov et al. 2021).

Type species – *Ericiomyces syringoforeus* Karpov & Reñé, Mycol. Prog. 20: 107 (2021); Fig. 30

Notes – This genus possesses a previously unobserved syringe-and-funnel organelle, which fully develops in the encysted zoospore, that penetrates the dinoflagellate host, perhaps paralyzing it (Karpov et al. 2021). The developing zoosporangium is covered by short, spiny protrusions along the entirety of its surface, a trait reflected in the generic etymology (*ericio*; Greek, "hedgehog").

Globomycetaceae Letcher, Mycol. Res. 112: 776 (2008)
Index Fungorum Identifier: 511775

Sporangium spherical with a single discharge pore. Rhizoids are sparingly branched. Zoospore with a single lipid globule partially covered with a fenestrated cisterna. The kinetosome and the non-flagellated centriole are parallel and connected by fibrillar material with a zone of convergence approximately 0.075 mm in width, centrally located between the two structures. Kinetosome-associated structure (KAS) is absent. Microbody is simple or lobed. Distinct thick-membraned spherical vesicles with uniformly electron-dense contents occur in the peripheral cytoplasm (Letcher et al. 2008c).

Family type – *Globomyces* Letcher, Mycol. Res. 112: 777 (2008)

Ecology & life modes – Observed on pollen baits added to aquatic and soil samples in Argentina (Letcher et al. 2008c) and the USA (Simmons et al. 2020).

Notes – Letcher et al. (2008c) described this family as distinct from other genera in *Rhizophydiales* based on molecular phylogenetics and zoosporic ultrastructural features. The family comprises two genera that were further delineated based on phylogenetic monophyly and slight ultrastructural variations.

Globomyces Letcher, Mycol. Res. 112: 777 (2008)
Index Fungorum Identifier 511780

Sporangium spherical with a single discharge pore. Zoospore contains a single lipid globule partially covered with a prominent fenestrated cisterna. Microbody is lobed (Letcher et al. 2008c).

Type species – *Globomyces pollinis-pini* (A. Braun) Letcher, Mycol. Res. 112: 777 (2008); Fig. 31

Basionym: *Chytridium pollinis-pini* A. Braun, Abh. K. Akad. Wiss. Berlin: 40 (1856) [1855]

Notes – This genus was described to accommodate a species previously described from pollen baits of aquatic and soil samples (Letcher et al. 2008c). Cultures are available from CZEUM

(Collection of Zoosporic Eufungi at the University of Michigan), and sequences are available in GenBank.

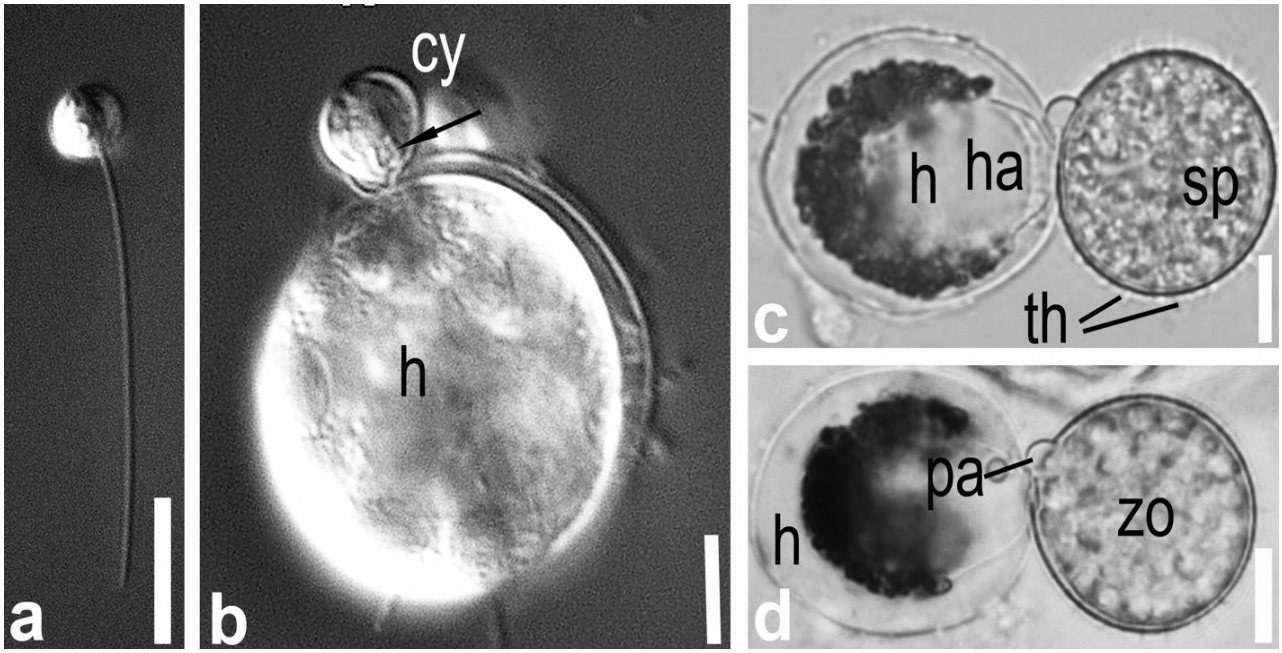


Figure 30 – Main stages of life cycle of *Ericiomyces syringoforum*. a zoospore. b cyst (cy) with a syringe (arrow) on the host (h) surface. c mature sporangium (sp) with thorns (th) and haustorium (ha) in the host. d sporangium with mature zoospores (zo) and papilla (pa). Scale bars: a, b = 5 μm, c, d = 10 μm.

Other genus in *Globomycetaceae*

Urceomyces Letcher, Mycol. Res. 112(7): 777 (2008)

Index Fungorum Identifier 511781; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Urceomyces sphaerocarpus* (Zopf) Letcher 2008

Notes – On pollen baits of aquatic samples from Argentina (Letcher et al. 2008c). Cultures are available from CZEUM (Collection of Zoosporic Eufungi at the University of Michigan), and sequences are available in GenBank.

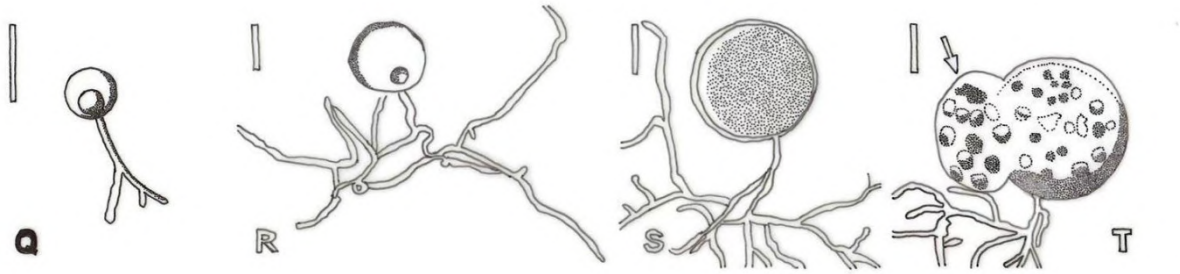


Figure 31– *Globomyces pollinis-pini* (ARG 068) a Germling. b Developing thallus. c Immature thallus. d Mature thallus with cleaved zoospores beginning to discharge (arrow). Scale bars 10 μm (redrawn from Letcher et al. 2008c).

Gorgonomycetaceae Letcher, Mycol. Res. 112: 767 (2008)

Index Fungorum Identifier 511768

Sporangia at maturity are spherical with numerous elongate and sinuous discharge tubes. Rhizoids are branched. Zoospore contains a single lipid globule partially covered with a fenestrated cisterna. Kinetosome and non-flagellated centriole are parallel and connected by fibrillar material with a zone of convergence approximately 0.010–0.025 mm in width, centrally located between the two structures. Kinetosome-associated structure (KAS) is absent. Microbody is lobed. Mitochondria one to five, with a portion anterior to the kinetosome (Letcher et al. 2008c).

Family type – *Gorgonomyces* Letcher, Mycol. Res. 112: 767 (2008)

Ecology & life modes – Species have been isolated from pollen and chitin baits added to aquatic samples from Argentina (Letcher et al. 2008c), USA (Simmons et al. 2020), and Thailand (Hurdeal et al. 2023).

Notes – This family contains one genus, *Gorgonomyces.* In addition to its phylogenetic and ultrastructural distinctiveness, members described thus far possess tubular projections from the developing spherical zoosporangium that make it easy to distinguish from most other families in *Rhizophydiales* (Letcher et al. 2008c).

Gorgonomyces Letcher, Mycol. Res. 112: 767 (2008)
Index Fungorum Identifier 511769

Sporangium spherical with one or two broad discharge tubes when on an algal host, or up to 30 elongate discharge tubes when on artificial media. KAS absent. Microbody lobed. Mitochondria one to five, with a portion anterior and proximal to the kinetosome (Letcher et al. 2008c).

Type species – *Gorgonomyces haynaldii* (Schaarschm.) Letcher, Mycol. Res. 112: 767 (2008); Fig. 32

Notes – Letcher et al. (2008c) believed that dissimilarity of some isolates in their molecular phylogeny was evidence for further speciation within the lineage, perhaps at different locations with similar habitats. Hurdeal et al. (2023) proved just that, describing a new species isolated from pollen baits of an aquatic sample from Thailand. Cultures are available from CZEUM (Collection of Zoosporic Eufungi at the University of Michigan), and sequences are available in GenBank.

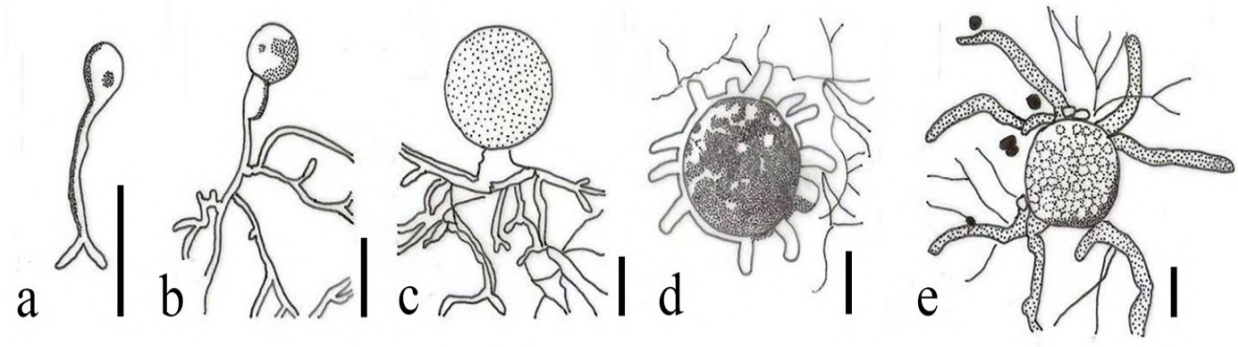


Figure 32 – *Gorgonomyces haynaldii* (ARG 026) a Germling. b Young developing thallus with swollen rhizoidal axis. c Immature thallus. d Mature thallus developing multiple discharge tubes. e Mature thallus with fully developed discharge tubes. Scale bars a-d = 10 μm (redrawn from Letcher et al. 2008c).

Halomycetaceae Letcher & M.J. Powell, Mycologia 107: 819 (2015)
Index Fungorum Identifier 811430

Thallus monocentric, eucarpic. Sporangium with few to many discharge papillae. Rhizoids are apophysate or non-apophysate. Zoospores with single or multiple lipid globules, a simple or fenestrated MLC cisterna, a microbody, and a microtubular root (Letcher et al. 2015a).

Family type – *Halomyces* Letcher & M.J. Powell, in Letcher, Powell & Davis, Mycologia 107: 819 (2015)

Ecology & life modes – This family contains genera that are primarily associated with pollen and keratin baits of primarily estuary, saline, and freshwater aquatic samples, with exceptions for wet, muddy, or agricultural soils, from Argentina, Brazil, Canada, Germany, South Africa, and the USA (Letcher et al. 2015a, Simmons et al. 2020).

Notes – At the time of its description, the monophyly of *Halomycetaceae* was not supported. However, further molecular analyses of a wider sampling of the *Rhizophydiales* showed *Paranamyces* to be phylogenetically distant from the other *Halomycetaceae* genera (Simmons et al. 2020). Future research may justify the description of an additional family to accommodate *Paranamyces*.

Halomyces Letcher & M.J. Powell, Mycologia 107: 819 (2015)
Index Fungorum Identifier 811463

Thallus monocentric, eucarpic. Sporangium spherical, 13.8–26.5 mm diam., with few (2–3) discharge papillae. Rhizoids are branched, tapering, non-apophysate, but with a swollen rhizoidal axis. Zoospores spherical, 2.7–3.6 mm diam., with a single lipid globule, a MLC fenestrated cisterna, a lobed microbody, endoplasmic reticulum ramifying through the ribosomal aggregation, a narrow zone of convergence in the fibrillar bridge between the kinetosome and non-flagellated centriole, and a microtubular root of 4–5 stacked microtubules (Letcher et al. 2015a).

Type species – *Halomyces littoreus* (Amon) Letcher & M.J. Powell, in Letcher, Powell & Davis, Mycologia 107: 819 (2015)

Basionym: *Rhizophydium littoreum* Amon, Mycologia 76(1): 137 (1984)

Notes – The generic name reflects the saline environments from which the ex-type isolate and additional members of the family have been observed and isolated. Sequences are available in GenBank.

Other genera in *Halomycetaceae*

Paludomyces Letcher & M.J. Powell, in Letcher, Powell & Davis, Mycologia 107(4): 819 (2015)
Index Fungorum Identifier 811465; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Paludomyces mangrovei* (Ulken) Letcher & M.J. Powell 2015

Notes – On pollen and keratin baits added to a mangrove swamp sediment sample from São Paulo, Brazil (Letcher et al. 2015a). Sequences are available in GenBank.

Paranamyces Letcher & M.J. Powell, in Letcher, Powell & Davis, Mycologia 107(4): 823 (2015)
Index Fungorum Identifier 811469; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Paranamyces uniporus* Letcher & M.J. Powell 2015

Notes – On pollen and keratin baits added to wet soils and estuary soils in Argentina and the USA (Letcher et al. 2015a). Cultures are available from CZEUM (Collection of Zoosporic Eufungi at the University of Michigan), and sequences are available in GenBank.

Ulkenomyces Letcher & M.J. Powell; in Letcher, Powell & Davis, Mycologia 107(4): 821 (2015)
Index Fungorum Identifier 811467; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Ulkenomyces aestuarii* (Ulken) Letcher & M.J. Powell 2015

Notes – On pollen and keratin baits added to estuary sediment from Bremen, Germany, mud from British Columbia, Canada, and farm soils from Northern Cape Province, South Africa (Letcher et al. 2015a). Culture is available from CZEUM (Collection of Zoosporic Eufungi at the University of Michigan), and sequences are available in GenBank.

Kappamycetaceae Letcher, Mycol. Res. 110: 912 (2006)
Index Fungorum Identifier 82155

Thallus eucarpic, monocentric. Sporangium and resting spore are endogenous with the zoospore cyst. Rhizoids thread-like, branched, and compact. Zoospores contain a ribosomal mass, a single lipid globule, a microbody, a nucleus, and a single mitochondrion. Kinetosome and non-flagellated centriole lie parallel or slightly angled and contain a densely granular core located centrally in each structure (Letcher et al. 2006).

Family type – *Kappamyces* Letcher & M.J. Powell, Nova Hedwigia 80: 125 (2005)

Ecology & life modes – *Kappamyce* is monotypic with *Kappamyces*, originally described from pollen baits of soils along streams in Virginia and Georgia, USA (Letcher & Powell 2005a). In subsequent studies, *Kappamyces* has proven to be rather ubiquitous and easily isolated, found on pollen baits of soil samples in Brazil (Jesus & Pires-Zottarelli 2020, Simmons et al. 2020), Argentina, Australia, and throughout the USA (Simmons et al. 2020).

Notes – *Kappamyces* was originally described as a new genus of *Chytridiales*, sister to the "*Rhizophydium* clade", based on zoosporic ultrastructural characters and molecular phylogenetics (Letcher & Powell 2005a). When this clade was elevated to *Rhizophydiales* by Letcher et al. (2006) and described *Kappamycetaceae* to accommodate *Kappamyces*

Kappamyces Letcher & M.J. Powell, Nova Hedwigia 80: 125 (2005)
Index Fungorum Identifier 28952

Thallus monocentric, eucarpic, with an epibiotic sporangium and resting spore and a compact endobiotic mass of thread-like rhizoids. Resting spores are thick-walled, spherical, hyaline, sessile or stalked, with a single large globule. Zoospores spherical, containing a ribosomal mass, a single lipid globule, a microbody, a nucleus, and a single mitochondrion, all enveloped in a double-membrane system; thick-membraned vesicles, 0.2-0.3 μm diam., with electron-opaque contents, either surrounding the kinetosome and non-flagellated centriole or occurring in the peripheral cytoplasm; kinetosome and non-flagellated centriole parallel, or proximal end of non-flagellated centrioles lightly angled toward the kinetosome. Both the kinetosome and the non-flagellated centriole have an electron-opaque core (Letcher & Powell 2005a).

Type species – *Kappamyces laurelensis* Letcher & M.J. Powell, Nova Hedwigia 80: 127 (2005)

Notes – Species of *Kappamyces* are relatively small and can complete a full cycle of zoospore release, encystment, development of zoosporangium, and subsequent release within 48 hours. *Kappamyces* was monotypic until the recent description of *K. microporosus* from pollen baits of soil from São Paulo, Brazil (Jesus & Pires-Zottarelli 2020). Cultures are available from CZEUM (Collection of Zoosporic Eufungi at the University of Michigan) and sequences are available in GenBank.

Operculomycetaceae Doweld, Index Fungorum 118: 1 (2014)
Index Fungorum Identifier 550461

Thallus monocentric, eucarpic; rhizoids extensively branched, commonly arising from a single main axis. Sporangia apically operculate. Zoospores spherical, posteriorly uniflagellate, with a prominent multilayered J-shaped laminated spur curving over the anterior end of the kinetosome, kinetosome and non-flagellated centriole not parallel, at an acute (15-20Âº) angle, microtubule roots and fenestrated cisternae lacking. Saprophytic on keratin, chitin, and pollen (Doweld 2014b).

Family type – *Operculomyces* M.J. Powell, Letcher & Longcore, Mycologia 103: 856 (2011)

Ecology & life modes – The family contains a single species, *Operculomyces laminatus*, isolated from a snake skin keratin bait from garden soil in Maine, USA (Powell et al. 2011).

Notes – Powell et al. (2011) introduced a monospecific genus in *Rhizophydiales*. Doweld (2014u), however, introduced *Operculomycetaceae* to accommodate the genus.

Operculomyces M.J. Powell, Letcher & Longcore, Mycologia 103: 856 (2011)
Index Fungorum Identifier 519309

Saprophytic. Thallus monocentric, eucarpic; rhizoids branched; sporangium operculate; zoospores posteriorly uniflagellate, spherical, with a prominent multilayered spur curving over the anterior end of the kinetosome; monophyletic within the *Rhizophydiales* (Powell et al. 2011).

Type species – *Operculomyces laminatus* M.J. Powell, Letcher & Longcore, Mycologia 103: 860 (2011)

Notes – In addition to the genus being distinct within *Rhizophydiales* by molecular phylogenetics and a suite of zoosporic ultrastructural characters, *Operculomyces* is also recognizable for its zoosporangium possessing a large, apical operculum, which commonly remains attached after zoospore release (Powell et al. 2011). Culture is available from CZEUM (Collection of Zoosporic Eufungi at the University of Michigan), and sequences are available in GenBank.

Pateramycetaceae Letcher, Mycol. Res. 112: 778 (2008)
Index Fungorum Identifier 511776

Zoospore contains a single lipid globule partially covered with a fenestrated cisterna. Kinetosome and non-flagellated centriole are parallel and connected by fibrillar material with a zone of convergence approximately 0.010–0.025 mm in width centrally located between the two structures. Kinetosome-associated structure (KAS) is absent. Mitochondrion has single a lobe, which lies above and proximal to the kinetosome. Microbody lobed. Walled, moderately electron-dense vesicles occur in the peripheral cytoplasm, often proximal and lateral to the kinetosome. From aquatic habitats, saprophytic on pollen (Letcher et al. 2008c).

Family type – *Pateramyces* Letcher, Mycol. Res. 112: 779 (2008)

Ecology & life modes – The family contains a single species, *Pateramyces corrientinensis*, from pollen baits of aquatic lake samples from Corrientes Province, Argentina (Letcher et al. 2008c).

Notes – At the time of its description, *Pateramycetaceae* was unique in *Rhizophydiales* as the only operculate family in the order (Letcher et al. 2008c), until the description of *Operculomycetaceae* (Doweld 2014b). The family is also distinguished by forming a distinct molecular phylogenetic lineage and by unique zoosporic ultrastructural characteristics.

Pateramyces Letcher, Mycol. Res. 112: 779 (2008)
Index Fungorum Identifier 511782

Sporangium spherical with a single discharge pore. Zoospore contains a single lipid globule partially covered with a fenestrated cisterna. Mitochondrion single (Letcher et al. 2008c).

Type species – *Pateramyces corrientinensis* Letcher, Mycol. Res. 112(7): 779 (2008)

Notes – Letcher et al. (2008) noted that *Pateramyces* is similar to *Operculomyces* (Powell et al. 2011), in that operculation is not often observed in genera of the *Rhizophydiales*, but is dissimilar in genetic sequence. In a larger phylogeny of *Rhizophydiales*, the disparity of these two genera has remained true, indicative of this trait likely evolving independently. Sequences are available in GenBank.

Protrudomycetaceae Letcher, Mycol. Res. 112: 773 (2008)
Index Fungorum Identifier 511772

Sporangia spherical to anatropous with one to three prominent discharge papillae. Rhizoids are peg-like on algae or branched on agar. Zoospore contains a single lipid globule partially covered with a fenestrated cisterna. Kinetosome and non-flagellated centriole are parallel and connected by fibrillar material with a zone of convergence approximately 0.010–0.025 mm in width, centrally located between the two structures. Kinetosome-associated structure (KAS) is absent. Mitochondria are numerous. Microbody is lobed around mitochondria proximal to the lipid globule (Letcher et al. 2008c).

Family type – *Protrudomyces* Letcher, Mycol. Res. 112: 773 (2008)

Ecology & life modes – This family is comprised of isolates cultured from pollen baits of aquatic samples in Ontario, Canada, Argentina, and the USA (Letcher et al 2008c, Simmons et al. 2020).

Notes – Letcher et al. (2008c) noted that additional taxa may exist in the lineage, given the molecular dissimilarity observed in the family.

Protrudomyces Letcher, Mycol. Res. 112: 773 (2008)
Index Fungorum Identifier 511777

Sporangium spherical to anatropous with one to three protruding discharge pores. Zoospore contains a single lipid globule partially covered with a fenestrated cisterna. Kinetosome-associated structure (KAS) is absent. Mitochondria numerous. Microbody lobed around mitochondrion proximal to lipid globule (Letcher et al. 2008c).

Type species – *Protrudomyces lateralis* (A. Braun) Letcher [as *'laterale'*], Mycol. Res. 112: 774 (2008)

Basionym: *Chytridium laterale* A. Braun, Abh. K. Akad. Wiss. Berlin: 41 (1856) [1855]

Notes – Cultures are available from CZEUM (Collection of Zoosporic Eufungi at the University of Michigan), and sequences are available in GenBank.

Rhizophydiaceae Letcher, Mycol. Res. 110: 909 (2006)
Index Fungorum Identifier 82157

Zoospore contains a single lipid globule partially covered with a cisterna. The kinetosome and the non-flagellated centriole are parallel and are connected by fibrillar material with a zone of convergence approximately 0.075 mm in width, centrally located between the two structures. Kinetosome-associated structure is present as a laminated, curved spur. Sporangium spherical at maturity, with multiple discharge pores or papillae. Rhizoids branched (Letcher et al. 2006).

Family type – *Rhizophydium* Schenk ex Rabenh., Flora Europaea algarum aquae dulcis et submarinae 3: 280 (1868) [1867]

Ecology & life modes – This family contains the type of the *Rhizophydiales*, *Rhizophydium*, which is a historically ubiquitous genus on multiple substrates in terrestrial and aquatic samples (see Letcher et al. 2006 for review). Of the molecularly confirmed cultures, members of the family have been observed on multiple substrates from Argentina, Australia, Brazil, the USA (Simmons et al. 2020), and Oman (Hassett et al. 2020).

Notes – Even after the delineation of the *Rhizophydiales* and multiple families (Letcher et al. 2006), *Rhizophydiaceae* still represents a ubiquitous lineage with molecular diversity that is likely to justify the description of multiple genera or species (Simmons et al. 2020).

Rhizophydium Schenk ex Rabenh., Flora Europaea algarum aquae dulcis et submarinae 3: 280 (1868) [1867]; Figs. 33q & r
Index Fungorum Identifier 20484

Thallus epi- and endobiotic, monocentric, eucarpic, generally monophagous; the epibiotic part forming the rudiment of the sporangium or resting spore, the endobiotic part forming a branched or rarely unbranched rhizoidal system; sporangium inoperculate, sessile, or rarely on an extrametrical stalk, uni- or multiparous, the wall occasionally deliquescing wholly or in part; zoospores formed within the sporangium, posteriorly uniflagellate, generally with a single globule; resting spore thick-walled, contents with one or more globules, borne like the sporangium, asexually formed or sexually after receiving the contents of a small adnate contributing thallus which persists as a cyst, upon germination functioning as a sporangium or prosporangium (Sparrow 1960).

Type species – *Rhizophydium globosum* (A. Braun) Rabenh., Flora Europaea algarum aquae dulcis et submarinae 3: 280 (1868) [1867]

Notes – The revisionary taxonomy of this genus resulted in the description of the first new order in *Chytridiomycota* in over 25 years (Letcher et al. 2006). Besides, most of the families in the

Rhizophydiales are derived from one or several species previously assigned to *Rhizophydium*. Further assessments of taxa, specifically those reported on natural substrates before isolation efforts, electron microscopy, and molecular phylogenetics, are necessary before delimiting which species are verified within the genus. Additionally, new species are being described under the current criteria (Hassett et al. 2020). Cultures are available from CZEUM (Collection of Zoosporic Eufungi at the University of Michigan), and sequences are available in GenBank.

Staurastromycetaceae Van den Wyng., K. Seto & Rojas-Jim., Protist 168: 399 (2017)
Index Fungorum Identifier 819821

Zoospore with aggregated ribosomes partially covered with endoplasmic reticulum. Endoplasmic reticulum ramifying ribosomal aggregation; microbody-lipid globule complex, including a single lipid globule partially covered by microbody and fenestrated cisternae; microbody simple; multiple mitochondria spherical shaped, outside ribosomal aggregation; nonflagellated centrioles lightly angled or almost parallel to kinetosome (Van den Wyngaert et al. 2017).

Family type – *Staurastromyces* Van den Wyng., K. Seto & Rojas-Jim., Protist 168: 399 (2017)

Ecology & life modes – Parasitic on a *Staurastrum* desmid in a freshwater lake in Brandenburg, Germany (Van den Wyngaert et al. 2017).

Notes – *Staurastromycetaceae* is a monotypic family that represents a unique lineage in *Rhizophydiales* and possesses a distinct zoosporic ultrastructural suite of characters (Van den Wyngaert et al. 2017).

Staurastromyces Van den Wyng., K. Seto & Rojas-Jim., Protist 168(4): 399 (2017)
Index Fungorum Identifier 819822

Zoospore with aggregated ribosomes partially covered with endoplasmic reticulum; endoplasmic reticulum ramifying ribosomal aggregation; microbody-lipid globule complex including a single lipid globule partially covered by microbody and fenestrated cisternae; microbody simple; multiple mitochondria spherical shaped, outside ribosomal aggregation; nucleus partially inserted into ribosomal aggregation, associated with microbody; multivesicular body outside ribosomal aggregation at peripheral cytoplasm; kinetosome and nonflagellated centrioles lightly angled or almost parallel, connected by fibrillar bridge without minimal zone of convergence; microtubular root consisting of stacked microtubules, extending from kinetosome to fenestrated cisternae; kinetosome associated structure absent (Van den Wyngaert et al. 2017).

Type species – *Staurastromyces oculus* Van den Wyng., K. Seto & Rojas-Jim., Protist 168: 399 (2017)

Notes – In a molecular phylogeny, *Staurastromyces* is sister to the *Pateramycetaceae* (Letcher et al. 2008a). However, molecular and morphological dissimilarity, most conspicuous being the lack of an operculum, sets *Staurastromyces* apart from that family, and Van den Wyngaert et al. (2017) described a new family to accommodate this genus. Sequences are available in GenBank.

Terramycetaceae Letcher, Mycol. Res. 110: 911 (2006)
Index Fungorum Identifier 82156

Zoospore contains a single lipid globule partially covered by a cisterna. Kinetosome and non-flagellated centriole are connected by fibrillar material with a zone of convergence of fibrils approximately 0.010–0.025 µm in width, centrally located between the two structures. Kinetosome-associated structure is present as a solid, non-laminar, curved spur. Sporangium is spherical to angular at maturity, with multiple, slightly or prominently raised discharge papillae. Rhizoids are robust and branched. Saprobic on pollen or keratin; primarily from terrestrial habitats (Letcher et al. 2006).

Family type – *Terramyces* Letcher, Mycol. Res. 110: 911 (2006)

Ecology & life modes – Species are distributed globally (Letcher et al. 2006), observed on pollen baits of soils from Brazil (Jerônimo et al. 2019), Thailand (Hurdeal et al. 2023), Australia, England, New Zealand, and USA (Letcher et al. 2006, Simmons et al. 2020).

Notes – *Terramycetaceae* was one of the first families described in *Rhizophydiales*, based on limited thallus morphology variation, with molecular phylogenetics and zoosporic ultrastructure characters being more heavily emphasized for its delineation (Letcher et al. 2006). Given its ubiquity and relative ease of culturing, the family has proven to be one of the most widely sampled taxa in the *Rhizophydiales* (Simmons et al. 2020).

Terramyces Letcher, Mycol. Res. 110: 911 (2006)
Index Fungorum Identifier 29046

Sporangium angular, with multiple, slightly raised discharge papillae. Zoospore contains a single lipid globule partially covered with a simple cisterna. Kinetosome-associated structure is a spur terminated with a spherical knob (Letcher et al. 2006).

Type species – *Terramyces subangulosus* (A. Braun) Letcher, Mycol. Res. 110: 911 (2006)

Notes – *Terramyces* reported as a globally distributed genus by Letcher et al. (2006) and culturing efforts and molecular determination of isolates have proven this to be true by reporting species from five continents (Simmons et al. 2020, Hurdeal et al. 2023). Taxonomic diversity, however, remains low (Letcher et al. 2006, Hurdeal et al. 2023), and molecular phylogenetics (Simmons et al. 2020) suggests there could be additional species within *Terramyces*. Cultures are available from CZEUM (Collection of Zoosporic Eufungi at the University of Michigan) and sequences are available in GenBank.

Other genus in *Terramycetaceae*

Boothiomyces Letcher, in Letcher, Powell, Churchill & Chambers, Mycol. Res. 110(8): 911 (2006)
Index Fungorum Identifier 29047; Index Fungorum Identifier 811465; Index Fungorum (2025) and Species Fungorum (2025) accepted three species.

Type species – *Boothiomyces macroporosus* (Karling) Letcher 2006

Notes: On pollen baits of soils in Argentina, Australia, Brazil, Costa Rica (Letcher et al. 2006, Jerônimo et al. 2019, Simmons et al. 2020). Cultures are available from CZEUM (Collection of Zoosporic Eufungi at the University of Michigan) and sequences are available in GenBank.

Uebelmesseromycetaceae M.J. Powell & Letcher, Powell, Letcher, Chambers & Roychoudhury, Mycologia 107: 423 (2015)
Index Fungorum Identifier 810747

Thallus monocentric, eucarpic. Sporangium with a single inoperculate discharge pore. Zoospores with a shield-shaped kinetosome-associated structure and a layered cap over the anterior end of the kinetosome; the microbody-lipid globule complex includes multiple lipid globules with simple as well as fenestrated cisternae (Powell et al. 2015).

Family type – *Uebelmesseromyces* M.J. Powell & Letcher, Mycologia 107(2): 423 (2015)

Ecology & life modes – The family contains a single species, *Uebelmesseromyces harderi*, isolated from pollen baits of intertidal soil in British Columbia, Canada, and has been observed on pollen baits of samples in France, Italy, Scotland, Spain, the USA, and additional sites in Canada (see Powell et al. 2015).

Notes – The family was described based on molecular phylogenetics and zoosporic ultrastructural characters (Powell et al. 2015). Currently, *Uebelmesseromyces* comprises only one genus.

Uebelmesseromyces M.J. Powell & Letcher, Mycologia 107: 423 (2015)
Index Fungorum Identifier 810748

Thallus monocentric, eucarpic. Sporangium with a single inoperculate discharge pore; one to several rhizoidal axes, with or without apophyses emerging from the surface of the sporangium.

Zoospores with shield-shaped kinetosome-associated structure; microbody-lipid globule complex including multiple lipid globules with simple as well as fenestrated cisternae; nucleus and mitochondria partially embedded in the ribosomal aggregation (Powell et al. 2015).

Type species – *Uebelmesseromyces harderi* M.J. Powell & Letcher, in Powell, Letcher, Chambers & Roychoudhury, Mycologia 107: 423 (2015)

Notes – The genus was described to accommodate *Rhizophlyctis harderii*, which produces a resting sporangium with apical, long tubular appendages with branching tips. These appendages resemble interbiotic rhizoids common to *Rhizophlyctis* (*Rhizophlyctidales*), but Powell et al. (2015) concluded that the appendages did not penetrate pollen substrates to which they held and dismissed suggestions that they were part of the absorptive rhizoidal system. Molecular and ultrastructural investigation concluded the species was a member of *Rhizophydiales* (Powell et al. 2015). Cultures are available from CZEUM (Collection of Zoosporic Eufungi at the University of Michigan) and sequences are available in GenBank.

Spizellomycetes Tedersoo et al.
Spizellomycetales D.J.S. Barr
Powellomycetaceae D.R. Simmons, Mycologia 103: 1415 (2011)
Index Fungorum Identifier 519601

Thallus eucarpic, monocentric; sporangium exogenous with the zoospore cyst. Monophyletic clade within *Spizellomycetales* (Simmons 2011).

Family type – *Powellomyces* Longcore, D.J.S. Barr & Désauln., Canadian Journal of Botany 73: 1389 (1995)

Ecology & life modes – Genera in this family have been observed and isolated primarily from pollen baits of soils from Australia, Brazil, New Zealand, UK, USA, and the Canary Islands, and pollen baits of manure from horses and ruminant animals in farms and nature preserves in the USA (Simmons 2011, Simmons & Longcore 2012).

Notes – *Powellomycetaceae* was erected to recognize that exogenous development within the *Spizellomycetales* appears to have occurred only once under molecular phylogenetic hypotheses (Simmons 2011). Additional genera are recognized for ultrastructural differences (Simmons & Longcore 2012).

Powellomyces Longcore, D.J.S. Barr & Désauln., Canadian Journal of Botany 73: 1389 (1995)
Index Fungorum Identifier 27628

Nucleus of the zoospore centrally to posteriorly located and pointing to the kinetosome; small, diffuse spur connected to one side of kinetosome. Two arcs of electron-opaque material lie between kinetosome and nucleus; microtubules radiate into the zoospore cytoplasm from the outer arc (Longcore et al. 1995).

Type species – *Powellomyces hirtus* Longcore, D.J.S. Barr & Désauln., Canadian Journal of Botany 73: 1389 (1995)

Notes – When describing *Spizellomycetales*, Barr (1980) transferred *Entophlyctis* (which contained exogenously-developing, monocentric fungi in *Chytridiales*), to *Olpidaceae* in *Spizellomycetales*. After examining the zoosporic ultrastructure of *Entophlyctis* from freshwater substrates, Longcore (1995) proposed that *Entophlyctis* be reserved for these taxa, which were more representative of the type species and returned the genus to *Chytridiales*. However, Longcore et al. (1995) recognized that a new genus, *Powellomyces*, was necessary for soil-dwelling species with entophlyctis-like thallus morphologies and spizellomycetalean zoosporic ultrastructure. Many representative cultures of *Powellomyces* were isolated by zoosporic eufungal specialists, allowing the examination of 49 cultures of powellomyces-like fungi that found molecular and ultrastructural diversity sufficient for the description of three additional genera (Simmons 2011, Simmons & Longcore 2012). Cultures are available from CZEUM (Collection of Zoosporic Eufungi at the University of Michigan) and sequences are available in GenBank.

Other genera in *Powellomycetaceae*

Fimicolochytrium D.R. Simmons & Longcore, Mycologia 104(5): 1234 (2012)
Index Fungorum Identifier 564196; Index Fungorum (2025) and Species Fungorum (2025) accepted two species.

Type species – *Fimicolochytrium jonesii* D.R. Simmons & Longcore 2012

Notes – This genus was reported from pollen baits of soils and manure from USA (Simmons & Longcore 2012, Simmons et al. 2020). Cultures are available from CZEUM (Collection of Zoosporic Eufungi at the University of Michigan) and sequences are available in GenBank.

Geranomyces D.R. Simmons, Mycologia 103(6): 1415 (2011)
Index Fungorum Identifier 519610; Index Fungorum (2025) and Species Fungorum (2025) accepted four species

Type species – *Geranomyces variabilis* (Longcore, D.J.S. Barr & Désauln.) D.R. Simmons 2011

Notes – The members of *Geranomyces* were reported on pollen baits of soils and manure from Australia, Brazil, New Zealand, UK, USA, and the Canary Islands (Simmons 2011, Simmons & Longcore 2012, Simmons et al. 2020). Cultures are available from CZEUM (Collection of Zoosporic Eufungi at the University of Michigan) and sequences are available in GenBank.

Thoreauomyces D.R. Simmons & Longcore, Mycologia 104(5): 1232 (2012)
Index Fungorum Identifier 564194; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Thoreauomyces humboldtii* D.R. Simmons & Longcore 2012

Notes – From pollen baits of forest soils in Maine, USA (Simmons & Longcore 2012). Cultures are available from CZEUM (Collection of Zoosporic Eufungi at the University of Michigan) and sequences are available in GenBank.

Spizellomycetaceae D.J.S. Barr, Canadian Journal of Botany 58: 2384 (1980)
Index Fungorum Identifier 81997

Thallus eucarpic, monocentric. Sporangium, or prosporangium, and resting spore endogenous with the zoospore cyst (Barr 1980).

Family type – *Spizellomyces* D.J.S. Barr, Canadian Journal of Botany 58: 2384 (1980)

Ecology & life modes – Genera in this family are mostly found on pollen baits of soils and manure of horses and ruminants, primarily from Canada and USA, but also Argentina, Australia, England, Germany, Israel, New Guinea, South Africa, and Taiwan (Barr 1980, Davis et al. 2016b, Letcher & Powell 2018b, Letcher et al. 2018, Powell & Letcher 2018, Simmons et al. 2020). A notable exception is *Gaertneriomyces semiglobifer*, which has been observed as a parasite on downy mildew oospores from Israel (Powell et al. 2018b) and on azygospores of the gypsy moth pathogen *Entomophaga maimaiga* in Ohio (Hajek et al. 2013).

Notes – *Spizellomycetaceae* is the largest family of *Spizellomycetales*, with the number of genera recently doubling from Barr's (1980) original description (Letcher & Powell 2018b, Letcher et al. 2018, Powell et al. 2018b).

Spizellomyces D.J.S. Barr, Canadian Journal of Botany 58: 2384 (1980)
Index Fungorum Identifier 20543

Nucleus of the zoospore anterior, with a heel-like segment extending to near the kinetosome; microtubules radiate at random in the zoospore cytoplasm from one side of the proximal face of the kinetosome or a spur (Barr 1980).

Type species – *Spizellomyces punctatus* (W.J. Koch) D.J.S. Barr [as 'punctatum'], Canadian Journal of Botany 58: 2384 (1980)

Basionym: *Phlyctochytrium punctatum* W.J. Koch, J. Elisha Mitchell scient. Soc. 73: 109 (1957)

Notes – Barr (1980) introduced *Spizellomyces* to accommodate *Phlyctochytrium punctatum* W.J. Koch. The genus comprises seven species (Species Fungorum 2025).

Other genera in *Spizellomycetaceae*

Barromyces M.J. Powell & Letcher, Nova Hedwigia 107: 221 (2018)
Index Fungorum Identifier 822235; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Barromyces tenuis* (D.J.S. Barr) M.J. Powell & Letcher 2018

Notes – On pollen baits of crop soil in Nova Scotia, Canada (Powell et al. 2018b). Sequences are available in GenBank.

Brevicalcar Letcher & M.J. Powell, Nova Hedwigia 107: 117 (2018)
Index Fungorum Identifier 822132; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Brevicalcar kilaueaense* Letcher & M.J. Powell 2017; Fig. 33s

Notes – On pollen baits of tree and lava field detritus in Australia and Hawaii (Letcher & Powell 2018b) and soil in Maine, USA (Simmons et al. 2020). Cultures are available from CZEUM (Collection of Zoosporic Eufungi at the University of Michigan) and sequences are available in GenBank.

Bulbosomyces Letcher & Longcore, in Letcher & Powell, Nova Hedwigia 107: 119 (2018)
Index Fungorum Identifier 822134; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Bulbosomyces maxikinetosomus* Letcher & Longcore 2017

Notes – On pollen bait of soil in Maine, USA (Letcher & Powell 2018b). Culture is available from CZEUM (Collection of Zoosporic Eufungi at the University of Michigan) and sequences are available in GenBank.

Gaertneriomyces D.J.S. Barr, Canadian Journal of Botany 58: 2386 (1980)
Index Fungorum Identifier 20232; Index Fungorum (2025) and Species Fungorum (2025) accepted four species.

Type species – *Gaertneriomyces semiglobifer* Uebelm. ex D.J.S. Barr 1980

Notes – On pollen baits of soils and manure of horses and ruminants from Argentina, Australia, Canada, England, South Africa, and Taiwan (Barr 1980, Powell et al. 2018b), as a parasite on downy mildew oospores from Israel (Powell et al. 2018b) and zygospores of *Entomophaga maimaiga* in Ohio (Hajek et al. 2013). Cultures are available from CZEUM (Collection of Zoosporic Eufungi at the University of Michigan) and sequences are available in GenBank.

Gallinipes Letcher & M.J. Powell, Nova Hedwigia 107: 123 (2018)
Index Fungorum Identifier 822136; Index Fungorum (2025) and Species Fungorum (2025) accepted three species.

Type species – *Gallinipes danensis* Letcher & M.J. Powell 2017

Notes – On pollen baits of soils from USA and British Columbia, Canada (Letcher & Powell 2018b). Cultures are available from CZEUM (Collection of Zoosporic Eufungi at the University of Michigan) and sequences are available in GenBank.

Kochiomyces D.J.S. Barr, Canadian Journal of Botany 58: 2386 (1980)
Index Fungorum Identifier 20289; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Kochiomyces dichotomus* (Umphlett) D.J.S. Barr 1980

Notes – On pollen baits of soils from Canada and USA and sand dunes in New Brunswick, Canada (Barr 1980, Letcher & Powell 2018b, Simmons et al. 2020). Cultures are available from CZEUM (Collection of Zoosporic Eufungi at the University of Michigan) and sequences are available in GenBank.

Triparticalcar D.J.S. Barr, Canadian Journal of Botany 58: 2386 (1980)
Index Fungorum Identifier 20585; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Triparticalcar arcticum* (D.J.S. Barr) D.J.S. Barr 1980

Notes – On pollen baits of soils and manure of horses and ruminant animals from Canada and USA (Barr 1980, Davis et al. 2016b, Letcher & Powell 2018b, Simmons et al. 2020). Cultures are available from CZEUM (Collection of Zoosporic Eufungi at the University of Michigan) and sequences are available in GenBank.

Synchytriomycetes Tedersoo et al.
Synchytriales Doweld
Synchytriaceae J Schröt Nat. Pflanzenfamilien (German): 71 (1892)
Index Fungorum Identifier 81448

Members of the family possess a unicellular, endobiotic and holocarpic thallus and are almost exclusively parasitic. A complex life cycle (Karling 1977), often forming a prosorus and a sorus which contains the sporangia. At maturity, the whole thallus is converted into the reproductive organ, a sorus of sporangia. Endogenous zoospores are posteriorly uniflagellate. Sexual reproduction by conjugation of isogamous flagellated gametes, resulting in a thick-walled resting spore. Upon germination, the resting spore functions as a sporangium. In many *Synchytriaceae*, a resting spore/sporangium may also form, which resembles prosori or sori in its micromorphology. During germination, this may function either as a prosorus or a sorus (Karling 2013).

Family type – *Synchytrium* de Bary & Woronin, Verh. Naturf. Ges. Freiburg 3(2): 46 (1863)

Ecology and Life modes – Although members of the family have a worldwide distribution, occurrence is limited to aquatic and moist terrestrial habitats due to the requirement of water for zoospore dispersal and infection. They are parasites of flowering plants, ferns, algae, mosses, and diatoms.

Notes – The family, introduced by Schröter (1892), comprises four genera, *viz.*, *Carpenterophlyctis* Doweld, *Endodesmidium* Canter, *Johnkarlingia* Pavgi & S.L. Singh and *Synchytrium* de Bary & Woronin. Although the genera appear distinct, molecular phylogenetic studies have yet to be performed for unambiguous identification.

Synchytrium de Bary & Woronin, Verh. Naturf. Ges. Freiburg (German) 3(2): 46 (1863)
Index Fungorum Identifier 20560

Thallus is a non-filamentous, uninucleate, globose protoplasmic mass surrounded by a thin wall. They are endobiotic holocarpic organisms with characteristic inoperculate sporangia that release motile flagellated spores. During reproduction, the whole vegetative cell is converted into the reproductive structure. A sorus is formed when the colonial thallus splits into many sporangia or gametangia that are always encased in a single membrane. The fungus produces persistent resting (winter) sporangia (sori) that acts as a sporangium upon germination. The breakdown of warts on the sporangial wall releases the sori into the soil. Each sorus has two inner membranes, the innermost of which is thin and transparent, surrounded by an outer, fragile membrane made of disorganized host cells. Upon release, zoospores attach to a host cell, penetrate it by means of a narrow germ tube and become enveloped in host cytoplasm (Karling 1964b, Alexopoulos et al. 1996, Heckman et al. 2001).

Notes – The genus was established by de Bary & Woronin (1863) and members are obligately biotrophic microfungi commonly infecting algae, mosses, ferns, and flowering plants

(Callan & Carris 2004). *Synchytrium* species fall into two broad categories: short-cycled and long-cycled. Short-cycled species show two lines of development: (i) sori, sporangia, zoospore (ii) resting spore, sori, zoospore. Long-cycled species follow a general pathway going through the steps, prosori/sori, sporangia, zoospore, resting spore, prosori/sori, sporangia, zoospore (Karling 2013).

Identification of *Synchytrium* species is challenging due to their morphological plasticity and inability to grow in culture. As a result, various unrelated criteria have been used as adjuncts to identification and classification. These are characteristics of the galls induced in the host and other cellular host reactions; hosts, host range, and specificity; and environmental conditions in which the species occur. Since all these features exhibit considerable variation imposed by the growth environment, overlaps between species are highly likely (Karling 2013). Investigations based on the 18S, 28S, and 5.8 subunits of rDNA of *Synchytrium* found them to cluster together and hence are designated as the "*Synchytrium* clade" (James et al. 2006b). Smith et al. (2014) presented an 18S rDNA phylogeny of 14 *Synchytrium* species representing Karling's (1953) subgenera, suggesting that species of *Synchytrium* are monophyletic.

Members of *Synchytrium* show worldwide distribution, living in aquatic and moist terrestrial habitats. Cultures of some species are available on the Alabama Chytrid Culture Collection (UACCC) and CZEUM (Collection of Zoosporic Eufungi at the University of Michigan), and sequences in GenBank. There are 250 species (Smith et al. 2014), making it the largest genus of the family.

Type species – *Synchytrium taraxaci* de Bary & Woronin 1863

Other genera in *Synchytriaceae*

Carpenterophlyctis Doweld, Index Fungorum 30: 1 (2013)

Index Fungorum Identifier 550266; Index Fungorum (2025) and Species Fungorum (2025) accepted two species.

Type species – *Carpenterophlyctis cannae* (Mundk. & Thirum.) Doweld 2013

Endodesmidium Canter, Trans. Br. mycol. Soc. 32(1): 72 (1949)

Index Fungorum Identifier 20207; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Endodesmidium formosum* Canter 1949

Johnkarlingia Pavgi & S.L. Singh, in Singh & Pavgi, Mycopathologia 69(1-2): 53 (1979)

Index Fungorum Identifier 20283; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Johnkarlingia brassicae* S.L. Singh & Pavgi 1979

Micromyces P.A. Dang., Botan. Zbl. 38: 530 (1889)

Index Fungorum Identifier 20330; Index Fungorum (2025) lists 23 epithets, and Species Fungorum (2025) accepts eleven species.

Type species – *Micromyces zygogonii* P.A. Dang., Botan. Zbl. 38: 531 (1889)

Micromycopsis Scherff., Arch. Protistenk. 54: 202 (1926)

Index Fungorum Identifier 20331; Index Fungorum (2025) lists eight epithets, and Species Fungorum (2025) doesn't accept any species.

Type species – *Micromycopsis cristata* Scherff., Arch. Protistenk. 54: 202 (1926)

Notes – Hyde et al. (2024) accepted this genus, but Species Fungorum (2025) regarded it as a synonym of *Micromyces* P.A. Dang.

Chytridiomycota* family *incertae sedis

Quaeritorhizaceae Longcore, D.R. Simmons & T.Y. James

Index Fungorum Identifier 833714

Based on light microscopy: Endogenous, monocentric sporangium with single major rhizoidal axis plus later-developing, interbiotic rhizoids; one to several broad, short or long, inoperculate discharge papillae. Zoospores are spherical when in motion. Resting spores with a single large lipid globule. Zoospore ultrastructure: nucleus enclosed by aggregated ribosomes; mitochondria lie outside of ribosomal mass. One to several adjoining lipid globules; simple rumposome. Non-flagellated centriole is nearly parallel and attached to the kinetosome from which extends a microtubule root to the rumposome and a splayed array of microtubules. Plug in flagellar transition zone limited to the space interior to microtubule doublets. Small, striated inclusion in cytoplasm (Longcore et al. 2020).

Family Type – *Quaeritorhiza* Longcore, D.R. Simmons & T.Y. James; Fig. 33t

Ecology & life modes – Pathogen of green algae. This family contains a single species, *Quaeritorhiza haematococci*, described from a culture isolated from a commercially grown population of *Haematococcus pluvialis* (Longcore et al. 2020).

Notes – Longcore et al. (2020) established *Quaeritorhizaceae* to accommodate *Quaeritorhiza*, based on SSU and LSU phylogeny. The family currently comprises only one genus.

Quaeritorhiza Longcore, D.R. Simmons & T.Y. James, in Longcore, Qin, Simmons & James, Mycologia 112(3): 611 (2020)

Index Fungorum Identifier 833680

Endogenous, monocentric sporangium with a single major rhizoidal axis plus later-developing, interbiotic rhizoids; one to several broad, short or long, inoperculate discharge papillae. Zoospores are spherical when in motion. Resting spores with a single large lipid globule. Zoospore ultra-structure: nucleus enclosed by aggregated ribosomes; mitochondria lie outside of the ribosomal mass. One to several adjoining lipid globules; simple rumposome. The non-flagellated centriole is nearly parallel and attached to the kinetosome from which extends a microtubule root to the rumposome and a splayed array of microtubules. Plug in flagellar transition zone limited to the space interior to microtubule doublets. Small, striated inclusion in cytoplasm (Longcore et al. 2020).

Type species – *Quaeritorhiza haematococci* Longcore, D.R. Simmons, T.Y. James & S. Qin (2020)

ENTOMOPHTHOROMYCOTA Humber

Entomophthoromycotina Humber

Entomophthoromycetes Humber

Entomophthorales G. Winter

Ancylistaceae Pfitzer, Monatsber. Königl. Preuss. Akad. Wiss. Berlin: 396 (1872)

Index Fungorum Identifier IF 585354

Vegetative growth is by aseptate (coenocytic) or irregularly septate mycelium. Nuclei are small 3–5 µm long during interphase, with a prominent nucleolus and lacking heterochromatin; they are usually difficult to observe during mitosis. Conidiophores are simple unbranched, or rarely branched, with a single conidium formed terminally per branch. Primary conidia are unitunicate, released forcibly by papillar eversion. Resting spores are usually zygospores resulting from gametangial contact of neighboring hyphal cells or by scalariform conjugations between hyphae; formed in axis of hypha or in a conjugation tube (Humber 2012, Gryganskyi et al. 2013).

Family type – *Ancylistes* Pfitzer. 1872

Ecology and life modes – Pathogenic on algae, desmids and tardigrade (Reukauf 1912, Berdan 1938, John 1955, Gryganskyi et al. 2022).

Notes – *Ancylistaceae* was established by Pfitzer (1872). Three new genera (*Capillidium*, *Micrconidiobolus* and *Neoconidiobolus*) were erected and accommodated in *Ancylistaceae* (Nie et al. 2020). Subsequently, Cai et al. (2021) erected another genus, *Azygosporus*. Recently, Gryganskyi et al. (2022), based on molecular phylogeny, excluded *Azygosporus, Capillidium,*

Conidiobolus, Neoconidiobolus and *Micrconidiobolus* from *Ancylistaceae*, leaving two genera *Ancylistes*, and *Macrobiotophthora*, in the family. Placement of the above-mentioned genera is discussed in other sections.

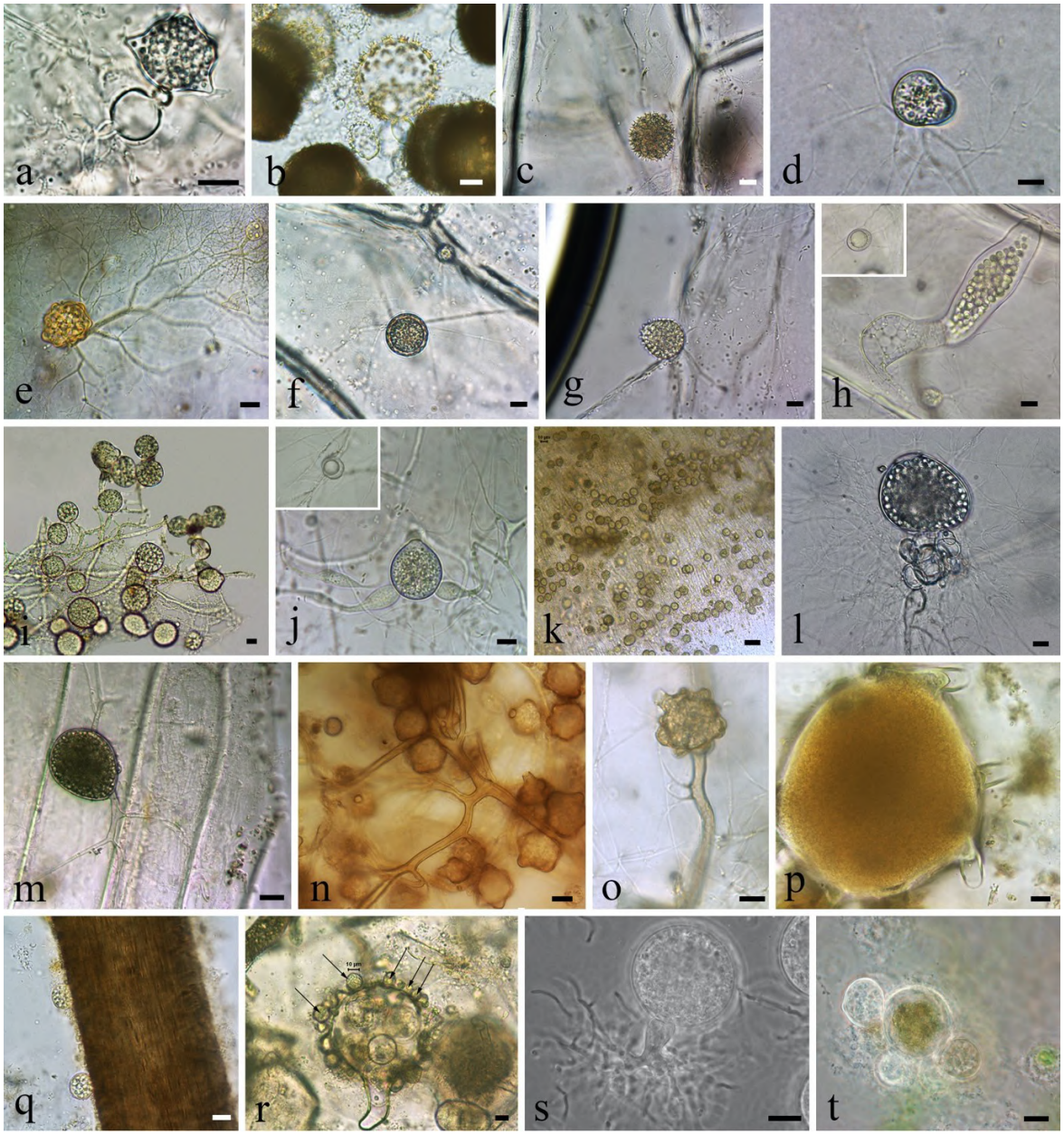


Figure 33 – a-g *Chytridiomycetes* a-c *Chytridiaceae;* a *Phlyctochytrium furcatum.* b *Phlyctochytrium aureliae* c *Phlyctochytrium aureliae*. d-g *Chytriomycetaceae;* d *Chytriomyces appendiculatus.* e *Entophlyctis lobata.* f *Entophlyctis luteolus.* g *Fayochytriomyces spinosus.* h-m *Cladochytriomycetes;* h *Cladochytriaceae, Karlingiella elongata.* i-k *Nowakowskiellaceae;* i,j *Nowakowskiella elegans.* k *Nowakowskiella multispora.* l, m *Septochytriaceae;* l *Catenochytridium* sp. m *Septochytrium variabilis.* n,o *Polychytriomycetes, Polychytriaceae, Polychytrium aggregatum.* p *Rhizophlyctidomycetes, Rhizophlyctidaceae, Rhizophlyctis rosea* q,r *Rhizophydiomycetes, Rhizophydiaceae.* q *Rhizophydium keratinophilum.* r *Rhizophydium* sp. s *Spizellomycetes, Spizellomycetaceae, Brevicalcar kilaueaense.* t *Synchytriomycetes, Quaeritorhizaceae, Quaeritorhiza haematococci.* Scale bars: a-t = 10 µm.

Ancylistes Pfitzer, Monatsber. Königl. Preuss. Akad. Wiss. Berlin: 396 (1872)
Index Fungorum Identifier IF 20030

Mycelium consisting of one to several septate, straight or slightly wavy, tubular hyphae of variable width, irregularly branching and anastomosing in the isthmus of the host or scarcely in other places by short lateral branches. Conidia are spherical, hyaline and produced at the tips of conidiophores and forcibly discharged into the air. Columella conical, subtended by a vacuole and extending into the mature conidium before it is discharged, collapsing afterwards. Conidia give rise to secondary or tertiary conidia directly or germinating by tube. Resting spores is zygospores resulting from gametangial contact of neighboring hyphal cells or by scalariform conjugations between hyphae; zygote is formed in a protuberance of the female gametangium and is retracted from its wall; wall of this protuberance is smooth or with 9–10 truncate warts; zygote is oval, spherical, and thick-walled with plenty of refractive globules; germination is unknown.

Type species – *Ancylistes closterii* Pfitzer

Notes – *Ancylistes* was established by Pfitzer (1872) for a single species, *A. closterii*, parasitizing *Closterium acerosum.*

Other genus in *Ancylistaceae*

Macrobiotophthora Reukauf, Centbl. Bakt. Parasitenk, Abt. I 63: 390 (1912)

Index Fungorum Identifier 20315; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Macrobiotophthora vimariensis* Reukauf 1912

Notes – *Macrobiotophthora vermicola* has been transferred to *Neoconidiobolus* (Nie et al. 2020).

Batkoaceae Gryganskyi, A.E. Hajek & Stajich, Journal of Fungi 8: 789 (2022)

Index Fungorum Identifier IF 844345

Mycelia hyaline, hyphae septate and branched. Hyphal bodies hypha or ameboid-like, subglobose to elongate, multinucleate, nuclei staining with aceto-orcein. Primary conidiophores are positively phototropic, unbranched, bearing a single apical primary conidium. Primary conidia are multinucleate, globose in shape, with a prominent conical papilla, single-celled and discharged forcibly. Replicative conidia are similar but smaller than primary conidia. Zygospores are hyaline or yellowish and globose in shape. Hyaline globose chlamydospores are also produced. Rhizoids may be present or absent (Gryganskyi et al. 2022).

Family type – *Batkoa* Humber 1989.

Ecology & life modes – Pathogenic on coleopterans, dipterans, lepidopterans, and homopterans (Humber 1989), with nearly a global distribution. Some species cause co-epizootics in anternfly (*Lycorma delicatula*, *Fulgoridae*, *Hemiptera*) (Clifton et al. 2019, Souza et al. 2021).

Notes – *Batkoaceae* was erected by Gryganskyi et al. (2022) to accommodate a single genus, *Batkoa* Humber, based on molecular data. Species of *Batkoa* produce ballistospores and are entomopathogenic.

Batkoa Humber, Mycotaxon 34 (2): 446 (1989); Fig. 34

Index Fungorum Identifier IF 25280

Colourless mycelia, ameboid-like, subglobose to elongate, multinucleate hyphal bodies. Primary conidiophores are simple, bearing a single multinucleate, globose a single primary conidium with a prominent conical papilla, single-celled and discharged forcibly.

Type species – *Batkoa apiculata* (Thaxt.) Humber 1989

Notes – *Batkoa* was erected by Humber (1989) with *B. apiculata* (Thaxter) Humber as the type species to accommodate *Empusa apiculata* Thaxter along with four new combinations. Since then, five more species have been added to the genus (Villacarlos & Keller 1997, Niell & Santamaría 2001, Huang et al. 2007, Keller 2007). Members can be easily isolated on simple culture media (Gryganskyi et al. 2022). Eleven species are accepted in the genus, and molecular data are available.

Capillidiaceae Y. Nie, Stajich & K.T. Hodge, Journal of Fungi 8: 789 (2022)
Index Fungorum Identifier IF 844346

Saprophytic, mycelia hyaline. Primary conidiophores are simple, unbranched, rarely branched bearing single primary conidia. Primary conidia multinucleate, hyaline, globose, pyriform to obovoid and forcibly discharged. Two types of replicative conidia, the first similar and smaller than primary conidia, the secondary (capilliconidia) arise singly or multiple, off-axis at the tip of slender, elongated conidiophores, and are not forcibly discharged. Zygospores present or absent, if present, formed in axial alignment with conjugating segments, globose to subglobose, often smooth, sometimes rough, hyaline or yellowish.

Family Type – *Capillidium* B. Huang & Y. Nie

Ecology & Life modes – Species of *Capillidiaceae* are saprophytic on woody substrates (mainly leaves). It probably has some role in decomposing wood.

Notes – *Capillidiaceae* was established by Gryganskyi et al. (2022) to accommodate a single genus *Capillidium* based on morphological and molecular data. Species of *Capillidium* peculiarly produce capillioconidia protruding from elongated, slender conidiophores (Nie et al. 2020).

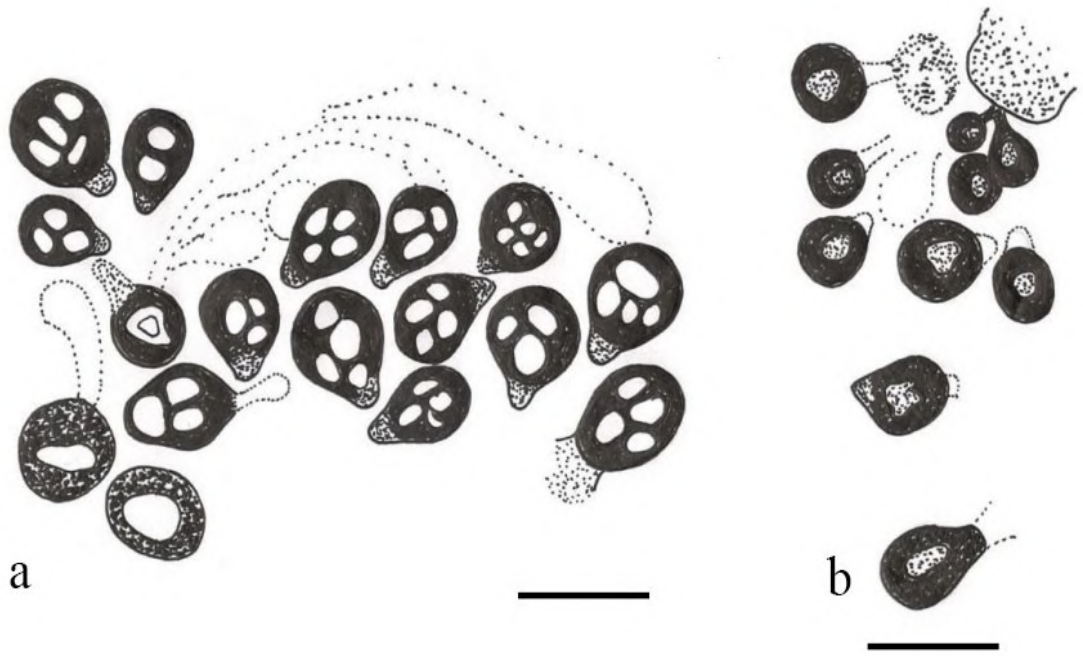


Figure 34 – *Batkoa hydrophila*. a Primary conidia. b Formation of primary conidia. Scale bars a, b = 30 μm (Redrawn from Keller 2007).

Capillidium B. Huang & Y. Nie, MycoKeys 66: 62 (2020); Fig. 35
Index Fungorum Identifier IF 831596

Mycelia with simple conidiophores bearing multinucleate, hyaline, globose, pyriform to obovoid primary conidium apically. Capilliconidia arises from elongate and slender conidiophores. Zygospores either present or absent. *Capillidium* possesses high morphological diversity such as conidiophore in *C. heterosporum* are branched and bear 2–6 capilliconidia whereas in other speciesthey are unbranched and have single capilliconidia; the size of primary conidia varies from 18 μm to 44 μm; Microconidia present in *C. adiaretum*. Resting spores present in *C. adiaretum*, *C. bangalorense* and *C. rhysosporum* and absent in rest of the species (Nie et al. 2020).

Type species – *Capillidium heterosporum* (Drechsler) B. Huang & Y. Nie 2020

Notes – *Conidiobolus* subgen. *Capillidium* Ben-Ze'ev & Kenneth was established to include species with capilliconidia (Ben-Ze'ev & Kenneth 1982a). Based on molecular phylogeny and the ability to form ellipsoidal secondary conidia (capilliconidia). Nie et al. (2020) raised this subgenus to genus with *Capillidium heterosporum* (Drechsler) B. Huang & Y. Nie as the type species, along with six new combinations. Nie et al. (2022) added three species to the genus, thus raising the number of members to ten.

Completoriaceae Humber, Mycotaxon 34(2): 453 (1989)
Index Fungorum Identifier IF 82027

Vegetative structures small, botryose, irregular hyphal bodies that probably lack cell walls. Nuclei filled with condensed chromatin at interphase and relatively of large size. Conidiophores short, unbranched, arising directly from vegetative cells, without a conidiogenous cell. Conidia unitunicate, more or less globose with a rounded papilla; release by papillar eversion. Resting spores globose (ontogeny and germination unknown), formed in the axis of parental cell (Humber 1989).

Family type – *Completoria* Lohde 1874

Ecology & life modes – Pathogenic on fern prothalii (Leitgeb 1881, Atkinson 1884, 1885)

Notes – *Completoriaceae* Humber was erected by Humber (1989) to accommodate a monotypic genus *Completoria* Lohde with *Completoria complens* Lohde as the type species. Since *Completoriaceae* is a monotypic family without molecular data, fresh collections are required to resolve its phylogenetic placement.

Completoria Lohde, Tagebl. Versamm. dt. naturf. Ärzte (Breslau) 47: 203-206 (1874)
Index Fungorum Identifier IF 20142

Description is similar to the family description.

Type species – *Completoria complens* Lohde

Notes – *Completoria* is the type genus of *Completoriaceae*, and it was established by Lohde (1874); parasite on fern (*Aspidium falcatum*) prothalii has been reported in a few instances (Leitgeb 1881). However, the genus was poorly studied, and to date, it is monotypic. Before the introduction of the family *Completoriaceae*, the genus was included in *Entomophthoraceae* because of distant relationships, with the presence of large nuclei without central nucleoli and thallus composed of short hyphal branches (Tucker 1981, BenZeev & Kenneth 1982b, Humber 1984, 1989). Since no molecular data are available for this genus, fresh collections are required to resolve its phylogenetic placement. The exclusion of *Completoria* from *Entomophthoraceae* renders all taxa in the family obligatory entomopathogenic.

Conidiobolaceae B. Huang, Stajich & K.T. Hodge, Journal of Fungi 8: 789 (2022); Fig. 36
Index Fungorum Identifier IF 844347

Saprobic, septate, branching hyphae forming hyaline mycelium. Hyphae multinucleate, with small nuclei that do not stain with aceto-orcein. Simple hyphal conidiogenous cells each develop one apical conidium, a ballistospore that is forcibly discharged by rapid circumscissile rupture and papillar eversion. Detached conidia are hyaline, single-celled, more or less globose, with an everted blunt conical papilla where they were once attached to the conidiophore. Microconidia often present in most species. Zygospores, present or absent, formed in axial alignment with conjugating segments, globose to subglobose (Gryganskyi et al. 2022).

Family type – *Conidiobolus* Bref. 1884

Ecology & life modes – Species of *Conidiobolaceae* are found worldwide, usually as saprobes on herbs, woody plants and soil in terrestrial habitats (Gryganskyi et al. 2022). A few species, such as *Neoconidiobolus osmodes* (Drechsler) B. Huang & Y. Nie (previously known as *Conidiobolus osmodes* Drechsler), cause epizootics in the larvae of *Tipula paludosa* (*Tipulidae*: *Diptera*) (Gökçe & Er 2003). While *Conidiobolus coronatus* and *C. incongruous* generally grow saprobically in soil or plant detritus, they occasionally act as an entomopathogen causing mycoses

in humans and animals, domestic or wild (El-Shabrawi et al. 2014, Weiblen et al. 2016). Additionally, they have been reported as a pathogen of adult mosquitoes (Montalva et al. 2016).

Notes – *Conidiobolaceae* was established based on a combined 4-gene (18S, 28S, *tef-1α*, and mtSSU) and genome dataset by Gryganskyi et al. (2022) to accommodate three genera, *Azygosporus* B. Huang & Y. Nie, *Conidiobolus* Bref and *Microconidiobolus* B. Huang & Y. Nie. Members of *Conidiobolaceae* are saprobic, ballistospore-forming fungi with a global distribution. They readily grow on simple culture media and form white to cream colonies. The primary ballistospores may germinate in three different ways: to form a much smaller ballistospore (microconidia) of similar form as the parent spore, to form a passively dispersed fusiform conidium atop a long, attenuated stalk, or to form a hyphal germ tube. Some species show opportunistic humans and other animals (Gryganskyi et al. 2022).

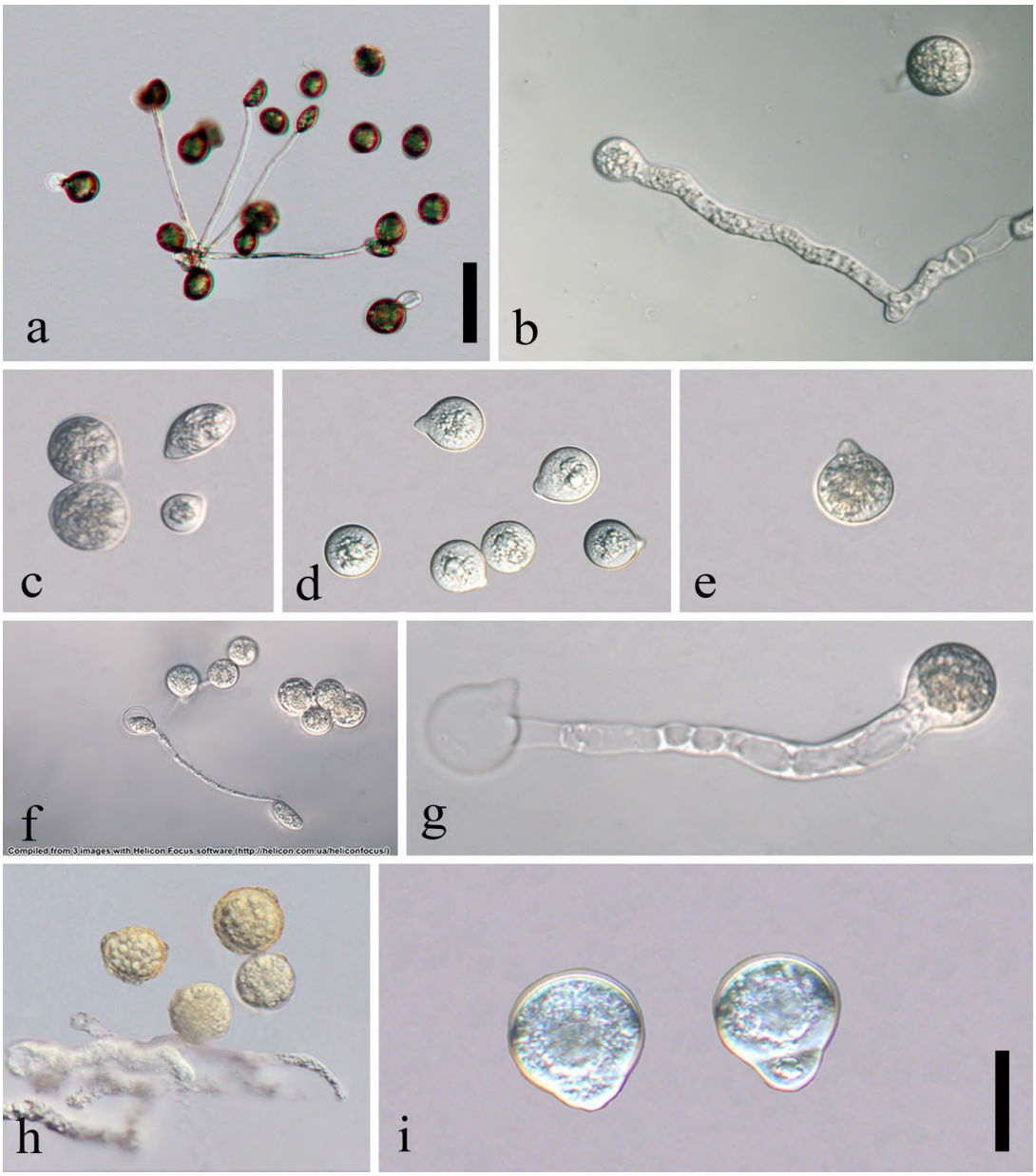


Figure 35 – *Capillidium heterosporum.* a Conidiophores branched at the base and bearing 4 capilliconidia. b-d *Capillidium jiangsuense.* b Primary conidiophores arising from mycelia segments. c Capilliconidia. d Primary conidia (only one). e-h *Capillidium macrocapilliconidium.* e Primary conidia. f Primary conidium bearing a single capilliconidium. g Primary conidia bearing a single secondary conidium. h Zygospores. i *Capillidium rhysosporum* primary conidia. Scale bar a = 100 μm i= 20 μm

Conidiobolus Bref., Mykol. Untersuch. 6(2): 35 (1884)
Index Fungorum Identifier IF 20144

Mycelia colourless, Primary conidiophores simple or branched dichotomously, positively phototropic, bearing a single or 2–4 primary conidia. Primary conidia forcibly discharged, multinucleate, colourless, pyriform, obovoid, globose to subglobose. Secondary conidia usually with shape of primary conidia but smaller, formed singly on short secondary conidiophores. Microspores arise from primary or secondary conidia. Villose appendaged globose conidia. Chlamydospores formed intercalarily within assimilative hyphae. Zygospores formed in axial alignment with one or two (homothallic or heterothallic) conjugating segments.

Type species – *Conidiobolus utriculosus* Bref.

Notes – *Conidiobolus* was established by Brefeld (1884) with *C. utriculosus* Bref. as the type species. The genus is characterized morphologically by simple sporophores, globose to pyriform multinucleate primary conidia, various types of secondary conidia and resting spores (Brefeld 1884, Humber 1997). Based on morphological and nutritional data, 38 species were accepted in the genus (Drechsler 1952, 1953, 1955, 1960, Srinivasan & Thirumalachar 1962, 1968). King (1976a, b, 1977), based on numerical taxonomy, accepted 27 species in *Conidobolus*. Since then, ten more species have been added to *Conidiobolus* (Bałazy et al. 1987, Bałazy 1993, Waters & Callaghan 1989, Huang et al. 2007, Waingankar et al. 2008, Nie et al. 2012, 2016, 2017, 2018). A total of 37 species are accepted by Nie et al. (2018).

Nie et al. (2020) revised *Conidiobolus* based on molecular phylogeny and transferred species to a newly erected genus *Capillidium*. In previous studies, this genus was included in *Ancylistaceae*, *Entomophthorales*, *Entomophthoromycetes*, *Entomophthoromycota* (Humber 2012, Gryganskyi et al. 2013, Benny et al. 2014). However, Gryganskyi et al. (2022), based on phylogenetic reconstruction data, removed *Conidiobolus sensu lato* from family *Ancylistaceae* and placed it in the newly erected family *Conidiobolaceae*.

Other genera in *Conidiobolaceae*

Azygosporus B. Huang & Y. Nie, in Cai, Nie, Zhao, Wang, Zhou, Liu & Huang, MycoKeys 85: 165 (2021)
Index Fungorum Identifier 840849; Index Fungorum (2025) and Species Fungorum (2025) accepted two species.

Type species – *Azygosporus parvus* (Drechsler) B. Huang & Y. Nie

Microconidiobolus B. Huang & Y. Nie, in Nie, Yu, Wang, Liu & Huang, MycoKeys 66: 68 (2020)
Index Fungorum Identifier 831597; Index Fungorum (2025) and Species Fungorum (2025) accepted three species.

Type species – *Microconidiobolus paulus* (Drechsler) B. Huang & Y. Nie

Entomophthoraceae Nowak., Synopsis der Drei Naturreiche. Ein Handbuch, Edn 2: 1258 (1874)
Index Fungorum Identifier 816371

Mycelial or hyphal bodies are without a cell wall, fusoid to catenate or irregularly amoeboid protoplast. Nuclei readily stained with aceto-orcin or bismarck brown are usually 5–12 µm in diameter. Conidiophores are simple unbranched, or dichotomously to digitately branched. Conidiogenous cells are born apically on each conidiophore. Primary conidia unitunicate or bitunicate, discharged forcibly. Resting spores formed as lateral or terminal buds connected by a narrow isthmus to parental cells (Humber 2012).

Family type – *Entomophthora* Fresen. 1856

Ecology & Life modes – Members of the family have been reported as pests of a broad range of insects

Notes – *Entomophthoraceae* was established by Nowakowski (1877). Eleven genera (*viz*., *Entomophaga* A. Batko, *Entomophthora* Fresen., *Erynia* (Nowak. ex A. Batko) Remaud. & Hennebert, *Eryniopsis* Humber, *Furia* (A. Batko) Humber, *Massospora* Peck, *Orthomyces* Steinkr.,

Humber & J.B. Oliv., *Pandora* Humber, *Strongwellsea* A. Batko & J. Weiser, *Tarichium* Cohn *sensu stricto* and *Zoophthora* A. Batko) are accepted in the family (Humber 2012, Gryganskyi et al. 2013, Wijayawardene et al. 2018). Recently, Gryganskyi et al. (2022) excluded *Batkoa* Humber from *Entomophthoraceae* and included it in the newly erected family *Batkoaceae*.

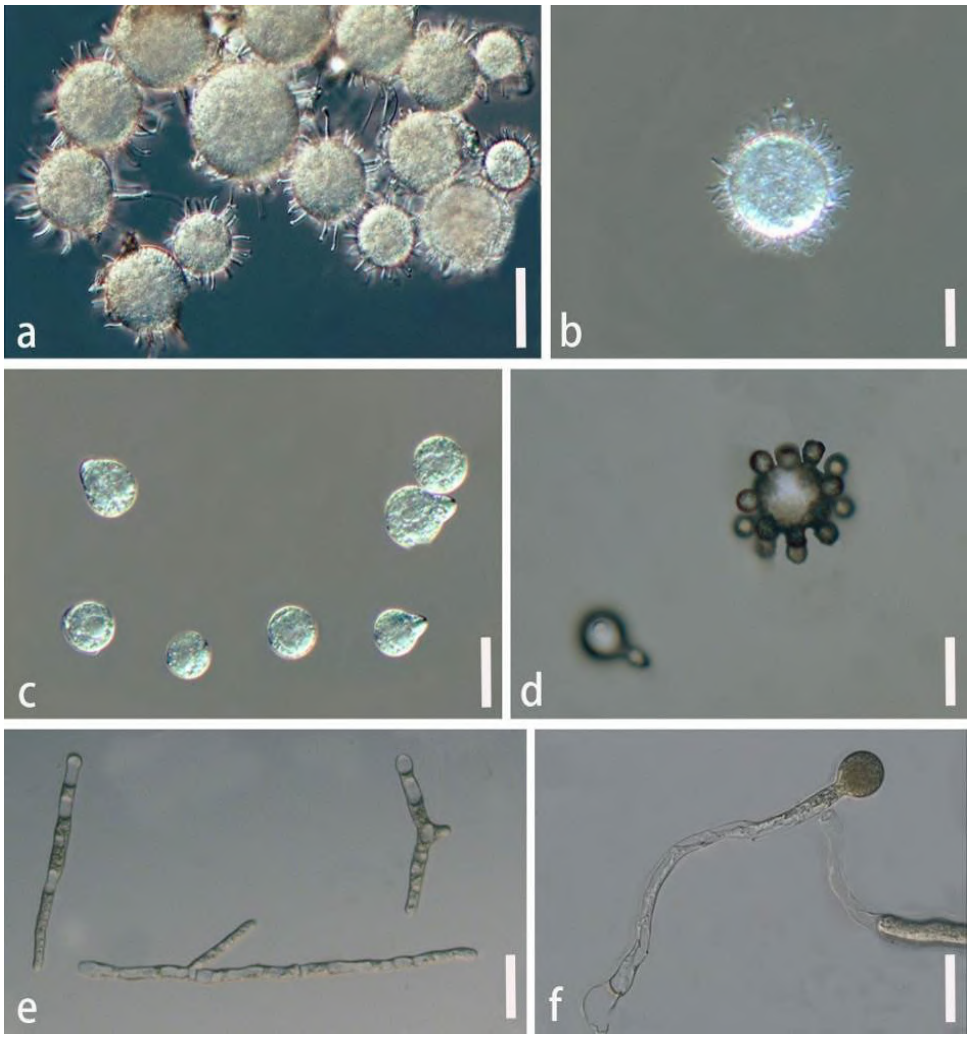


Figure 36 – Representative characters of *Conidiobolaceae*. a *Conidiobolus longivillosus* (villose spores). b *Conidiobolus coronatus* (villose spore). c *Azygosporus macropapillatus* (primary conidia). d *Conidiobolus* sp. (microconidia). e *Conidiobolus taihushanensis* (mycelium). f *Conidiobolus bifurcatus* (primary conidiophore). Scale bars: a –f = 20 μm.

Entomophthora Fresen., Bot. Ztg. 14: 883 (1856)
Index Fungorum Identifier IF 816371

The hyphal bodies are ellipsoidal to short club-shaped and germinate with a single germ tube. Conidiophores are unbranched. Produce primary and secondary conidia. Resting spores are present (Dustan 1924, Keller 2002).

Notes – *Entomophthora* was established by Fresenius (1856) to accommodate a fungus described by Cohn (1855) as *Empusa muscae* Conn, as Fresenius argued that the name *Empusa* had already been given to an orchid genus. Brefeld (1877) used these names to define two different genera; before this, these two names were used synonymously. Nowakowski (1881) suggested that *Entomophthora* has branched conidiophores, while *Empusa* has unbranched ones. In his classification, Lakon (1919) accepted and defined three genera: *Empusa* and *Lamia* with unbranched conidiophores, the latter having cystidia and rhizoids, and *Entomophthora* with branched conidiophores and rhizoids. Later, Batko (1964a,b,c,d,e), in his classification of the

arthropod pathogenic *Entomophthorales*, restricted the boundaries of *Entomophthora* to include only species with rhizoids and muscae-type conidia, designating *Entomophthora muscae* as the type species, thus making *Empusa* a synonym (same type species) (Batko 1964a). Disagreements regarding the taxonomy of *Entomophthora* persisted until 1980 due to the high degree of morphological similarity among many species and varied interpretations of the most important morphological features for species differentiation (Macleod 1963, Batko & Weiser 1965). Eventually, Remaudière & Keller (1980) proposed that fungal species producing campanulate primary conidia and forcibly discharging them should be classified as *Entomophthora*.

Species of *Entomophthora* are pathogenic to insects, including species in orders of Diptera, Hemiptera, Raphidoptera, Thysanoptera, Plecoptera, Hymenoptera and Coleoptera (Eilenberg et al. 1987, Elya & De Fine 2021). These fungi play an important role in naturally controlling and regulating the population of their hosts. Many species of *Entomophthora* cause epizootics in pest flies, and they have the potential for use in biocontrol (Mullens et al. 1987, Steinkraus et al. 1993, Watson & Petersen 1993, Klingen et al. 2000). There are 140 species listed in Species Fungorum (last accessed on 11-06-2025), but most of the species have been transferred to other genera. Cultures and molecular data are available (Gryganskyi et al. 2013, 2022, Nie et al. 2020, Elya & De Fine 2021, Möckel et al. 2022).

Other genera in *Entomophthoraceae*

Entomophaga A. Batko, Bull. Acad. Polon. Sci., Cl. II. sér. sci. biol. 12: 325 (1964)
Index Fungorum Identifier 20218; Index Fungorum (2025) lists 29 epithets, but Species Fungorum (2025) accepted 19 species.

Type species – *Entomophaga grylli* (Fresen.) A. Batko

Erynia (Nowak. ex A. Batko) Remaud. & Hennebert, Mycotaxon 11(1): 301 (1980)
Index Fungorum Identifier 20224; Index Fungorum (2025) lists 84 epithets, but Species Fungorum (2025) accepted 23 species.

Type species – *Erynia ovispora* (Nowak.) Remaud. & Hennebert

Eryniopsis Humber, Mycotaxon 21: 258 (1984)
Index Fungorum Identifier 25639; Index Fungorum (2025) and Species Fungorum (2025) accepted four species.

Type species – *Eryniopsis lampyridarum* (Thaxt.) Humber

Furia (A. Batko) Humber, Mycotaxon 34(2): 450 (1989)
Index Fungorum Identifier 25300; Index Fungorum (2025) lists 18 epithets, but Species Fungorum (2025) accepted 14 species.

Type species – *Furia virescens* (Thaxt.) Humber

Massospora Peck, Ann. Rep. N.Y. St. Mus. nat. Hist. 31: 44 (1878) [1876]
Index Fungorum Identifier 2032; Index Fungorum (2025) and Species Fungorum (2025) accepted 13 species.

Type species – *Massospora cicadina* Peck

Orthomyces Steinkr., Humber & J.B. Oliv., in Steinkraus, Oliver, Humber & Gaylor, J. Invert. Path. 72(1): 5 (1998)
Index Fungorum Identifier 27887; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Orthomyces aleyrodis* Steinkr., Humber & J.B. Oliv.

Strongwellsea A. Batko & J. Weiser, J. Invert. Path. 7: 463 (1965)

Index Fungorum Identifier 20554; Index Fungorum (2025) and Species Fungorum (2025) accepted eight species.

Type species – *Strongwellsea castrans* A. Batko & J. Weiser

Tarichium Cohn, Beitr. Biol. Pfl. 1(1): 69 (1875)
Index Fungorum Identifier 20566; Index Fungorum (2025) lists 42 epithets, but Species Fungorum (2025) accepted 26 species.

Type species – *Tarichium megaspermum* Cohn

Zoophthora A. Batko, Bull. Acad. Polon. Sci., Cl. II. sér. sci. biol. 12: 323 (1964)
Index Fungorum Identifier 20601; Index Fungorum (2025) lists 94 epithets, but Species Fungorum (2025) accepted 39 species.

Type species – *Zoophthora radicans* (Bref.) A. Batko

Meristacraceae Humber, Mycotaxon 34(2): 456 (1989)
Index Fungorum Identifier IF 82028

Walled hyphae may be simple or somewhat branched and grow vegetatively inside the host, coenocytic first and then becoming septate after the death of the host or when the fleshy content of the host is completely exhausted. Each segment of the hypha is capable of giving rise to either conidiophore or resting spore. Conidiophore is simple, unbranched and bearing numerous conidia. Primary conidia are single-walled and discharged forcibly by papillar eversion, by fluid discharge from a swollen subtending cell, or passively released from a short sterigmatic extension of conidiophore. Secondary conidia may or may not be produced if produced they resembled with primary conidia, discharged forcibly or passively dispersed from an elongated strongly narrowed conidiophore. Resting spores (zygospores) are formed as a result of conjugation of neighboring hyphal cells or scalariform conjugations between adjacent hyphae. During interphase nuclei are small, usually 3-5µm long with a prominent central nucleolus, nucleoplasm having a very minute quantity of condensed chromatic granular material, staining lightly with aceto-orcein or Bismarck brown.

Family type – *Meristacrum* Drechsler, J. Wash. Acad. Sci. 30: 250 (1940)

Ecology and life modes – Members of *Meristacraceae* are pathogenic on soil invertebrates, particularly nematodes.

Notes – *Meristacraceae* was introduced by Humber (1989) to accommodate *Meristacrum* Drechsler as the type genus, along with *Ballocephala* Drechsler and *Zygnemomyces* K. Miura. Later, *Ballocephala* and *Zygnemomyces* were excluded from *Meristacraceae* based on the bifurcate septa with lenticular plugs in their vegetative hyphae and shifted to *Kickxellomycotina* Benny (Saikawa 1989, Saikawa et al. 1997). Two genera *Meristacrum* and *Tabanomyces* are accepted in *Meristacraceae* (Humber 2012, Gryganskyi et al. 2013, Benny et al. 2014, Wijayawardene et al. 2022).

Meristacrum Drechsler, J. Wash. Acad. Sci. 30: 250 (1940)
= *Tabanomyces* Couch, R.V. Andrejeva, Laird & Nolan, Proc. natn Acad. Sci. U.S.A. 76(5): 2302 (1979)
Index Fungorum Identifier IF 20325

Hyphae developed within the host tissue, simple to somewhat branched, continuous at first but at later stages dividing into segments which give rise to sporophores, the terminal portion giving rise to a few to several cells in a basipetal manner, each of which gives rise to a single spore and are forcibly discharged through papillar eversion. Secondary spores are replicative or detached passively. Resting spores, Azygospores or zygospores are produced from hyphal segments or conjugation of spherical gametangia (Drechsler 1940).

Notes – *Meristacrum* was established by Drechsler (1940) with *M. asterospermum* Drechsler as the type from leaf mould of deciduous woodland invading *Rhabditis*, *Aphelenchoides* and *Plectus*; two species are accepted in the genus.

Type species – *Meristacrum asterospermum* Drechsler, J. Wash. Acad. Sci. 30: 251 (1940); Fig. 37

Neoconidiobolaceae X.Y. Liu, Stajich & K.T. Hodge, Journal of Fungi 8: 789 (2022); Fig. 38
Index Fungorum Identifier IF 844348

Saprobic with hyaline mycelium. Primary conidiophores are simple, occasionally branched, positively phototropic, bearing a single apical primary conidium. Primary conidia multinucleate, hyaline, globose, pyriform to obovoid, discharged forcibly. Replicative conidia are similar and smaller than primary conidia. Chlamydospores are globose, formed terminally on hyphae or from globose cells by thickening the wall. Zygospores are globose to ellipsoidal, smooth, hyaline, rarely pale yellowish, produced in axial alignment with two conjugating segments (Gryganskyi et al. 2022).

Family Type – *Neoconidiobolus* B. Huang & Y. Nie, MycoKeys 66: 70 (2020).

Ecology & Life modes – Species of *Neoconidiobolaceae* are found growing on plant detritus, leaf litter and soil and play an important role in recycling organic matter.

Notes – *Neoconidiobolaceae* was erected by Gryganskyi et al. (2022) to accommodate a monotypic genus *Neoconidiobolus* B. Huang & Y. Nie based on morphological and molecular data. Before the establishment of this family, *Neoconidiobolus* was included in *Ancylistaceae*. Species of families *Neoconidiobolaceae* and *Conidiobolaceae* show resemblance in lacking both microconidia and capilliconidia. All the species of *Neoconidiobolus* have hyaline, globose, pyriform to obovoid primary conidia, forcibly discharged. Two types of resting spores are produced: zygospores and chlamydospores.

Neoconidiobolus B. Huang & Y. Nie, MycoKeys 66: 70 (2020)
Index Fungorum Identifier IF 831598

Mycelia colourless. Primary conidiophores are usually simple unbranched, sometimes branched from hyphal knots or differentiated from aerial hyphae, bearing a single primary conidium. Primary conidia are multinucleate, colourless, globose, pyriform to obovoid and discharged forcibly. Replicative conidia similar and smaller than primary conidia. Chlamydospores globose, formed terminally on hyphae or from globose cells by thickening of the wall. Zygospores formed in axial alignment with two conjugating segments, globose to ellipsoidal, smooth, colourless, rarely pale yellowish (Nie et al. 2020, 2021).

Type species – *Neoconidiobolus thromboides* (Drechsler) B. Huang & Y. Nie

Notes – *Neoconidiobolus* was established by Nie et al. (2020) with *Neoconidiobolus thromboides* (Drechsler) B. Huang & Y. Nie as type to accommodate *Conidiobolus thromboides* Drechsler, along with nine other new combinations. Nie et al. (2021, 2022) added two new species and two new combinations, thus raising the number of species to 14. All species were accepted in the genus, and molecular data are available.

Neozygitomycetes Humber
Neozygitales Humber
Neozygitaceae Ben Ze'ev, R.G. Kenneth & Uziel, Mycotaxon 28(2): 321 (1987)
Index Fungorum Identifier IF 81840

Vegetative growth as hyphal bodies that may or may not have a cell wall. Conidiophores unbranched, cylindrical or somewhat clavate. Conidia unitunicate, 4 or 7–11 nucleate, discharged by papillar eversion, melanized; may form secondary capilloconidia. Zygospores bud from the point of conjugation of two hyphal bodies, melanized (Ben Ze'ev & Uziel 1987).

Family type – *Neozygites* Witlaczil

Ecology and life modes – Taxa in the family are usually parasitic on homopteran, mites and thrips (Witlaczil 1885, Ben Ze'ev & Uziel 1987). A few members are exploited as biocontrol agents in forestry and agriculture against aphid pests (Montalva et al. 2014, Barta & Cagáň 2006).

Notes – *Neozygitaceae* was introduced by Ben-Ze'ev Ben Ze'ev & Uziel (1987), comprising two genera, *Apterivorax*, and *Neozygites* (= *Thaxterosporium*) (Humber 2012, Gryganskyi et al. 2013) and appears to be parasitic on mites and plant lice.

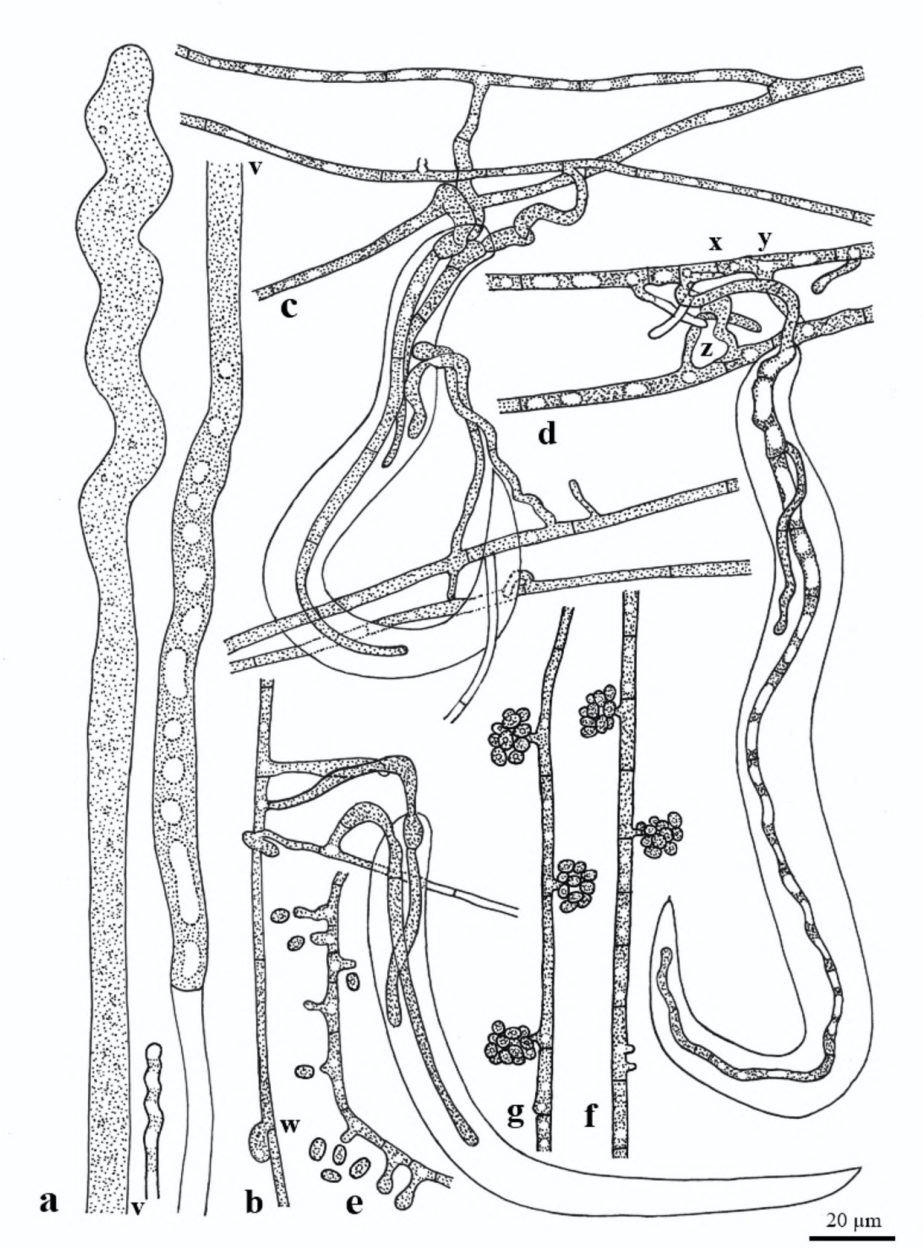


Figure 37 – *Meristacrum asterospermum.* Drawn to a uniform magnification with the aid of a camera lucida; X 1000 throughout. a Sporiferous termination of a conidiophorous filament of *Meristacrum asterospermum*, showing its distal disposition in an extended helicoid spiral. b Specimen of *Plectus communis* which, after its disablement by a protozoan parasite, is being invaded besides by two hyphae of *Cephalosporium* sp.; (v,w), a short spurlike hyphal branch. c Another disabled specimen of *P. communis*, penetrated by five hyphal branches of *Cephalosporium* sp. d Specimen of *P. parvus* Bastian, disabled by protozoan parasite and then further invaded by a branching filament of *Cephalosporium* sp.; (x-z), three oblique partial septa. e Superficial hypha of *Cephalosporium* sp. with several spore-producing sterigmata. f, g, Submerged filaments showing clusters of spores at the tips of lateral sterigmata. (Owing to lack of space, 'v' shown in two parts,

which are connected in ‘v’. The small sketch, in which the lower portions of the successive turns are stippled, is intended to show more clearly the direction of rotation in the helicoid termination (Redrawn from Dreschler 1940).

Neozygites Witlaczil, Arch. Mikr. Anat. 24: 599 (1885)
Index Fungorum Identifier: IF 20366

Spherical or rod-shaped hyphal bodies with or without the wall; simple conidiophores; spherical to obovate primary conidia with 3–8 nuclei; the presence of capilliconidia with typically bent capillary tubes; spherical or ellipsoidal, binucleate, dark brown to black zygospores, rarely azygospores; cystidia always absent, rhizoids normally absent.

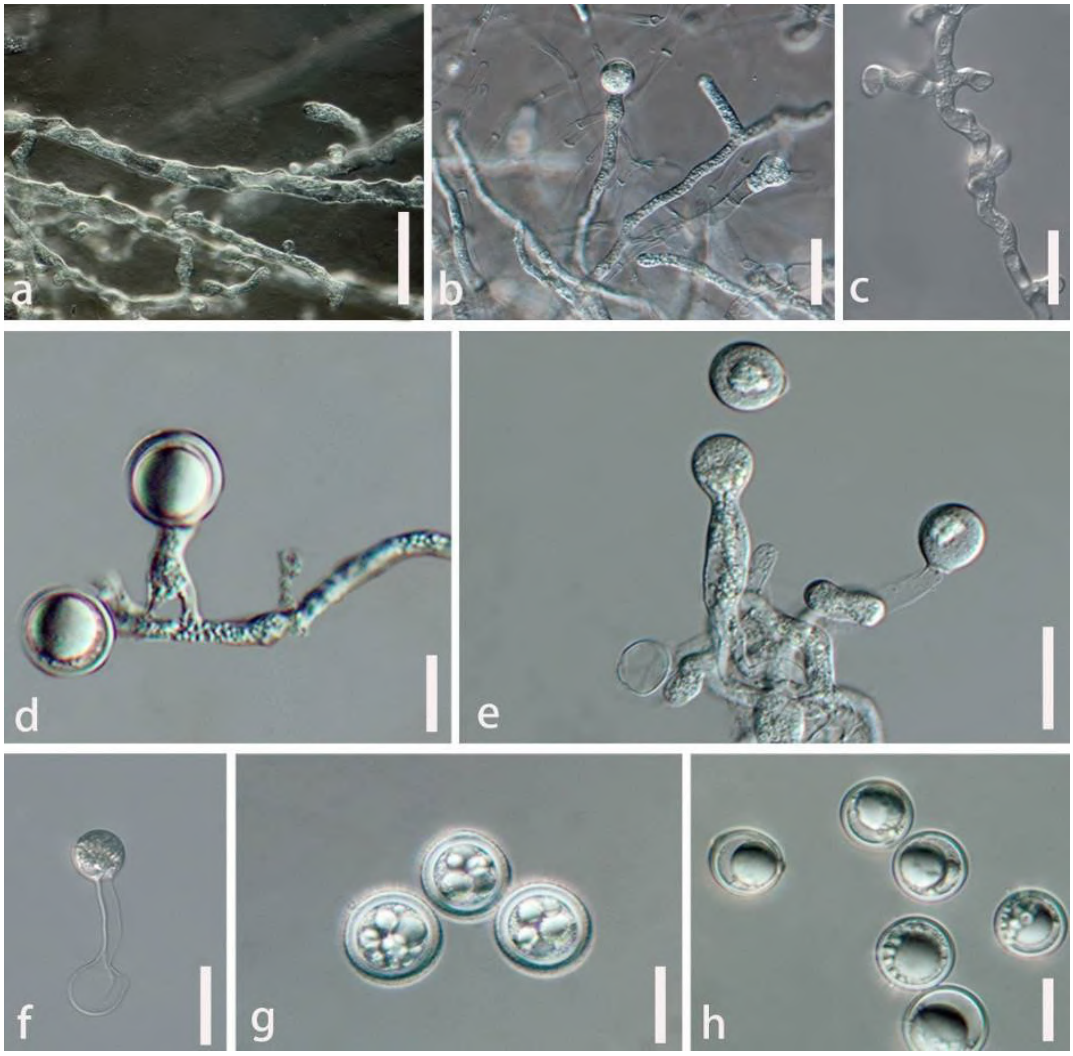


Figure 38 – Representative characters of *Neoconidiobolaceae*. a *Neoconidiobolus osmodes* (mycelium). b *Neoconidiobolus pachyzygosporus* (primary conidiophore). c *Neoconidiobolus mirabilis* (mycelium). d *Neoconidiobolus stilbeus* (zygosporus). e *Neoconidiobolus stromoideus* (primary conidiophore). f *Neoconidiobolus kunyushanensis* (secondary conidia). g *Neoconidiobolus osmodes* (zygosporus). h *Neoconidiobolus sinensis* (zygosporus). Scale bars: a –h = 20 μm.

Notes – *Neozygites* was erected by Witlaczil (1885) with *N. aphidis* from the cadaver of *Aphis arundinis* on *Phragmites communis.* The genus is characterized by nuclear structure, and the nuclear behaviour during mitosis of *Neozygites* differs from that of the other *Entomophthorales* (Butt & Heath 1988, Butt & Humber 1989). Therefore, the genus was placed in a distinct family, *Neozygitaceae* Ben-Ze'ev & Kenneth (Ben-Ze'ev et al. 1987).

No taxonomic subdivision has been recognized, but there is a difference between homopteran pathogens in this genus, most of which have ovoid zygospores with smooth surfaces, and the pathogens of mites and thrips, all of which have globose or subglobose resting spores with roughened surfaces. The narrow host ranges of *Neozygites* species increase their potential value as biological control agents of different forestry and agricultural aphid pests that do not threaten non-target organisms like plants, beneficial arthropods, and vertebrates (Barta & Cagáň 2006, Montalva et al. 2014). *Neozygites* species are rare and difficult to culture. To date, only mites and thrips pathogens of this genus have been cultured *in vitro* (Butt & Humber 1989, Keller 1997, Grundschober et al. 1998, Delalibera 2003, Leite et al. 2003). None of the *Neozygites* species infecting aphids has been cultured *in vitro* (Keller 1991, 1997, Humber 2016).

Other genera in *Neozygitaceae*

Apterivorax S. Keller, Sydowia 57(1): 47 (2005)

Index Fungorum Identifier 28942; Index Fungorum (2025) and Species Fungorum (2025) accepted two species.

Type species – *Apterivorax sminthuri* (S. Keller & Steenb.) S. Keller

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

Archaeosporomycetes Sieverd., G.A. Silva, B.T. Goto & Oehl

Archaeosporales C. Walker & A. Schüßler

Ambisporaceae C. Walker, Vestberg & Schüßler emend. R.J. Bills & J.B. Morton, Mycorrhiza 25: 494 (2015); Fig. 39

≡*Appendicisporaceae* C. Walker, Vestberg & Schüßler, Mycol. Res. 111:254 (2007); **nom. illegit.** (Arts 53.1, 53.3)

Index Fungorum Identifier 510208

Dimorphic species forming glomoid, acaulosporoid, or both glomoid and acaulosporoid spore types. Glomoid morph formed singly in soil or in loose clusters, germinating through the subtending hypha. Glomoid spores are hyaline with 1–3 layers in the spore wall. Acaulosporoid spores are hyaline to yellow, formed at the top of a short branch (pedicel) of the neck of a sporiferous saccule; after detachment from the neck, the spores with the pedicel resemble glomoid spores. Acaulosporoid spores germinate through a germ tube emerging from a germinal shield (orb) formed on the inner wall (Spain et al. 2006). Intraradical hyphae, arbuscules and vesicles stain pale blue in trypan. Glomoid morph is not known for all species (Błaszkowski et al. 2021b).

Family type – *Ambispora* C. Walker, Vestberg & Schüßler emend. R.J. Bills & J.B. Morton Mycorrhiza 25: 494 (2015)

Notes – Spain et al. (2006) introduced *Appendicispora* Spain et al. to accommodate three dimorphic species producing both acaulosporoid and glomoid spores (*Appendicispora appendicula*, *A. gerdermanii* and *A. jimgerdermanii*). Walker et al. (2007a) introduced *Ambispora* typified by *Am. fennica* C. Walker et al., a dimorphic fungus with the acaulosporoid morph indistinguishable from that of *Ap. gerdemannii* (S.L. Rose et al.) Spain et al. The genus was placed in the family *Ambisporaceae* (Walker et al. 2007a), forming a clade sister to *Archaeosporaceae* in *Archaeosporales*. Subsequently, Walker et al. (2007b) established *Appendicisporaceae* with all species described in *Ambispora*. *Appendicispora* appeared later to be a homonym of a genus in *Ascomycota*, *Appendicospora* K.D. Hyde (Hyde 1995). Consequently, *Ambispora* was resurrected, and *Appendicisporaceae* synonymized with *Ambisporaceae* (Walker 2008). Of the eleven species assigned to *Ambispora*, Bills & Morton (2015) recognized only three. Nevertheless, we recognize five species: *A. leptoticha* (N.C. Schenck & G.S. Sm.) C. Walker et al., *A. gerdemannii* (S.L. Rose et al.) C. Walker et al., *A. granatensis* Palenz. et al., *A. nicolsonii* (C. Walker et al.) Oehl et al. and *A. reticulata* Oehl & Sieverd. However, additional phylogenetic analysis of *A. appendicula* (Spain et al.) C. Walker, *A. jimgerdemannii* (Spain et al.) C. Walker, *A. callosa* (Sieverd.) C. Walker et al., *A. fecundispora* (N.C. Schenck & G.S. Sm.) C. Walker and *A. nicolsonii* using isolates from type locations (or their vicinities) should be performed to clarify if the species recognized by Spain et al.

(2006) are valid. The phylogenetic analysis of *A. reticulata* still requires effort to confirm its affinity in *Ambispora*. The family represents a complex species group because of their spore diversity, life cycle, morphology and phylogeny.

The family is worldwide distributed, including both terrestrial and aquatic ecosystems (Queiroz et al. 2020, Polo-Marcial et al. 2021, 2024), with the highest number of records in tropical zones of North and South America (Stürmer et al. 2018).

Genome available for *A. leptoticha* FL130A and *A. gerdemannii* MT106 (Montoliu-Nerin et al. 2021), and transcriptome available for *A. leptoticha* JA116 (Beaudet et al. 2018).

Ambispora C. Walker, Vestberg & Schüßler emend. R.J. Bills & J.B. Morton Mycorrhiza 25: 494 (2015)
≡*Appendicispora* Spain, Oehl & Sieverd. Mycotaxon 97: 168 2006
Index Fungorum Identifier 510209
Description as in *Ambisporaceae*.

Type species – *Ambispora gerdemannii* (S.L. Rose et al.) R. Bills & J.B. Morton, Mycol. Res. 111(2): 148 (2007)

Notes – As in *Ambisporaceae*, since the family has only one genus.

Archaeosporaceae J.B. Morton & D. Redecker, Mycologia 93(1): 182 (2001); Fig. 40
Index Fungorum Identifier 82112

Archaeosporaceae species produce monomorphic (acaulosporoid and entrophosporoid spore type) or dimorphic (acaulosporoid and glomoid spore type) glomerospores (Morton & Redecker 2001), singly or rarely in small, loose clusters without a peridium in the soil, occasionally inside roots (Schenck et al. 1986, Oehl et al. 2019, Schüßler & Walker 2019). Spores are globose, subglobose to irregular, small, hyaline. Acaulosporoid spores, possessing two walls, each with 2–3 layers, develop laterally on the neck of a sporiferous saccule. The saccule is hyaline, globose to subglobose or oblong to irregular, has a single-layered hyaline wall, usually covered with granular material, and is generally collapsed and detached in most mature spores. Glomoid spores are rarely observed (Oehl et al. 2015a, 2019, Schüßler & Walker 2019). They are produced terminally or intercalary on cylindrical subtending hyphae. Pore is often closed by a septum arising from the second layer of the spore wall. Amyloid or dextrinoid reactions to Melzer's reagent are not observed (Walker et al. 2007a). Mycorrhizal structures stain weakly in trypan blue, and vesicles have not been observed yet. Differs from *Ambisporaceae* and *Polonosporaceae* Błaszk. et al., in the number of spore walls (two-walled vs. three-walled) and the nucleotide composition of sequences of the SSU-ITS-LSU nrDNA region.

Family type – *Archaeospora* (R.N. Ames & Linderman) J.B. Morton & D. Redecker, Mycologia 93(1): 183 (2001)

Notes – *Archaeosporaceae* was introduced by Morton & Redecker (2001) based on morphological and phylogenetic analysis of three species with dimorphic spore development previously described in *Acaulospora*: *A. trappei* (type species), *A. leptoticha* and *A. gerdemannii*. With the support of molecular and morphological data, Spain et al. (2006) transferred *Ar. leptoticha* and *Ar. gerdemannii* to *Ambispora* (see *Ambisporaceae* section). Considering the morphology of the bi-walled spores produced laterally on the neck of a sporiferous saccule, the weak staining reaction of mycorrhizal structures and the absence of vesicles, two more species of *Acaulospora* were transferred to *Archaeospora*: *A. myriocarpa* (Spain et al.) Oehl et al. and *A. undulata* (Sieverd.) Sieverd. et al. (Oehl et al. 2011a). However, these species require additional molecular and phylogenetic analysis to confirm their affiliation with the genus. Using morphological and ontogenetic characters, Sieverding & Oehl (2006) established the genus *Intraspora* Oehl & Sieverd. within *Archaeosporaceae* to accommodate *I. schenckii* (Sieverd. & S. Toro) Oehl & Sieverd., previously classified as *Entrophospora schenckii* in the family *Entrophosporaceae* Oehl & Sieverd. With the subsequent acquisition of SSU sequences for this species, Schüßler & Walker (2010) transferred it to *Archaeospora*, synonymizing the genus *Intraspora*. Based on spore morphology

and phylogeny of the ITS/LSU regions, Oehl et al. (2015a) described the new monospecific genus *Palaeospora* Oehl et al. with the type species *P. spainii* Oehl et al. Phylogenetically, the new genus formed a clade basal to *A. trappei* (R.N. Ames & Linderman) J.B. Morton & D. Redecker and *I. schenckii* (maintained as separate genera). More recently, *Archaeospora* was enriched with the species *A. europea* Oehl et al. and *A. ecuadoriana* A. Schüßler & C. Walker (Oehl et al. 2019, Schüßler & Walker 2019), supported by molecular data. Due to the phylogenetic position of the latter species, *P. spainii* was included within *Archaeospora*, and hence, Schüßler & Walker (2019) advocated the emendation of *Palaeospora* as a synonym of *Archaeospora*. Till now, the phylogenetic position of *A. trappei*, the type species of the genus, is uncertain since sequences from several isolates with similar morphology are scattered within and outside the *Archaeospora* clade (Schüßler & Walker 2019). This could suggest the presence of cryptic species or an unresolved phylogeny of the true *A. trappei*. Analysis of Tedersoo et al. (2024) based on a large dataset of eDNA ribosomal sequences enlarged the family with two potential new genera.

Archaeosporaceae is one of the earliest diverging clades in *Glomeromycota* (Morton & Redecker 2001). Recently, mycorrhizal propagules with characteristics similar to *Archaeosporaceae* were found in fossil plants from the Devonian, leading to the proposition of a new fossil taxon in this family, *Archaeosporites rhyniensis* C. Walker et al. (Harper et al. 2020).

The family presents a worldwide distribution in a variety of habitats, including forests, grasslands, deserts and wetlands in over 20 countries. Only a few experiments have been conducted so far to assess the influence of *Archaeosporaceae* spp. on plant performance. However, *A. myriocarpa* was highly effective in promoting the growth of cassava and coffee plants in greenhouse and field trials (Sieverding 1990). Furthermore, *A. trappei* promoted herbivory tolerance in *Plantago lanceolata* (Bennett et al. 2009) and increased phosphorus uptake and growth in three tree species (Helgason et al. 2008).

Archaeospora (R.N. Ames & Linderman) J.B. Morton & D. Redecker, Mycologia 93(1): 183 (2001)

Index Fungorum Identifier 28457

As in the *Archaeosporaceae* description.

Type species – *Archaeospora trappei* (R.N. Ames & Linderman) J.B. Morton & D. Redecker, Mycologia 93(1): 183 (2001)

≡*Acaulospora trappei* R.N. Ames & Linderman, Mycotaxon 3(3): 566 (1976)

Notes – As in the *Archaeosporaceae* notes.

Geosiphonaceae Engl. & E. Gilg, Syllabus, Edn 9 & 10 (Berlin): 24 (1924) emend. A. Schüßler; Fig. 43

Index Fungorum Identifier 81542

Geosiphonaceae was introduced by Engler & Gilg (1924) to accommodate *Geosiphon pyriformis* (Kütz.) F. Wettst. (Drude & Schorler 1916), initially described as a symbiosis between a heterotrophic siphonal algae and the cyanobacteria *Nostoc*.

The morphological and ontogenetic characterization of *G. pyriformis* spores remains unclear, requiring further analysis. There are no diagnostic characteristics that uniquely separate these spores from those of other species in *Glomeromycota*. The fungus presents a restricted occurrence limited to Germany and Austria (Schüßler 2002). The findings of *G. pyriformis* in wet ecosystems of Germany suggest that this species prefers such habitats and may occur in other regions of the world. The genome of *G. pyriformis* reveals ancestral traits related to the emergence of the AM symbiosis, and the gene counts, estimated genome size, and genome statistics are all similar to those of model AMF species (Malar et al. 2021).

Family type – *Geosiphon* F. Wettst., Öst. bot. Z. 65: 152 (1915)

Notes – The fungal nature of *G. pyriformis* was reported by Knapp (1933), suggesting that it was a type of lichen. Mollenhauer (1992) was the first to suggest a relationship between *Geosiphon* F. Wettst. and AMF, based on the similarities of the reproductive structures (spores). Schüßler et al.

(1994) validated the hypothesis by comparing the spore morphology of *Geosiphon* and *Glomus* species. The family *Geosiphonaceae* was placed in the order *Geosiphonales* Caval.-Sm. and class *Geomycetes* Caval.-Sm. (*Ascomycota*) designated by Cavalier-Smith (1998). However, genetic data showed that this fungus belonged to the order *Glomales* (Gehrig et al. 1996). Thus, based on new morphological and molecular evidence, Schüßler (2002) emended the family and placed it in the order *Archaeosporales*. According to the description, *G. pyriformis* produces hypogeous coenocytic mycelium. Forming typical glomoid, globose to subglobose asexual spores, produced singly or in loose clusters. It is a biotrophic organism, forming symbiotic relationships with photoautotrophic organisms. Currently, only one species is known, establishing endocytobiosis with cyanobacteria (*Nostoc*).

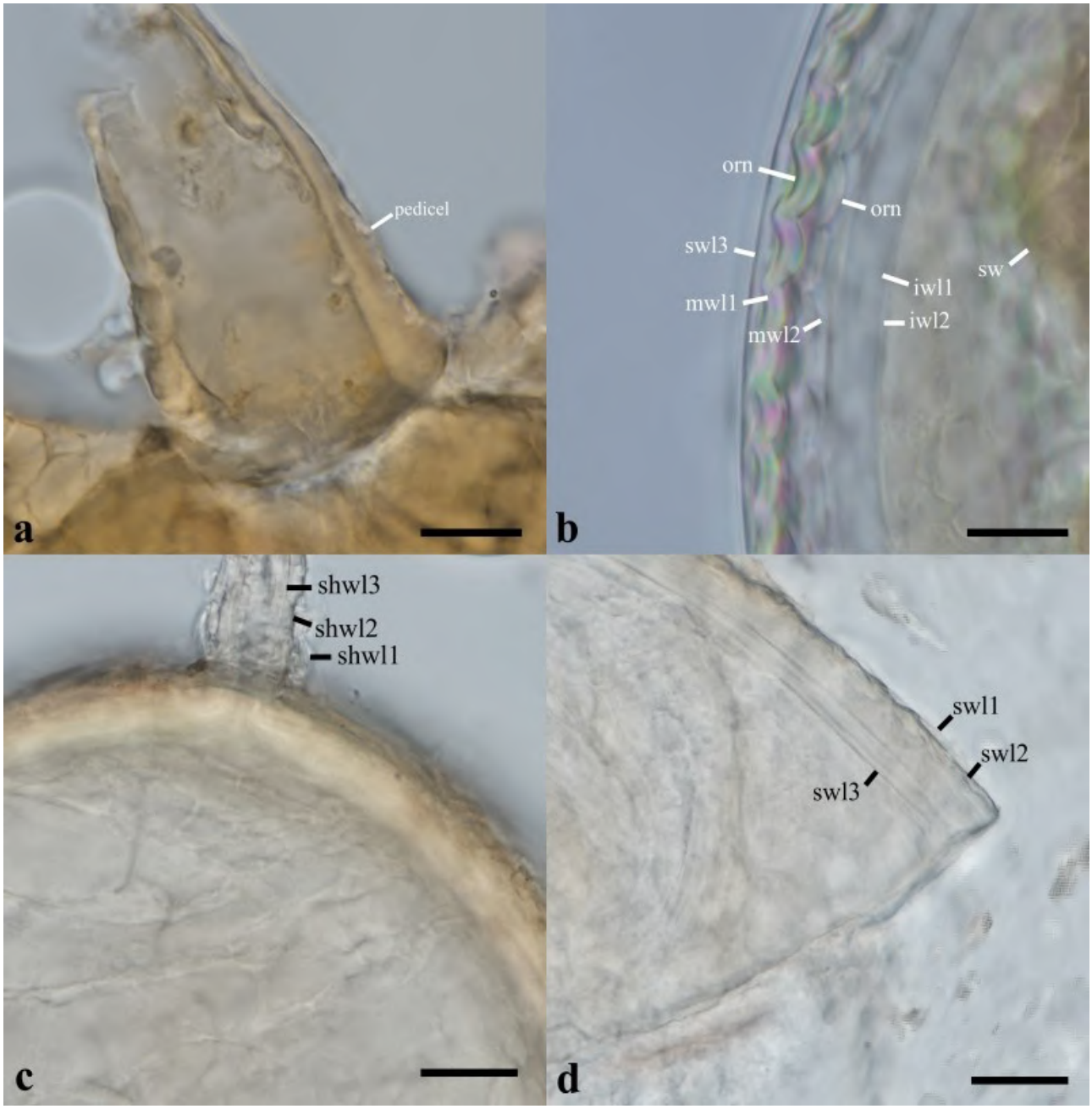


Figure 39 – *Ambisporaceae*. a Pedicel formed at the spore base connecting the spore and sporiferous saccule in *A. appendicula*. b Spore with 3 walls and ornamentation (orn) in the middle wall (mw). c Glomoid spore produced by *A. appendicula* with three subtending hyphal wall layers (shwl1–3). d Details of spore wall with three layers (swl1–3). Scale bars: a–d = 10 µm.

Geosiphon F. Wettst., Öst. bot. Z. 65: 152 (1915)
Index Fungorum Identifier 20238

As in the family *Geosiphonaceae* description.

Type species – *Geosiphon pyriformis* (Kütz.) F. Wettst., Öst. bot. Z. 65: 153 (1915) emend. A. Schüßler

≡*Botrydium pyriforme* Kütz., Spec. alg. (Lipsiae): 486 (1849)

Notes – As in the family *Geosiphonaceae* notes.

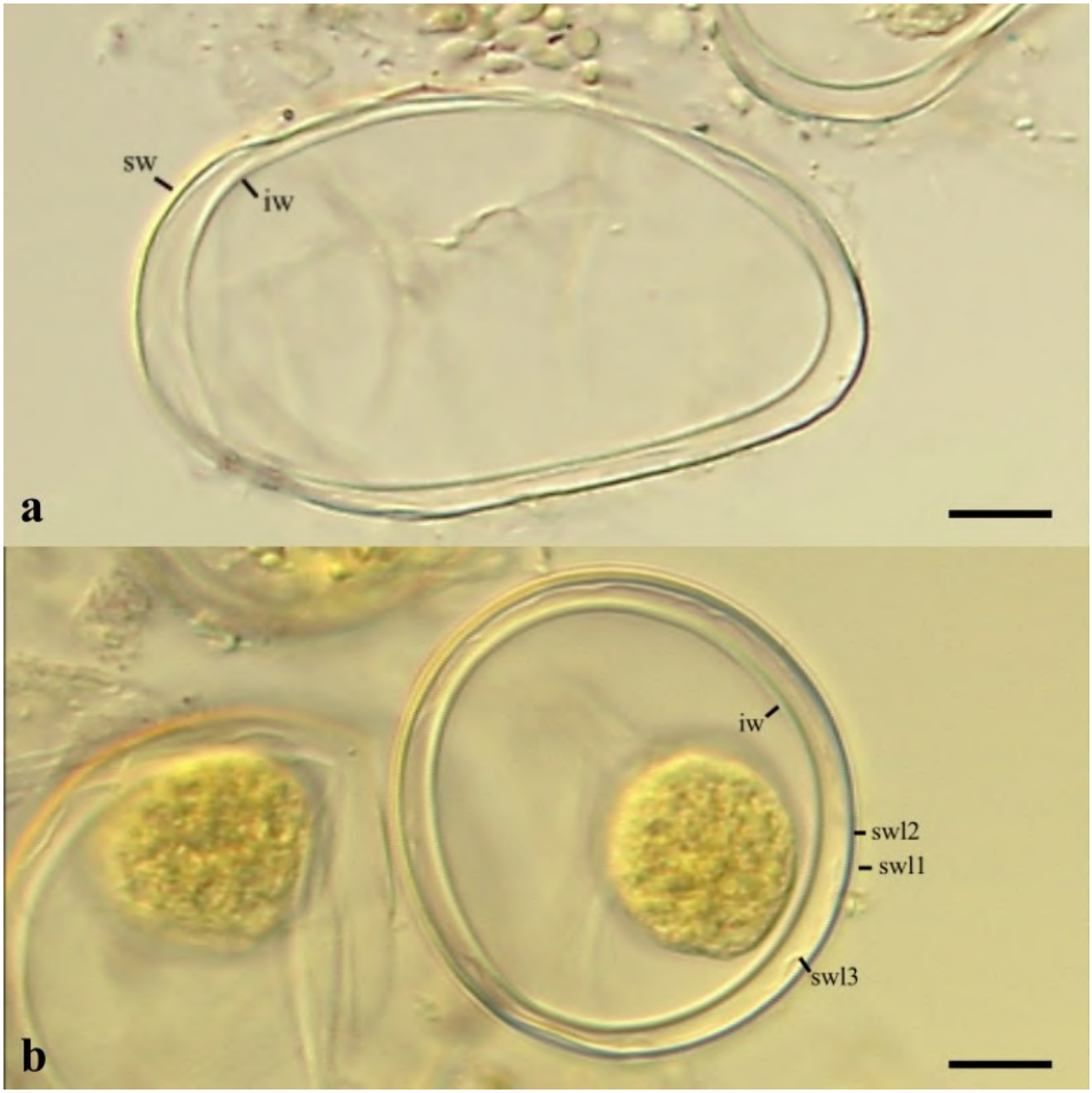


Figure 40 – *Archaeosporaceae*. a Spores in cluster of *Archaeospora myriocarpa* with two walls (sw, iw) and details of the outer wall with three layers (swl1–3). b Detail of spore walls (sw, iw) in *A. myriocarpa*. Scale bars: a, b = 10 µm.

Polonosporaceae Błaszk., Niezgoda, B.T. Goto & Magurno, Mycol. Prog. 20(8): 946 (2021); Fig. 42
Index Fungorum Identifier 840255

Acaulosporoid spores formed singly in soil, arise laterally from the neck of a sporiferous saccule continuous with an extraradical mycorrhizal hypha. Spores are hyaline to white, glistening, globose to subglobose with three spore walls. Outer spore wall with two layers. Layer 1 evanescent,

hyaline, continuous with the wall of the sporiferous saccule. Layer 2 laminate, smooth, hyaline to white. The middle spore wall consists of one flexible to semi-flexible, hyaline layer. Inner spore wall with two hyaline, smooth layers, flexible to semi-flexible. Layer 1 is usually tightly adherent to the lower surface of layer 2 and difficult to see. In Melzer's reagent, layer 2 of the outer spore wall sometimes stains reddish white. Germination orb not found. Sporiferous saccule hyaline, globose to subglobose. Saccule wall is a hyaline, smooth, 0.5–1.0 μm thick layer. Cicatrix has a slightly raised collar when seen in cross view, or circular when observed in plain view. Differs from *Archaeosporaceae* in the characteristics of spore walls and the nucleotide composition of sequences of the SSU–ITS–LSU nrDNA region and the *rpb1* gene.

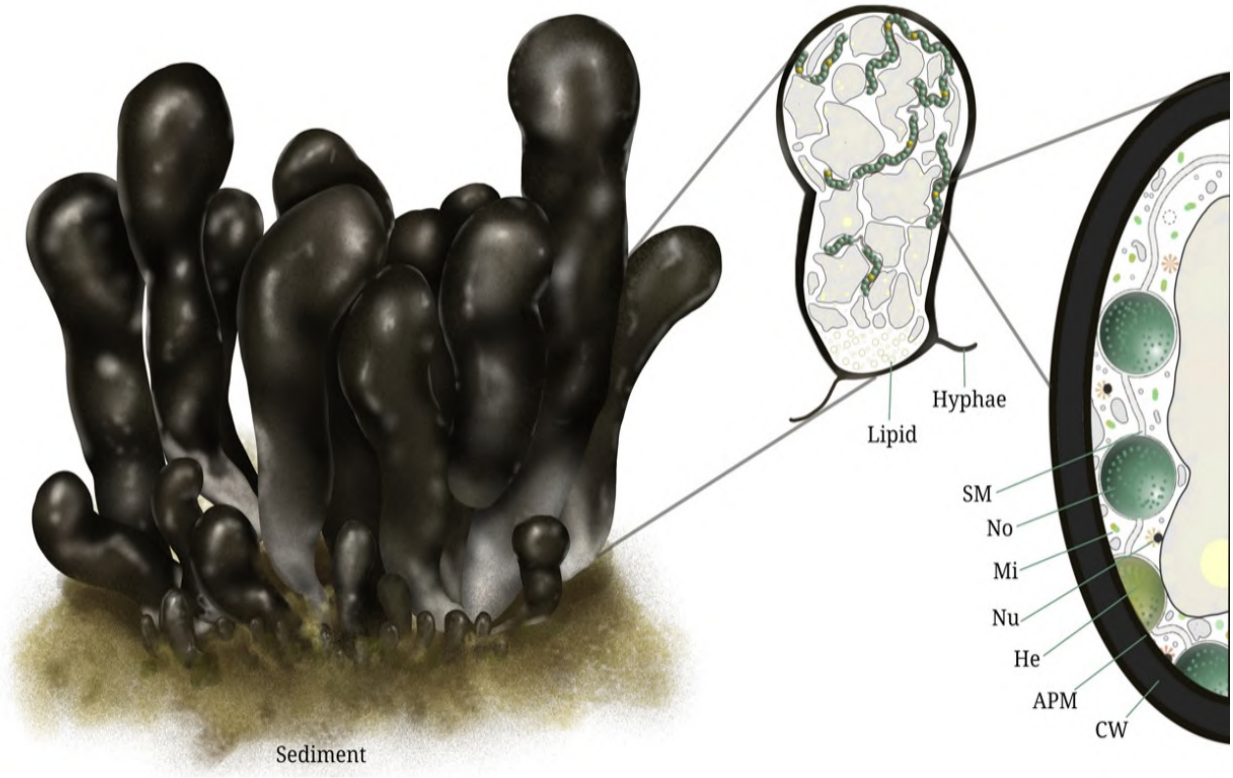


Figure 41 – *Geosiphonaceae*. *Geosiphon pyriformis* developing in wet soils, with detail of the internal sub-cellular structures associated with cyanobacteria (SM: symbiosome-membrane, No *Nostoc* algae, Mi: mitochondrion, Nu: nucleus, He: heterocyst, APM: arbuscular fungal plasma membrane, CW: cell-wall) (Redrawn using software Ibis paintX. Original image is from Kluge et al. 2002).

Family type – *Polonospora* Błaszk., Niezgoda, B.T. Goto & Magurno, Mycol. Prog. 20(8): 946 (2021)

Notes – Phylogenetic analyses of SSU–ITS–LSU and *rpb1* sequences obtained from spores grown in trap cultures placed *Acaulospora polonica* in a new clade at the rank of family in *Archaeosporales*. The new family is monospecific and, therefore, its morphological characterization is based on *Polonospora polonica* only. Nevertheless, environmental sequences support the existence of at least three more genera and species not yet described (Błaszkowski et al. 2021a).

Polonospora Błaszk., Niezgoda, B.T. Goto & Magurno, Mycol. Prog. 20(8): 946 (2021)
Index Fungorum Identifier 840256

As in the *Polonosporaceae* description.

Type species – *Polonospora polonica* (Błaszk.) Błaszk., Niezgoda, B.T. Goto & Magurno Mycol. Prog. 20(8): 947 (2021)

≡*Acaulospora polonica* Błaszk. 1988

Notes – As in the *Polonosporaceae* notes.

Glomeromycetes Caval.-Sm. emend. Oehl, G.A. Silva, B.T. Goto & Sieverd.
Diversisporales C. Walker & A. Schüssler, **emend**. Oehl, G.A. Silva & Sieverd.
Acaulosporaceae J.B. Morton & Benny Mycotaxon 37:471–491 (1990); Fig. 43
Index Fungorum Identifier 82037

Acaulosporoid, kuklosporoid and the recently described "entrosacculoid" spores are produced singly in soil, occasionally in aggregates or in sporocarps. Rarely found in the roots of the host (Lin et al. 2022). Upon detaching from the spore, the sporiferous saccule leaves one scar (acaulosporoid) or two scars (kuklosporoid). Spores are yellow to orange-red or colourless (hyaline), smooth or ornamented, globose or subglobose, sometimes ovoid, cylindrical or irregular. The spore structure consists of three walls (spore wall (sw), middle wall (mw), inner wall (iw)), smooth or ornamented, usually with 1–3(–5) layers in the spore wall (Goto et al. 2013). The outer wall (sw) has the outermost layer continuous with the wall of the neck of the saccule. The ornamentations, when present, are usually located in the second layer of the outer wall (swl2). Ornamentations consist of projections, depressions or double ornamentations. The middle wall is composed of two layers (mwl1–2), hyaline, flexible to semi-flexible, sometimes rigid, generally adhered. The inner wall has three layers and its surface is ornamented with granular outgrowths ("beaded layer"), except *A. intravesiculata* and *A. gedanensis*, in which this layer is smooth. Generally, the inner wall reacts to Melzer's reagent. Germ tube emerging from a plate-shaped pre-germination structure formed by a coiled hypha and associated with the upper surface of the inner wall, penetrating first the overlying middle wall and then the spore wall.

Family Type – *Acaulospora* Gerd. & Trappe, Mycological Memoir 5:31–33 (1974).

Notes – Originally, *Acaulosporaceae* was included with two genera (*Acaulospora* and *Entrophospora* R.N. Ames & R.W. Schneid. emend. Błaszk. et al.). With the revision by Sieverding & Oehl (2006), *Entrophospora* was transferred to the new family *Entrophosporaceae*, except for the species *E. colombiana* Spain & N.C. Schenck, *E. kentinensis* C.G. Wu & Y.S. Liu and *E. schenckii*. *Entrophospora colombiana* and *E. kentinensis* were included in the new genus *Kuklospora* Oehl & Sieverd., while *E. schenckii* was included in the new genus *Intraspora* in *Archaeosporaceae*, as *I. schenckii*. Later, with the transfer of *K. colombiana* and *K. kentinensis* to *Acaulospora*, *Kuklospora* remained monospecific (*K. spinosa*). The description of *K. spinosa* was based only on the morphology and ontogeny of the spores (Cai et al. 2013). Therefore, the lack of molecular data does not allow to unveil the phylogenetic relationship with *Acaulospora*, and consequently to validate the genus. Its distribution is restricted to the place of description: Sichuan, China, isolated from the rhizosphere of *Prunus mume*. For these reasons, we consider the species as *incertae sedis* requiring additional analysis.

In the last two decades, seven *Acaulospora* species were transferred to the genera *Ambispora* (*Am. appendicula*, *Am. jimgerdemannii*, *Am. nicolsonii*), *Archaeospora* (*Ar. myriocarpa*, *Ar. trappei*, *Ar. undulata*) and *Polonospora* (*P. polonica*). *Acaulosporaceae* includes 66 species (da Silva et al. 2022, Park et al. 2021, Stürmer et al. 2022) with a cosmopolitan distribution, occurring in different ecosystems (terrestrial and aquatic), with records in approximately 61 countries. *Acaulosporaceae* is one of the most dominant AMF families in natural and agricultural sites. A global niche model by Davison et al. (2021) showed that *Acaulosporaceae* generally had an optimal niche in low pH and low-temperature conditions. Under these and other stressful conditions, they probably play an important role for their host plants through arbuscular mycorrhizal symbiosis. Inoculation with *Acaulospora* has been seen to increase plant growth and nutrition (Sieverding & Toro 1990, Séry et al. 2016, Huang et al. 2020), regulating the synthesis of important plant biomolecules such as phenolics and saponins (Muniz et al. 2021) and promoting the phytostabilization in heavy metal contaminated soils (González-Chávez et al. 2019). Furthermore,

the glycoprotein GRSP associated with *A. scrobiculata* showed suppressing properties versus plant pathogens *in vitro* (Sharma et al. 2017). Inoculation of *Schizolobium parahyba* – an Amazon forest native tree – with a combination of *Acaulospora* spp. and plant growth-promoting rhizobacteria increased wood yield under field conditions (Cely et al. 2016).

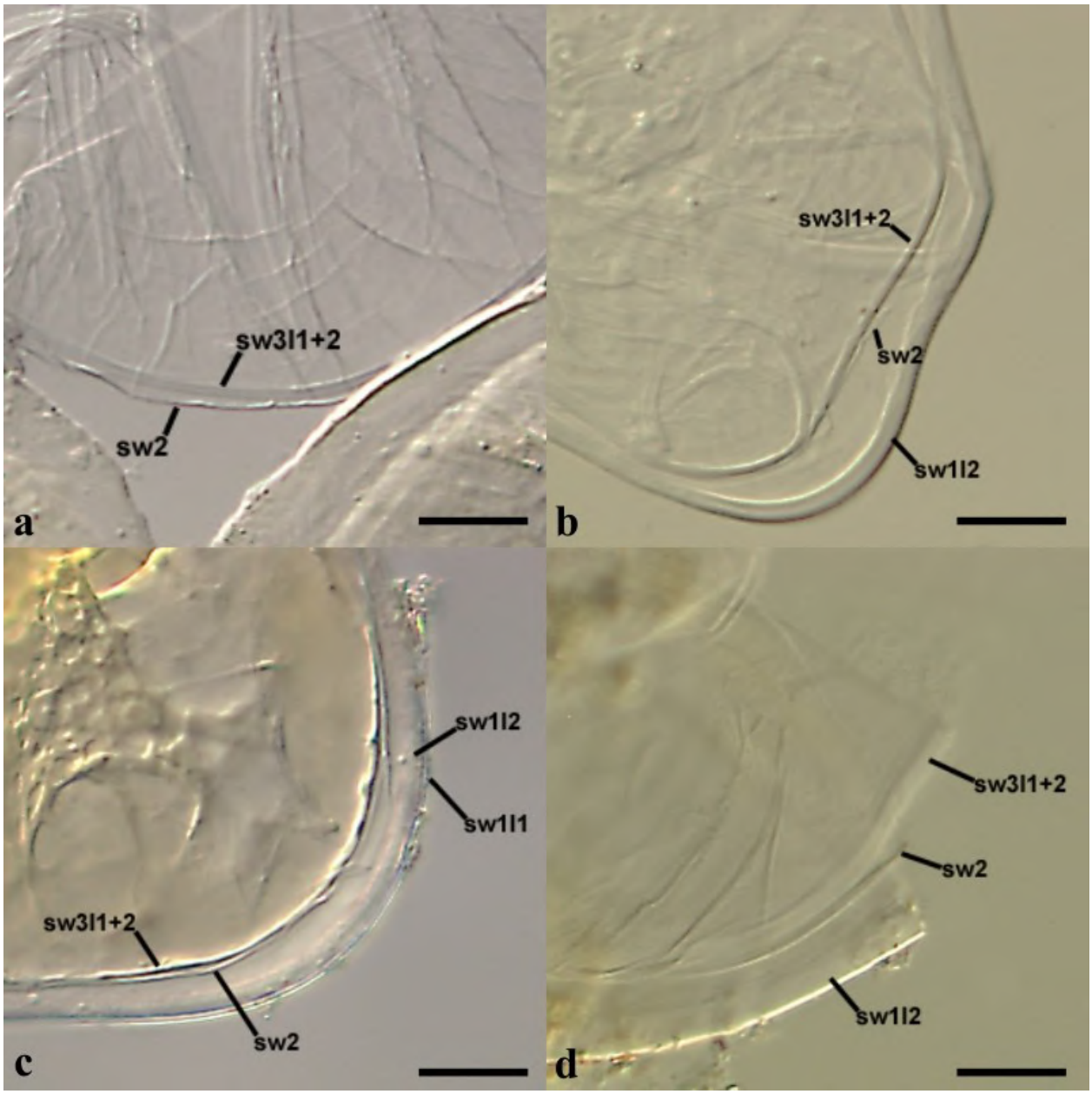


Figure 42 – *Polonosporaceae*. a *Polonospora polonica* produces spores with three walls. b–d Detail of spore wall in *P. polonica*. Scale bars: a–d = 10 μm.

Additionally, da Silva et al. (2022) concluded that the presence or absence of spore ornamentation is an evolutionarily convergent character because it does not correlate with the phylogeny of *Acaulospora* species.

Genome available for *A. morrowiae* Spain & N.C. Schenck CL551 and *A. colombiana* CL356 (Montoliu-Nerin et al. 2021); transcriptome available for *A. morrowiae* INVAM CR315B (Beaudet et al. 2018). Among the 66 species described, 51 have molecular data available in NCBI (e.g., SSU–ITS–LSU, *rpb1*, β*tub2*, *αtub2*, Chitin Synthase, Transcription Factor Ste12, Heat–Shock Protein 60 and Group I Intron (IGI) from the Cytochrome Oxidase 1 – COX1 gene).

Acaulospora Gerd. & Trappe, Mycologia Memoir 5:31–33 (1974)
≡*Kuklospora* Oehl & Sieverd., Journal of Applied Botany 80:74 (2006)
Index Fungorum Identifier 20003

As in *Acaulosporaceae* description.

Type species – *Acaulospora laevis* Gerd. & Trappe, Mycologia Memoir 5:33–34 (1974)

Notes – As in the *Acaulosporaceae*.

Diversisporaceae C. Walker & A. Schüßler emend. Oehl, G.A. Silva & Sieverd., Mycotaxon 116: 108 (2011); Fig. 44
Index Fungorum Identifier 82125

Diversisporaceae comprises species producing glomoid, otosporoid or tricisporoid spores. Glomoid spores are produced terminally on a subtending hypha, singularly, in small or large loose clusters or in compact epigeous and sub-hypogeous unorganized and irregular glomerocarps, containing hundreds to thousands of glomerospores, covered or not by a peridium. Glomoid spores are globose, subglobose, irregular, ovoid or ellipsoid, consisting of one wall (spore wall (sw)), including one to rarely four layers (swl1–4), that are genus and species-specific. The subtending hyphae are straight, cylindrical to funnel-shaped, and inflated or constricted at the spore base. Pore open or most frequently occluded by a conspicuous septum that arises from swl2–3. According to Oehl et al. (2011 b, c), spores that form terminally on subtending hyphae with a wall that is not entirely continuous with the hyphal mycelia wall, and whose inner wall layers form a septum at or a short distance from the base of the spore within the subtending hyphae, are referred to as a "diversisporoid" morph (typical of *Diversispora* and *Redeckera*). Otosporoid glomerospores are formed laterally on the persistent neck of a terminal or intercalary sporiferous saccule at some distance from the saccule terminus. They are singly in soil, globose, subglobose to rarely ovoid or irregular, consisting of two multiple-layered walls. Mycelial hyphae hyaline with an evanescent outer layer and an inner layer continuous with swl3 of the saccule stalk and the spore wall. Pore generally occluded by a plug-like septum arising directly at the spore base from the laminate swl3 and adherent to a thin swl4, resembling a ring or a cicatrix, being connected to the persistent saccule stalk. Tricisporoid spores are formed within the hyphal neck of a tightly attached terminal or intercalary sporiferous saccule, closely attached to the saccule terminus, often smaller than the mature spores attached. They have an outer and an inner wall, both multi-layered, and two cicatrices formed by the outer pigmented structural spore wall layer.

Family type – *Diversispora* C. Walker & A. Schüßler emend. Tedersoo & Magurno, Mycokeys 107:249-271 (2024)

Notes – Establishment of *Diversisporaceae* originated from the separation of the clade *Glomus* group C (*Glomus sensu lato*) as suggested by Schüßler et al. (2001). Using SSU nrDNA sequences, Schwarzott et al. (2001) pointed out that a new family (current *Diversisporaceae*) was needed to accommodate the species *Glomus versiforme*, *G. spurcum* and a species morphologically similar to *G. etunicatum*. These species, till then classified in *Glomeraceae*, were grouped in a monophyletic clade with the *Acaulosporaceae* and *Gigasporaceae* families. Schüßler et al. (2001) proposed a new order, *Diversisporales*, comprising *Acaulosporaceae*, *Gigasporaceae* and *Diversisporaceae*, but this order was not validly published. Walker & Schüßler (2004) validated *Diversisporales* and *Diversisporaceae* and proposed *Diversispora*, with *D. spurca* (=*G. spurcum*) designated as a generic type. Based on morphological evidence and SSU sequences, Palenzuela et al. (2008) introduced *Otospora* with the type species *O. bareai*, phylogenetically close to the *D. spurca* clade. Considering the formation of large glomerocarps with peridium and molecular evidence of the SSU–ITS–LSU nrDNA segment, Schüßler & Walker (2010) enriched *Diversisporaceae* with the genus *Redeckera*, with the type *R. megalocarpa* (basionym = *G. megalocarpum*), *R. fulvum* (basionym: *G. fulvum*) and *R. pulvinate* (basionym = *G. pulvinatum*). Oehl et al. (2011c) described *Tricispora*, transferring *Entrophospora nevadensis* to *T. nevadensis*. The validity of *Otospora* and *Tricispora* was questioned by Redecker et al. (2013) due to the quality of the material studied and the phylogenetic position among *Diversispora* species (Fig. 46).

Tedersoo et al. (2024), based on a wide dataset-based phylogenetic analysis, transferred *Otospora bareai* and *Tricispora nevadensis* to *Diversispora*. Over time, three more genera were included in *Diversisporaceae*, relying on analysis of the partial SSU–ITS–LSU region: *Corymbiglomus*, to accommodate *C. corymbiformis* (basionym = *Glomus corymbiformis*), *C. globiferum* (basionym = *G. globiferum*) and *C. tortuosum* (basionym = *G. tortuosum*) (Błaszkowski & Chwat 2013); *Sieverdingia*, where *C. tortuosum* was later transferred by Błaszkowski et al. (2019a); and *Desertispora* (Symanczik et al. 2018), where *Diversispora omaniana* was moved as a result of its partial 45S and *rpb1* phylogeny. Five genera and 41 species are accepted in *Diversisporaceae*, making it the third most representative family in terms of species richness of the *Glomeromycota*. Analysis of Tedersoo et al. (2024) based on a large dataset of eDNA ribosomal sequences enlarged the family with two potential new genera and, at the same time, pointed out possible incongruencies for *Redeckera* and *Corymbiglomus*.

The geographic distribution of *Diversisporaceae* encompasses at least 52 countries from different continents and conditions. *Diversisporaceae* species certainly play an important role in ecosystem productivity because of their common occurrence and wide distribution. Experiments conducted with *Diversispora* spp. and *S. tortuosa* showed an enhancement of heavy metals immobilization in polluted soils and a reduced transfer from root to shoots of the host plants (Liu et al. 2017, Li et al. 2022). Furthermore, other experiments showed an improved photosynthetic capacity of the hosts under salt stress conditions, probably due to better nutrient uptake and secretion of substances stimulating chloroplast development (Zhang et al. 2016, Xu et al. 2018).

Genome available for *D. epigaea* (B.A. Daniels & Trappe) C. Walker & A. Schüßler IT104 and *D. eburnea* (L.J. Kenn. et al.) C. Walker & A. Schüßler AZ414A (Sun et al. 2019b, Montoliu-Nerin et al. 2021); transcriptome available for *D. epigaea* (B.A. Daniels & Trappe) C. Walker & A. Schüßler INVAM W475–40 (Beaudet et al. 2018).

Diversispora C. Walker & A. Schüßler emend. Tedersoo & Magurno, Mycokeys 107:249-271 (2024)

Index Fungorum Identifier 28884

Glomerospores formed singly in soils, in small or large loose clusters or in compact epigeous and sub-hypogeous unorganized glomerocarps. Glomerospores arise blastically at the tip of sporogenous hyphae with one wall (glomoid) or laterally from sporiferous saccule with two walls (otosporoid) or intercalarly in the neck of sporiferous saccule with two walls (tricisporoid). Glomoid spores are globose, subglobose, irregular or ellipsoid, consisting of one wall (sw) with two to four layers (swl1–4). Swl1 might range from hyaline to deep yellow or yellowish brown, evanescent, flexible to semiflexible, smooth, permanent or short-lived, rarely ornamented, except for *D. pustulata* and *D. trimulares*, which exhibit blister-like outgrowths unevenly distributed on the spore surface. Swl2 can be hyaline, yellowish white to brownish red, laminate, flexible to semi-flexible, smooth and generally permanent. Swl3 is hyaline to pale or grayish yellow, laminate, flexible to semi-flexible, smooth, and usually tightly adherent to the lower surface of swl2. Rarely present, swl4 can be hyaline, flexible, permanent, uniform and loosely associated with the lower surface of swl3. Swl1–4 do not react in Melzer's reagent, except for *D. clara,* in which swl1–2 generally turn light to dark yellow. The single subtending hyphae is hyaline, yellowish white to brownish yellow, straight or recurved, cylindrical to funnel-shaped, sometimes slightly constricted at the spore base. Pore open or occluded by thickening of the subtending hyphal wall or by a straight or slightly invaginated septum continuous with swl2 or swl3. Glomerocarps are globose to subglobose or ovoid, grayish orange to light brown, covered or not by a peridium. Peridium thin, hyaline to pale yellow, only partially covering spore conglomerations.

Type species – *Diversispora spurca* (C.M. Pfeiff. et al.) C. Walker & A. Schüßler, Mycol. Res. 108 (9): 982 (2004)

Basionym = *Glomus spurcum* C.M. Pfeiff., C. Walker & Bloss 1996

Notes – *Diversispora,* typified by *D. spurca*, was erected by Walker & Schüßler (2004) mainly based on molecular phylogenetic analyses of SSU nrDNA sequences. The authors concluded that *Glomus spurcum* (Pfeiffer et al. 1996) was unrelated to *Glomeraceae* and instead represented a distinct genus-level lineage within the newly established family *Diversisporaceae* (Schüßler et al. 2001, Walker & Schüßler 2004). Later, Gamper et al. (2009) introduced *D. celata*, which is phylogenetically (based on SSU, ITS and LSU loci) close with *D. spurca* and with species recognized in *Glomus* (*G. versiforme, G. aurantium, G. eburneum*). Based on molecular phylogeny, Schüßler & Walker (2010) transferred four species of *Glomus* to *Diversispora* (*D. epigaea*, *D. eburnea*, *D. aurantia, D. trimurales*). Subsequently, Oehl et al. (2011b), incorporated seven additional *Glomus* species into *Diversispora* (*D. arenaria, D. gibbosa, D. insculpta, D. przelewicensis, D. pustulata, D. tenera, D. versiformis*), relying on both morphology of the spore base and subtending hypha, as well as molecular phylogeny. However, *D. versiformis*, originally described as *Endogone versiformis* (Karsten 1884) and later as *G. versiforme*, must be considered as a species of uncertain position in *Glomus sensu lato* because the available molecular data actually belonged to the wrongly synonymized species *G. epigaeum* BEG47 (currently *D. epigaea*) (Schüßler et al. 2011). Over time, new species have been described in the genus (Estrada et al. 2011, Symanczik et al. 2014, Błaszkowski et al. 2015a, 2022a, Balázs et al. 2015, Jobim et al. 2019, Guillén et al. 2020a, Lebeuf et al. 2023, Crossay et al. 2024, Niezgoda et al. 2024), with 27 species currently recognized based on molecular sequences (SSU–ITS–LSU, *rpb1*), and three species (*D. tenera, D. pustulata*, *D. przelewicensis*) supported solely by morphological characters of the glomerospores (Oehl et al. 2011b). Molecular inventories have shown numerous Operational Taxonomic Units (OTUs) belonging to undescribed species of this genus (Krüger et al. 2015, Islam et al. 2021). Based on the phylogenetic position of *Otospora bareai* and *Tricispora nevadensis* inside the *Diversispora* clade, Tedersoo et al. (2024) transferred both species with distinctive spore development (otosporoid and tricisporoid) to *Diversispora,* a genus whose species presented only glomoid spores. Thus, *Diversispora* presents distinct spore development such as in *Entrophosporales*.

Diversispora spp. are reported from tropical, subtropical and temperate terrestrial ecosystems (Posada et al. 2016, De Assis et al. 2018, Guillén et al. 2020a, Maazouzi et al. 2020) to lentic and lotic aquatic ecosystems (Kennedy et al. 2002, Moora et al. 2016). Some species currently have a distribution restricted to the type location (e.g., *D. insculpta, D. jakucsiae*, *D. peridiata*, *D. peloponnesiaca, D. sabulosa, D. slowinskiensis, D. valentina*), whereas *D. aurantia*, *D. celata*, *D. eburnea* and *D. spurca* extend the genus distribution to over 40 countries on different continents. Eighteen of the 30 currently recognized species in *Diversispora*, were originally discovered in sand dunes, especially in Poland (*D. aestuarii, D. arenaria*, *D. densissima*, *D. gibbosa*, *D. insculpta*, *D. marina, D. peridiata, D. slowinskiensis*, *D. vistulana*), Spain (*D. clara*, *D. valentina*), USA (*D. pustulata, D. trimurales*), Cuba (*D. varaderana*), Greece (*D. peloponnesiaca*), Hungary (*D. jakucsiae*), Israel (*D. aurantia*), and Lithuania (*D. sabulosa*). Other *Diversispora* species are also frequent and abundant in dune ecosystems (Yamato et al. 2012, Estrada et al. 2013, Dalpé et al. 2016).

Diversispora spp. can improve water and nutritional support, and relieve abiotic and biotic stresses of their plant hosts (Begum et al. 2019). Experimental research showed that *D. spurca* promoted growth and freeze tolerance of crested wheatgrass (Otgonsuren & Lee 2011) and ameliorated the effects of waterlogging on the growth, root system architecture and antioxidant enzyme activities of citrus plants (Wu et al. 2013). Furthermore, *D. epigaea* enhanced phosphorus use efficiency in sweet basil (Shabani et al. 2019) and promoted *Phragmites* growth in heavy cadmium pollution soil (Li et al. 2022). Due to the characteristic formation of epigeous glomerocarps (Jobim et al. 2019), *D. epigaea* was one of the earliest AMF species used in cytochemical, biochemical and molecular studies (Bonfante-Fasolo & Grippiolo 1984, Harrison & van Buuren 1995).

Other genera in *Diversisporaceae*

Corymbiglomus Błaszk. & Chwat, *Glomeromycota* (Kraków): 272 (2012)

Index Fungorum Identifier 564566; Index Fungorum (2025) lists four epithets, and Species Fungorum (2025) lists two species; DNA sequences available.

Type species – *Corymbiglomus corymbiforme* Błaszk. & Chwat 2012

Desertispora Błaszk., Kozłowska, Ryszka, Al-Yahya'ei & Symanczik, Mycol. Prog. 17(4): 444 (2018)

Index Fungorum Identifier 823563; Index Fungorum (2025) and Species Fungorum (2025) list only one epithet; DNA sequences available.

Type species – *Desertispora omaniana* (Symanczik et al.) Symanczik et al. 2018

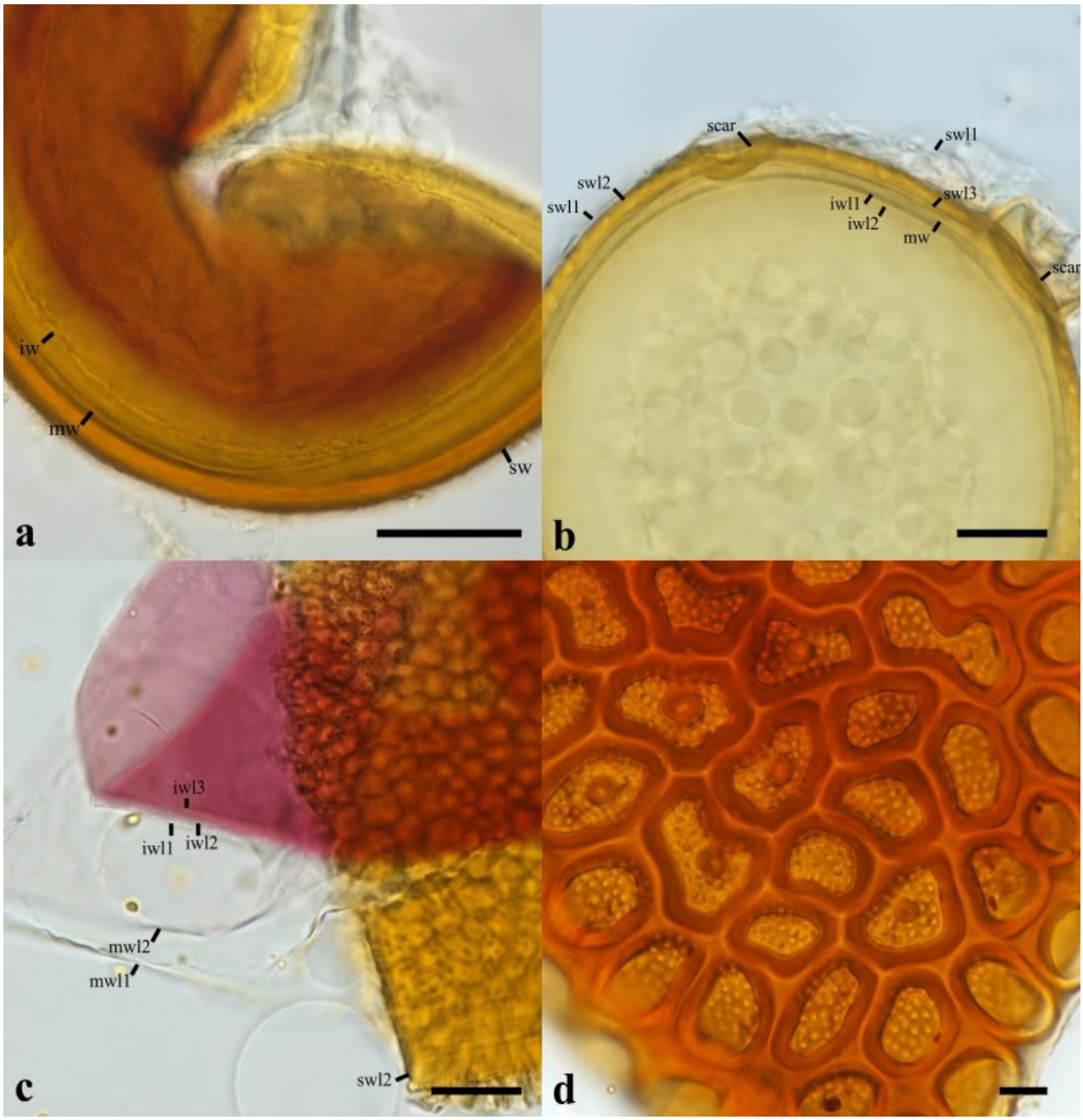


Figure 43 – *Acaulosporaceae*. a Acaulosporoid spore with three walls (sw, mw, iw). b Kuklosporoid spore produced by *A. kentinensis* with two scars and three walls. c Typical spore of *A. elegans* with three walls, and a "beaded" layer in the inner wall (iwl1). d Ornamentation pattern

of an undescribed *Acaulospora* species showing two ornamentation types in the outer spore wall. Scale bars: a = 20 µm, b–c = 10 µm, d = 5 µm.

Redeckera C. Walker & A. Schüßler, The *Glomeromycota*, A species list with new families and new genera (Gloucester): 44 (2010)
Index Fungorum Identifier 542402; Index Fungorum (2025) and Species Fungorum (2023) list six species; DNA sequences available for 3 species.

Type species – *Redeckera megalocarpa* (D. Redecker) C. Walker & A. Schüßler 2010

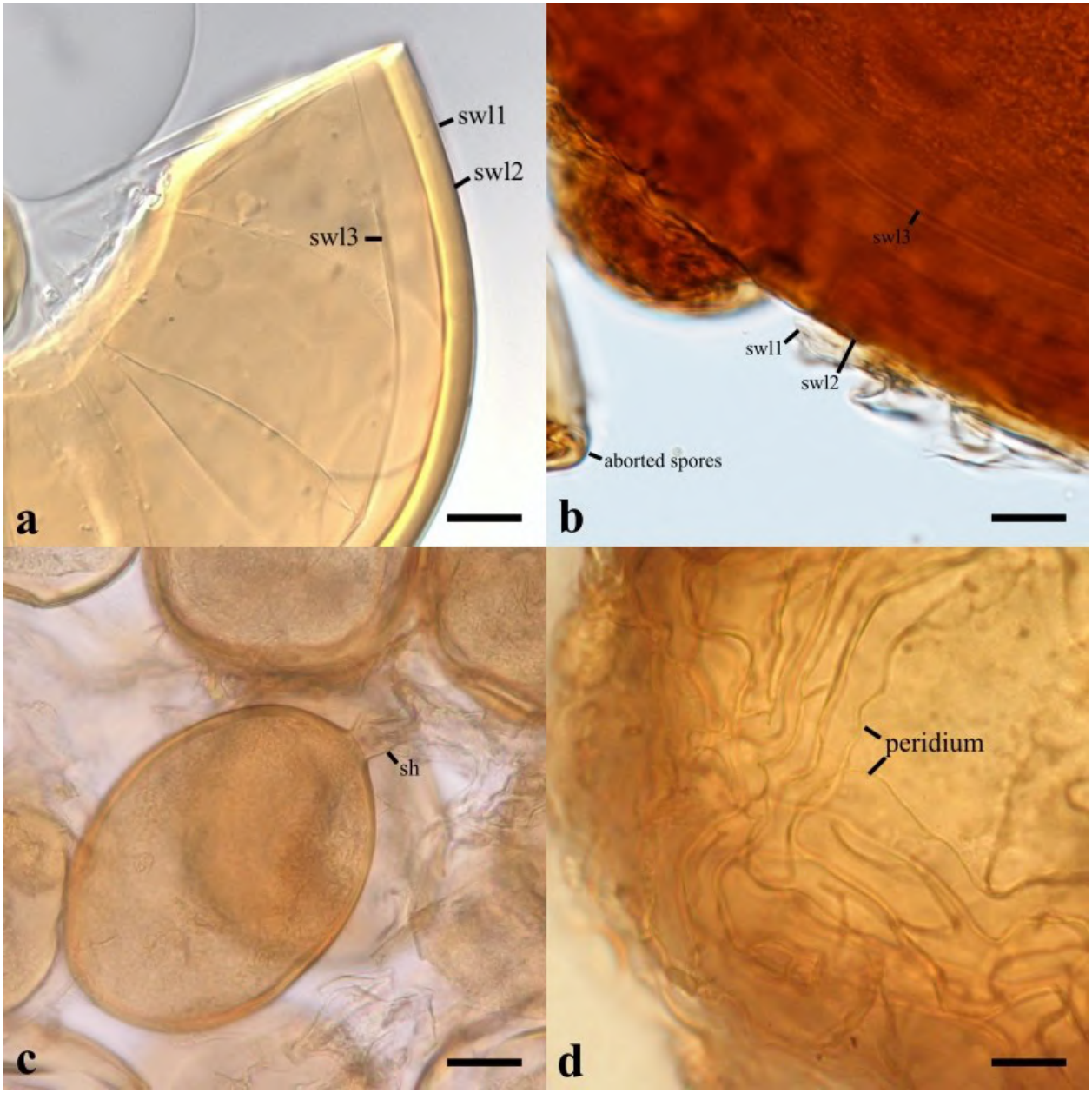


Figure 44 – *Diversisporaceae*. a *Diversispora* sp. with three layers in the spore wall (swl1–3) (courtesy of E. Furrazola). b *Corymbiglomus globiferum* with three layers on the spore wall (swl1–3) and aborted spores attached to the peridium surrounding spore. c Spore inside the glomerocarp of *Redeckera fulvum*. d Hyphae of peridium surrounding the spores of *Sieverdingia tortuosa*. Scale bars: a = 20 µm, b–d = 10 µm.

Sieverdingia Błaszk., Niezgoda & B.T. Goto, Mycol. Prog. 18(11): 1368 (2019)

Index Fungorum Identifier 832298; Index Fungorum (2025) and Species Fungorum (2025) list only one epithet; DNA sequences available.

Type species – *Sieverdingia tortuosa* (N.C. Schenck & G.S. Sm.) Błaszk., Niezgoda & B.T. Goto 2019

Pacisporaceae C. Walker, Błaszk., A. Schüßler & Schwarzott, in Walker & Schüßler, Mycol. Res. 108(9): 981 (2004); Fig. 45

Index Fungorum Identifier 82126

The family was introduced by Walker & Schüßler (2004) to accommodate pacisporoid species, which (i) produce glomoid spores with two, three-layered spore walls formed *de novo* (independently from each other) during the spore development, (ii) have an inner wall with amyloid properties, (iii) could form a germination shield (orb) on the upper surface of the inner wall. Spores ornamented with projections on the outer wall (*P. scintillans, P. dominikii, P. chimonobambusae, P. coralloidea*) or without ornamentation (*P. robigina, P. franciscana, P. patagonica*). The presence of orbs was found only in *P. scintillans* and *P. franciscana* (Oehl & Sieverding 2004, Błaszkowski 2012). Intra- and extraradical structures stain intensively in trypan blue. Cultures established from single spores showed that *P. scintillans* forms auxiliary cells morphologically resembling those of species of the genus *Scutellospora* (Błaszkowski 2012). Species of *Pacispora* are the only ones reported to form both structures - intraradical vesicles and extraradical auxiliary cells - in their mycelia (Błaszkowski 2012).

Family type – *Pacispora* Sieverd. & Oehl, Journal of Applied Botany and Food Quality, Angew. Bot. 78: 74 (2004)

Notes – *Pacisporaceae* was introduced by Walker & Schüßler (2004) to override the invalid name *Gerdemanniaceae* (Walker et al. 2004). Initially, Oehl & Sieverding (2004) introduced *Pacispora* in *Glomeraceae* to accommodate four new species (*P. franciscana, P. robigina, P. coralloidea, P. boliviana*) and three species previously described in *Glomus* (*G. scintillans*, *G. dominikii* and *G. chimonobambusae*), designating *P. scintillans* as the type species. This proposal was based only on morphology of the spore wall and the germinal shield (orb), a specialized structure associated with germination not previously detected in other glomoid-like spores. Concurrently, Walker et al. (2004), using SSU rDNA sequences, described *Gerdemannia* in the new family *Gerdemanniaceae*, based on the same type species *G. scintillans*. The paper by Oehl & Sieverding (2004) was effectively published a few days earlier, and therefore *Gerdemannia* has been determined to be a later homotypic synonym of *Pacispora*. As a consequence, the name *Gerdemanniaceae* was also considered illegitimate and a new family name, *Pacisporaceae*, was introduced (Walker & Schüßler 2004). Sequences of *P. franciscana* obtained later confirmed its phylogenetic position within the genus (Krüger et al. 2012). Mello et al. (2013), based on phylogenetic nrDNA analyses, transferred *P. boliviana* to *Paraglomus*. Currently, *Pacisporaceae* presents one genus with seven species, but only *P. franciscana* and *P. scintillans* possess molecular data.

Walker et al. (2004) analysis showed *Pacisporaceae* as a sister clade to *Gigasporales*, whose members also produce spores with inner wall(s) and germination shields. Another characteristic shared by pacisporoid and gigasporoid species is the formation of extraradical auxiliary cells (Błaszkowski 2012). Furthermore, analysis conducted using partial SSU–ITS–LSU sequences confirmed the phylogenetic placement as a sister clade to *Gigasporales*, even though it is weakly supported. Therefore, the current affiliation of *Pacisporaceae* to *Diversisporales sensu* Oehl et al. should be considered uncertain, requiring further investigation.

Members of the family are distributed worldwide, including countries in tropical, temperate and mediterranean regions, such as Argentina, Australia, Bolivia, Brazil, China, Ecuador, Ethiopia, Germany, India, Mexico, Morocco, Poland, Portugal, Spain, Switzerland, Taiwan and USA (Mello et al. 2013, Soteras et al. 2015, Yang et al. 2016, Melo et al. 2019, Garo et al. 2022, de Valgaz et al. 2022, Senapati et al. 2024). Nevertheless, many occurrences were detected solely according to identification by morphological analysis, therefore requiring confirmation.

Pacispora Sieverd. & Oehl, Journal of Applied Botany and Food Quality, Angew. Bot. 78: 74 (2004)

Index Fungorum Identifier 28842

As in *Pacisporaceae* description.

Type species – *Pacispora scintillans* (S.L. Rose & Trappe) Sieverd. & Oehl ex. C. Walker, Vestberg & A. Schüßler, Mycol. Res. 111(3): 255 (2007)

Basionym = *Glomus scintillans* S.L. Rose & Trappe, Mycotaxon 10(2): 417 (1980)

Notes – As in *Pacisporaceae* notes.

Sacculosporaceae Oehl, Sieverd., G.A. Silva, B.T. Goto, Sánchez-Castro & Palenz. Mycotaxon 117: 310 (2011); Fig. 46

Index Fungorum Identifier 561645

According to Oehl et al. (2011c), the diagnostic morphological features of members of *Sacculosporaceae* are spores which (i) arise inside the neck of closely adherent terminal or intercalary sporiferous saccules, (ii) have three spore walls, with the middle and inner walls formed *de novo*, and the outer wall surrounded by hyphal peridium (Błaszkowski et al. 1998), (iii) have two, often opposite, cicatrices that are closed by sublayers of the permanent structural layer of the outer wall after the detachment of the saccule from the spore, (iv) have no ornamentation on the upper surface of the outermost layer of the inner wall, and (v) do not react in Melzer's reagent. Germination is unknown.

Family type – *Sacculospora* Oehl et al., Mycotaxon 117: 311 (2011)

Notes – Based on molecular and morphological evidence, this family was introduced to accommodate *Sacculospora* (previously accommodated in *Entrophosporaceae*) from sand dunes of Poland (Oehl et al. 2011c). *Sacculospora baltica* differs from other entrophosporoid species in the formation of a hyphal mantle and structure of the outer and inner spore walls (Błaszkowski et al. 1998, Oehl et al. 2011c). Currently, *Sacculospora* also contains *S. felinovii*, originating from India, with distinguishing phenotypic and histochemical features of components of the spore walls, and phylogeny (Willis et al. 2016). Members of the family are distributed among countries in tropical and temperate regions: Brazil, Chile, Mexico, Poland, Spain, Switzerland, and India.

Sacculospora Oehl, Sieverd., G.A. Silva, B.T. Goto, Sánchez-Castro & Palenz. Mycotaxon 117: 311 (2011)

Index Fungorum Identifier 561646

As in *Sacculosporaceae* description.

Type species – *Sacculospora baltica* (Błaszk. et al.) Oehl et al., Mycotaxon 117: 311 (2011)

Notes – As in the *Sacculosporaceae* notes.

Entrophosporales Błaszk., Sánchez-García, B.T. Goto & Magurno

Entrophosporaceae (Oehl & Sieverd.), **emend**. Błaszk., Sánchez-García, B.T. Goto & Magurno; Fig. 47

Index Fungorum Identifier 521877

= *Claroideoglomeraceae* C. Walker & A. Schüßler. The *Glomeromycota* – a species list: 21.2010

Originally described by Sieverding & Oehl (2006), the family is characterized by producing entrophosporoid and glomoid spores, or just one of these morphs. Entrophosporoid spores have two spore walls, with only one persistent scar proximal to the spore saccule. Glomoid spores are formed at the tips of branching sporogenic hyphae of the wall of the sporiferous saccule and/or the neck of the sporiferous saccule of the entrophosporoid morph or continuous with extraradical mycorrhizal hyphae, occasionally interspersed within the hyphae. Extraradical spores produced singly, rarely in clusters with few spores. Spores with one spore wall consisting of two to five layers. One or two layers can stain in Melzer's reagent (Błaszkowski et al. 2022b). Entrophosporoid and glomoid

species produce mycorrhiza with arbuscles, vesicles, as well as intra- and extraradical hyphae staining dark in Trypan blue (Błaszkowski et al. 2022b).

Family Type – *Entrophospora* R.N. Ames & R.W. Schneid., **emend**. Błaszk., Sánchez-García, B.T. Goto & Magurno

Notes – In early taxonomic studies, genera of arbuscular mycorrhizal fungi were defined/established based on the mode of spore development/formation (Gerdemann & Trappe 1974). Even today, the mode of spore development remains a precious morphological criterium for the identification of AMF genera and species, especially when information about the number and types of wall layers is available. There are a few fungi described with entrophosporoid development. This mode was described to accommodate a species previously described as *Glomus infrequens* (Ames & Schneider 1979) after the revision of *Endogonaceae* (Gerdemann & Trappe 1974). *Entrophosporaceae* was introduced by Sieverding & Oehl (2006) based on morphology of two species: *E. infrequens* (Ames & Schneider 1979), the type species, and *E. baltica* (Błaszkowski et al. 1998). Other species, previously recognized as *Entrophospora*, were transferred to two new genera and accommodated in different orders of *Glomeromycota* (*Intraspora* was introduced to accommodate *E. schenckii* in *Archaeosporaceae – Archaeosporales* (see *Archaeosporaceae*), while *Kuklospora* was introduced to accommodate *E. colombiana* and *E. kentinensis* in *Acaulosporaceae – Diversisporales*). Originally, *Entrophosporaceae* was described based on (i) spores with two walls; (ii) the absence of a beaded wall; (iii) having a relatively thick inner wall and (iv) the presence of a plug at the point of insertion of the proximal hypha of the spore saccule. The phylogenetic data supported the description of the new family and clearly showed that *Entrophospora* does not belong to *Acaulosporaceae* as previously assumed because of the development of spores from a sporiferous saccule. Later, *Entrophosporaceae* and *Entrophospora* were recognized as taxa of uncertain systematic position in the order *Diversisporales*, *Kuklospora* synonymized with *Acaulospora* (da Silva et al. 2022), and *I. schenckii* was transferred to *Archaeospora* as *A. schenckii* (Schüßler & Walker 2010).

Schüßler & Walker (2010) introduced *Claroideoglomeraceae* with *Claroideoglomus* into *Glomerales*. The type species of *Claroideoglomeraceae* was *C. claroideum* (Schüßler & Walker 2010), originally described as *Glomus claroideum* (Schenck & Smith 1982). Oehl et al. (2011c) synonymized *Claroideoglomeraceae* with *Entrophosporaceae* based on phylogenetic analyses of sequences of *E. infrequens*, three species of *Claroideoglomus*, other representatives of *Glomerales*, and members of other families of *Glomeromycota*. *Claroideoglomus* remained in *Entrophosporaceae*, and *Entrophospora* with *E. infrequens* became the type species of this family. The same analyses also transferred *C. drummondii* and *C. walkeri* to the new genus *Albahypha*. Furthermore, *Glomus viscosum* was accommodated in a new genus, *Viscospora*, in *Entrophosporaceae*. *Entrophospora baltica* was accommodated in the new family *Sacculosporaceae* in *Diversisporales*, as *S. baltica*. Thus, *Entrophosporaceae* comprises four genera: *Albahypha*, *Claroideoglomus*, *Viscospora* and *Entrophospora*.

Redecker et al. (2013) rejected the family and two genera *Albahypha* and *Viscospora*, retaining *Claroideoglomeraceae*, transferring *Viscospora viscosa* to *Septoglomus viscosum* in *Glomeraceae* and returned *Entrophospora* to "as of uncertain position". The family was revised and reinstated later by Błaszkowski et al. (2022b) with the erection of a new order, *Entrophosporales*, where *Entrophosporaceae* was accommodated. Furthermore, *Albahypha* was not supported by the analysis of Błaszkowski et al. (2022b) and the dimorphic nature of *Entrophospora*/*Claroideoglomus* was proven after obtaining a culture producing both glomoid- and entrophosporoid- morphs, rendering the two genera synonyms. Currently, this family has only one genus with twelve species.

Genome available for *Entrophospora lutea* SA01 and *Entrophospora candida* NC172, NC268 (Montoliu-Nerin et al. 2020, 2021); transcriptome available for *Entrophospora claroidea* DAOM 234280 (Beaudet et al. 2018).

Entrophospora R.N. Ames & R.W. Schneid., Mycotaxon 8(2): 347 (1979)

Index Fungorum Identifier 20223

As in the description of *Entrophosporaceae*.

Type species – *Entrophospora infrequens* (I.R. Hall) R.N. Ames & R.W. Schneid., Mycotaxon 8(2): 348 (1979)

≡*Glomus infrequens* I.R. Hall, Trans. Br. Mycol. Soc. 68(3): 345 (1977)

Notes – As in the *Entrophosporaceae* notes.

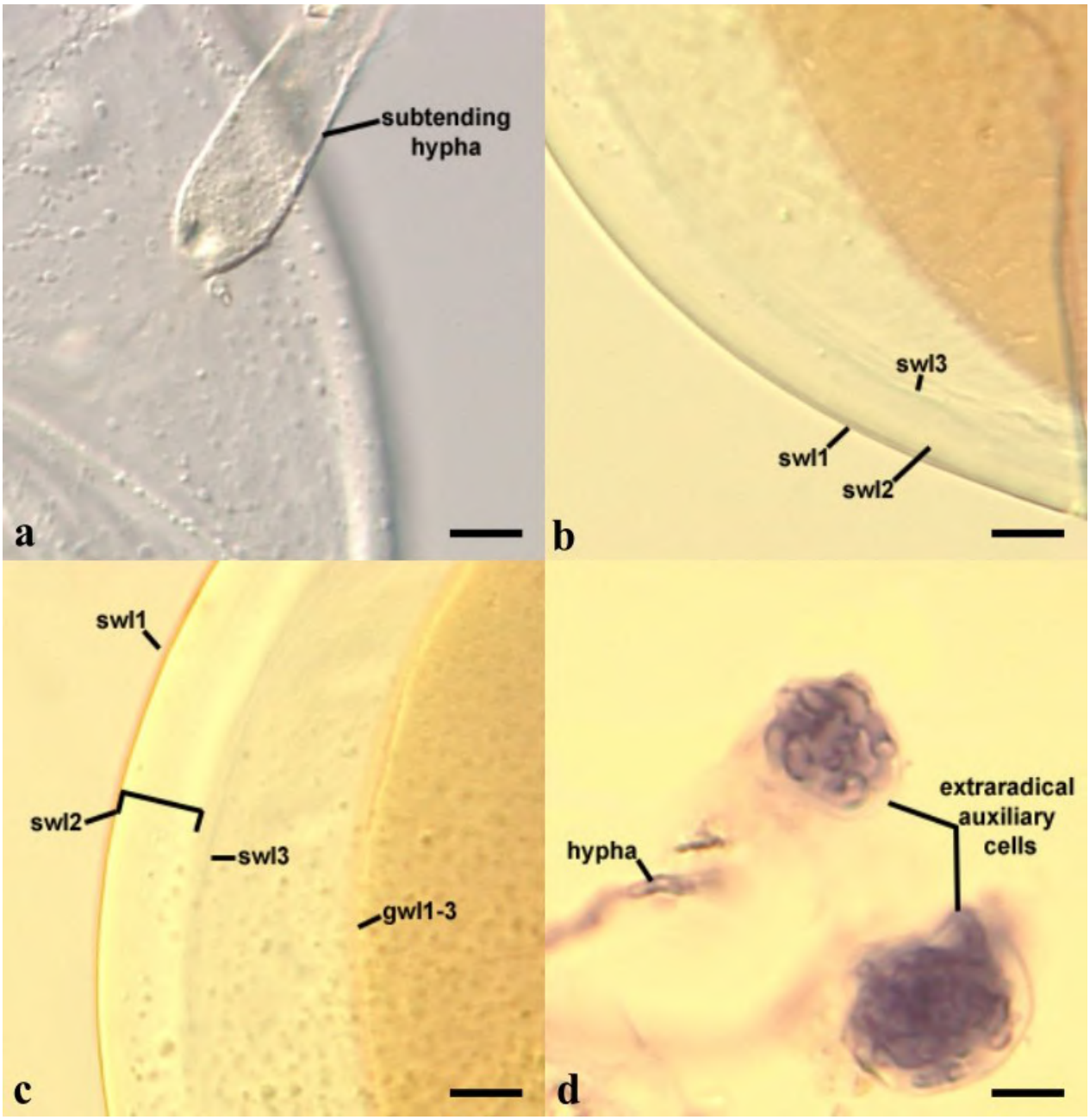


Figure 45 – *Pacisporaceae.* a Spore of *Pacispora scintillans* with subtending hypha. b–c Spore wall with three layers (swl1–3) and inner wall with three layers (gwl1–3) in *P. scintillans*. d Extraradical auxiliary cells formed by *P. scintillans*. Scale bars: a–d = 10 µm.

Gigasporales S.P. Gautam & U.S. Patel

Bulbosporaceae Magurno, F.A. de Souza, N.V.L. Oliveira & B.T. Goto ***fam. nov.***; Fig. 48

MycoBank 856868

Etymology: From Latin *bulbus*, referring to the onion-like, small sporogenous cells at the spore bases used by Marinho et al. (2014) as characteristic to describe the genus *Bulbospora*.

Diagnosis – Differs from other families in *Gigasporales* by the diagnostic small sizes of the spores (<100 µm diam.) and sporogenic cells (<25 µm diam.), and the nucleotide composition of sequences of the LSU nrDNA.

Description – Spores formed singly in soils and rarely in roots on sporogenous cells that arise from small sporogenous hyphae. Spores elliptical, oval to ovoid or subglobose, rarely globose. Spores small, <100 µm diam., with three walls and a germination shield/orb circular to oval, mono-lobed, hyaline to sub-hyaline. Germination shield (orb) formed on the outer surface of the inner wall. Sporogenous cells are subglobose to oblong, <25 µm diam., and generally persist on spores.

Distribution – *Bulbospora minima*, the only known species of the family, was originally found in a semi-arid area of the National Park Vale do Catimbau, Pernambuco State, Brazil (Marinho et al. 2014). Later, *B. minima* was reported occurring in different ecosystems in Brazil (de Pontes et al. 2017, Vieira et al. 2019a, b, Stürmer et al. 2022, da Nóbrega Veras et al. 2024). BLASTn search using the LSU nrDNA sequences available for the species (KJ944321-5) against the nucleotide collection of GenBank resulted in no closely related sequences (Identity <92.0%), suggesting that *B. minima* and *Bulbosporaceae* have a limited range of distribution.

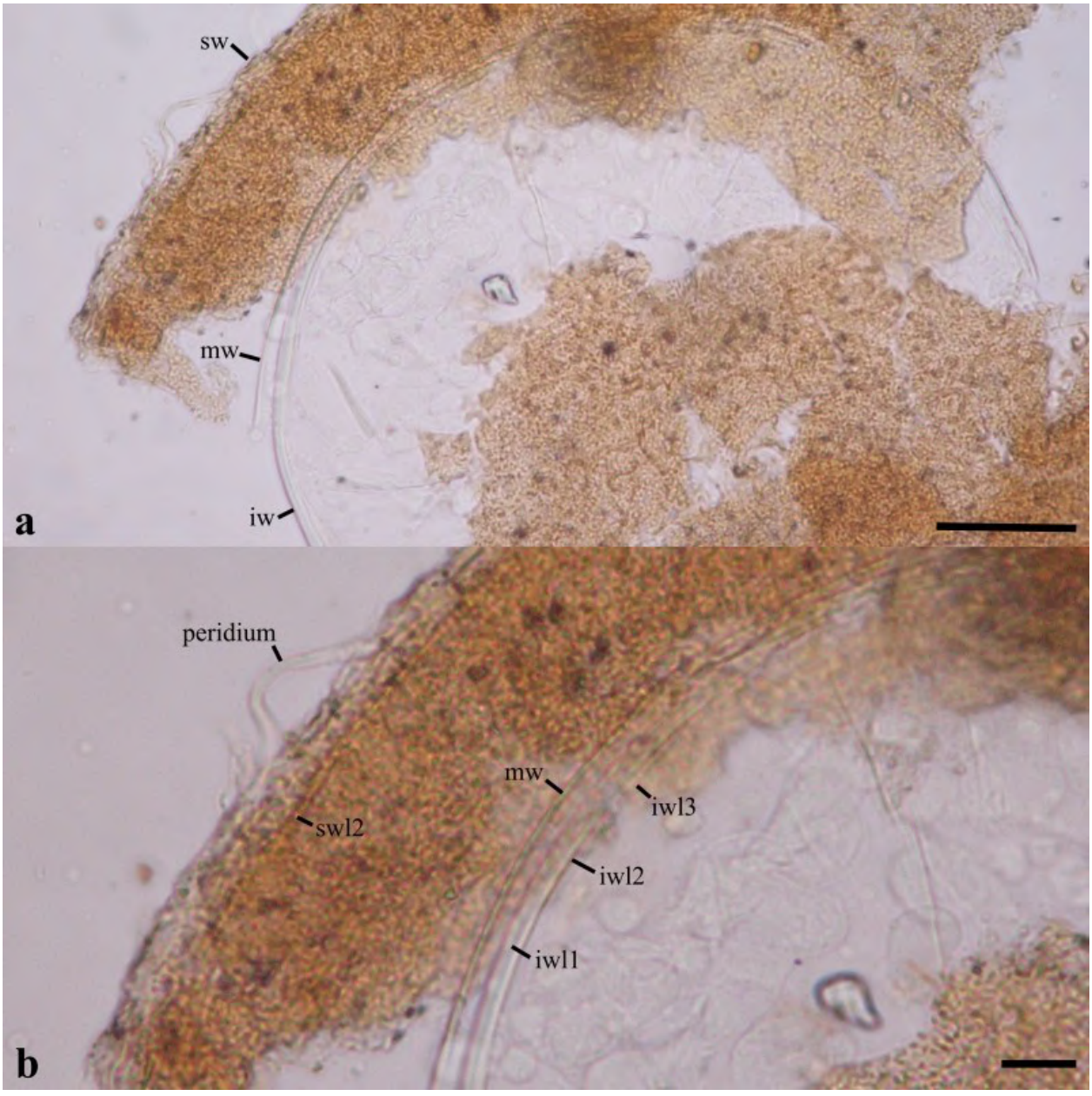


Figure 46 – *Sacculosporaceae.* a *Sacculospora baltica* with three walls (sw, mw, iw). b Spore wall layers of *S. baltica* with three–layered inner wall (iwl1–3) and delicate hyphae of peridium. Scale bars: a = 20 µm, b = 10 µm.

Family type – *Bulbospora* Oehl & G.A. Silva, Sydowia 66(2): 316 (2014)

Notes – Oehl et al. (2008) defined family *Scutellosporaceae* with a single genus *Scutellospora*. Later, *Orbispora* (Oehl et al. 2011d) and *Bulbospora* (Marinho et al. 2014) were included in the family based on newly discovered species. Both *Bulbospora* and *Orbispora* species share three walls and an orbital germinal shield (considered morphologically simplest as compared with other genera in *Gigasporales*), producing only one germ tube (Oehl et al. 2011d, Marinho et al. 2014). *B. minima* differs from *O. pernambucana* (≡ *Scutellospora pernambucana*), the closest relative morphologically by (i) spore size (<100 µm vs. >100 µm) and (ii) Melzer's reaction in the outer spore wall, absent in *O. pernambucana* (Marinho et al. 2014). Based on Marinho et al. (2014), the inclusion of sequences of *Bulbospora* in the phylogeny of *Gigasporales* rendered the family *Scutellosporaceae* not supported. Based on the phylogenetic analyses presented here (Fig. 4) and in Tedersoo et al. (2024, Supplementary material 2), *Bulbospora* does not have any sister relationship neither with the *Scutellosporaceae* clade nor other family clades in *Gigasporales*, therefore, a new family is necessary to accommodate this monospecific genus. *Scutellosporaceae* (*Scutellospora* and *Orbispora*) remain basal in the *Gigasporales* clade.

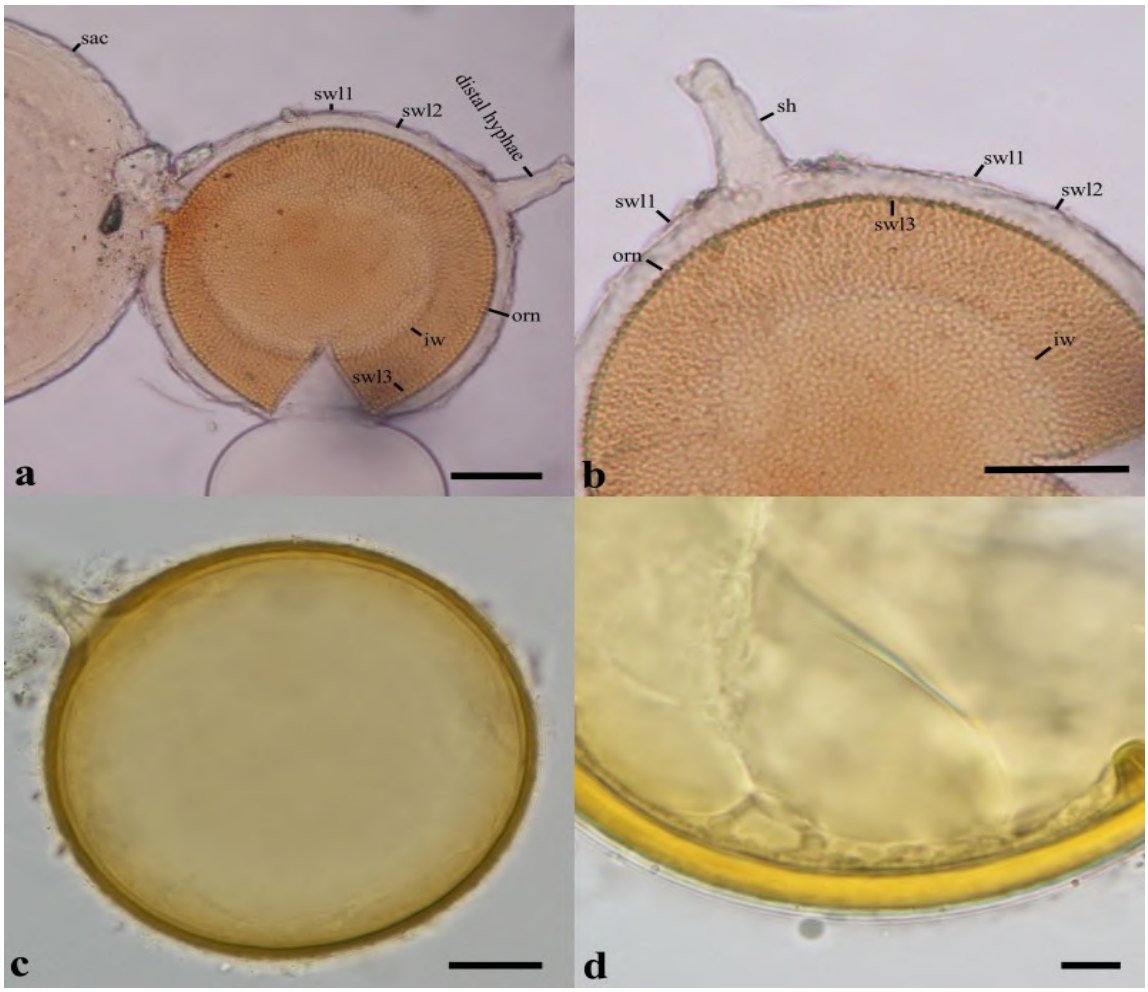


Figure 47 – *Entrophosporaceae.* a *Entrophospora infrequens* with sporiferous saccule (sac), spore wall layers (swl1–3), of which swl3 is ornamented (orn), and inner wall (iw). b Detail of spore wall layers (swl1–3; iw) and subtending hypha (sh) attached. c detail of subtending hypha of glomoid spores of *Entrophospora claroidea.* d Spores wall of *E. claroidea.* Scale bars: a, b, c = 20 µm, d = 10 µm.

Bulbospora Oehl & G.A. Silva, Sydowia 66(2): 316 (2014)
Index Fungorum Identifier 809231

As in *Bulbosporaceae* description.

Type species – *Bulbospora minima* Oehl, Marinho, B.T. Goto & G.A. Silva, Sydowia 66(2): 316 (2014)

Notes – As in *Bulbosporaceae* notes.

Dentiscutataceae Sieverd., F.A. Souza & Oehl, Mycotaxon 106: 340 (2009); Fig. 49
Index Fungorum Identifier 511962

The family was introduced to accommodate 12 species in three genera (*Dentiscutata*, *Fuscutata* and *Quatunica*) supported by morphological evidence (spore wall organization and morphology of the germination shields) and phylogenetic analysis of partial LSU sequences (Oehl et al. 2008). Later, Redecker et al. (2013) transferred *Quatunica erythropus* to *Dentiscutata*, invalidating the genus *Quatunica*. Other changes proposed by Redecker et al. (2013) in *Gigasporales* have been questioned (Wijayawardene et al. 2022, Tedersoo et al. 2024) see Fig. 51. The species in this family are characterized by producing (i) spores with 3 to 4 walls, the outer wall with several layers, one to two middle walls with two layers, and an inner wall with two or three layers, (ii) on the outer surface of the innermost wall a yellow-brown to brown germination shield with distinctive dented edges, which is violin-shaped and has two lobe-like compartments (*Fuscutata*) or is oval or heart-shaped with up to 30 small compartments, and (iii) lobes and compartments separated by folds, with one germ tube initiation each.

Family type – *Dentiscutata* Sieverd., F.A. Souza & Oehl, Mycotaxon 106: 340 (2009)

Notes – *Dentiscutataceae* was originally introduced to accommodate species of an evolutionary lineage formerly classified within the polyphyletic genus *Scutellospora sensu* Walker & Sanders (de Souza et al. 2005a, Oehl et al. 2008). The species produced large spores having two (e. g. *Dentiscutata* and *Fuscutata*) to three (e. g. *Quatunica*) inner walls and a pigmented germinal shield (Oehl et al. 2008). Oehl's et al. (2008) decision was based on phylogenetic analysis of partial sequences of LSU nrDNA and distinctive morphological characteristics to genus-level identification, this probably made the support of the three genera unconvincing. Later, this family received some criticism (Msiska & Morton 2009, Redecker et al. 2013). See Wijayawardene et al. (2022) for a detailed discussion of the *Gigasporales* phylogeny. However, the clade introduced as a family by Oehl et al. (2008) was accepted as a genus by Redecker et al. (2013). A recent analysis using environmental sequences supported *Dentiscutataceae* as a family clade (Tedersoo et al. 2024). It is important to stress that the three genera originally recognized in the family *Dentiscutataceae* have clear morphological characteristics to differentiate them (Oehl et al. 2008). Only *Intraornatosporaceae* (with *Intraornatospora* and *Paradentiscutata*) contains species with similar, dark-pigmented germinal shields, but the shields have no dentated edge. Moreover, the spore wall of these species has introverted ornamentation, so far not reported in members of *Dentiscutataceae* (Goto et al. 2012). Further analyses, using not yet sequenced species and additional gene markers, will help to clarify the phylogeny of this family and the generic clades' support. The last species described in the family were *Dentiscutata colliculosa* B.T. Goto & Oehl and *Fuscutata aurea* Oehl et al., both from Brazil (Goto et al. 2010a, Mello et al. 2012), suggesting tropical occurrence with several other species recorded in South America and Africa (Spain et al. 1989, Walker & Diederichs 1989, Spain & Miranda 1996, Tchabi et al. 2008, 2009, Goto et al. 2010a, b, Mello et al. 2012, Polo-Marcial et al. 2021, 2022). Robin-Soriano et al. (2024), carrying out a large inventory of glomeromycotean fungi in a hot desert region in northwestern Saudi Arabia, did not detect *Gigasporales* using metabarcoding and spore extraction approaches in both soil and roots. Besides, *Gigasporales* communities in maritime sand dunes are abundant and diverse (Jobim et al. 2016, da Silva et al. 2017, Stürmer et al. 2018).

Few species of *Dentiscutataceae* have been used in plant growth promotion tests. *Fuscutata heterogama* has shown a potential to promote the growth of plants of economic interest and to increase plant tolerance to nematode attacks (Silva et al. 2004, Anjos et al. 2010). Despite advances in genetic studies, there is only one report of albinism in the phylum *Glomeromycota* for *F. heterogama* (Almeida & Schenck 1990). Phylogenetic analysis showed that an albino isolate cultured at INVAM for more than 10 years has sequences matching those of *F. heterogama*, proving that the pigmentation of spores is not a useful diagnostic criterion for this species (Morton & Msiska 2010a).

Genome available for *F. heterogama* IL203A and *Dentiscutata erythropa* MA453B (Montoliu-Nerin et al. 2021).

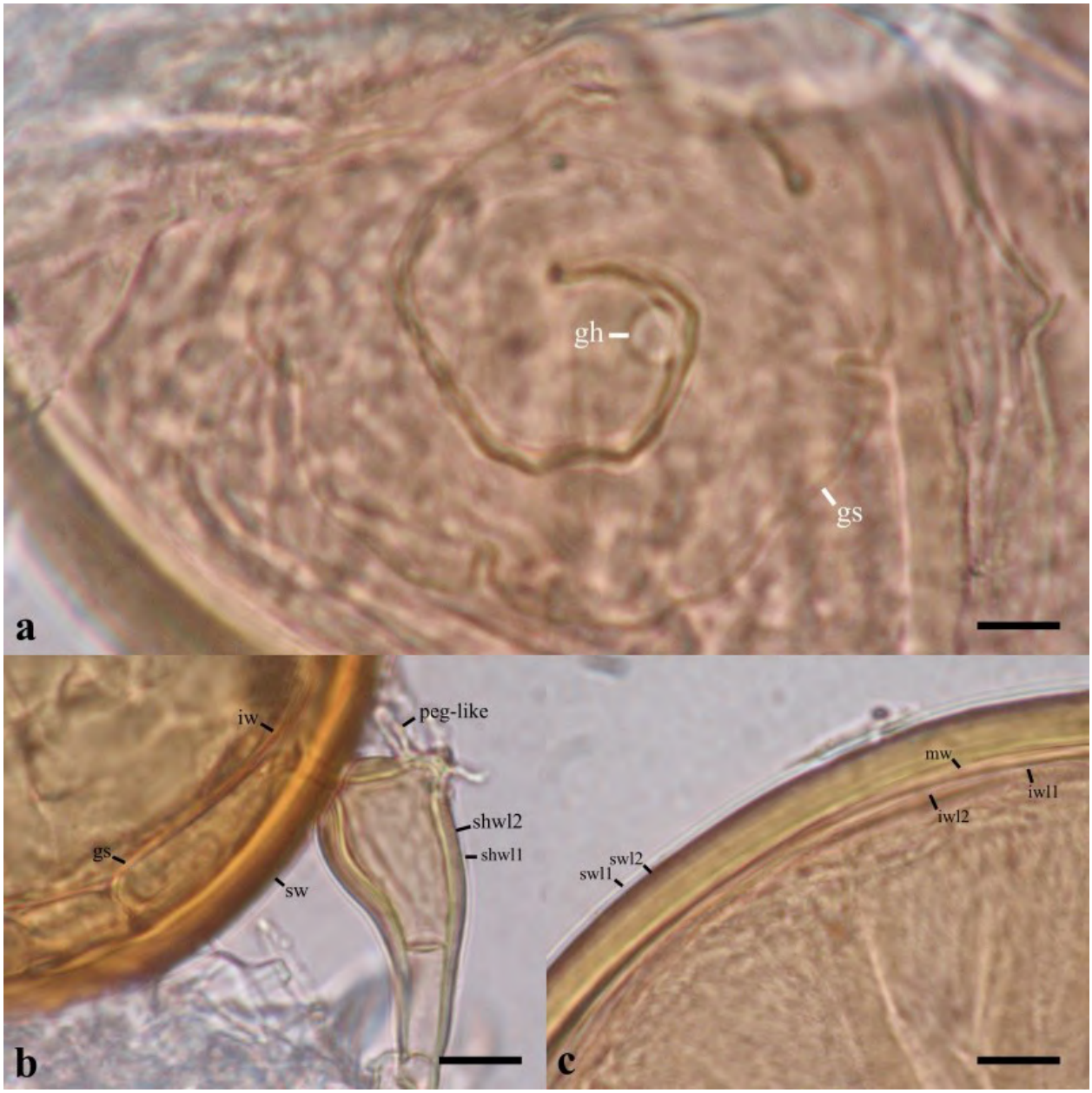


Figure 48 – *Bulbosporaceae.* a Helicoid germinal shield (gs) and germinal hole (gh) in *Bulbospora minima*. b Sporogenous cell wall with two layers (scwl 1 and 2) and germinal shield (gs) in the inner wall (iw). c Spore with 3 walls (sw, mw, iw). Scale bars: a = 5 μm, b–c = 10 μm.

Dentiscutata Sieverd., F.A. Souza & Oehl, Mycotaxon 106: 340 (2009) (2009)
Index Fungorum Identifier 511968

The genus was described by Oehl et al. (2008) as representing a monophyletic clade based on LSU nrDNA were the species produced spores with (i) a three- to five-layered outer wall continuous with the wall of the sporogenous cell, (ii) a one- to bi-layered middle wall and a two to three-layered inner wall, both being hyaline and formed *de novo* during spore development, (iii) a germination shield that arises on the outer surface of the inner wall, is yellow-brown to brown, ellipsoid (to oval), or rarely reniforme to cardioforme, has many (8–30) large folds separating the shield into 8–30 'small compartments', and (generally) a dentate like edge in planar view.

Type species – *Dentiscutata nigra* (J.F. Redhead) Sieverd., F.A. Souza & Oehl, Mycotaxon 106: 342 (2009)

Basionym: *Gigaspora nigra* J.F. Redhead, Mycologia 71(1): 187 (1979)

Notes – With eleven species, *Dentiscutata* is the third genus most diverse in *Gigasporales* in terms of species richness (https://biologiademicorrizas.wixsite.com/glomeromycota/gigasporales). However, several species lack phylogenetic confirmation. Furthermore, Tedersoo et al. (2024) transferred *D. cerradensis* and *D. reticulata* to *Fuscutata*, but as the type of the genus, *D. nigra*, has available only LSU nrDNA while *D. reticulata* does not, the transfer has to be confirmed. However, some taxa had an unreliable phylogenetic position in Tedersoo et al. (2024), requiring review as they were not supported by other phylogenies, including phylogenomic (Oehl et al. 2008, Borriello et al. 2014, Montoliu-Nerin et al. 2021). Tedersoo et al. (2024) and the phylogenetic analysis presented here call for a thorough revision of the genus, as it appears that only *D. nigra* remains included among the species with available molecular data. *Dentiscutata colliculosa*, *D. scutata* (C. Walker & Dieder.) Sieverd. et al., *D. biornata* (Spain et al.) Sieverd. et al., and *D. cerradensis* (now *Fuscutata*) were all originally described from semiarid, savanna to semi-humid regions in Brazil (Walker & Diederichs 1989, Goto et al. 2010a, Passos et al. 2021) and Colombia (e.g., Spain et al. 1989, Spain & Miranda 1996), indicating that the diversity of species with a brown germination shield is high in South American Tropical areas (Goto et al. 2010a).

Other genus in *Dentiscutataceae*

Fuscutata Oehl, F.A. Souza & Sieverd., Mycotaxon 106: 342 (2009)
Index Fungorum Identifier 511963; Index Fungorum (2025) and Species Fungorum (2025) list seven and six species, respectively; the difference between the two datasets is the *F. trirubiginopa*; DNA sequences are available for some species.

Type species – *Fuscutata heterogama* Oehl, F.A. Souza, L.C. Maia & Sieverd. 2009

Notes – A comprehensive discussion about *Fuscutata* can be found in Wijayawardene et al (2022). Three *Fuscutata* species were originally transferred from *Scutellospora* and the type species *F. heterogama* was designated by Oehl et al (2008). Recently, Tedersoo et al. (2024) transferred *D. cerradensis* and *D. reticulata* to *Fuscutata* (see above the discussion concerning that action).

Gigasporaceae Morton & Benny, Mycotaxon 37: 483 (1990); Fig. 50
Index Fungorum Identifier 82038

In *Gigasporaceae*, as well as in all members of *Gigasporales*, the glomerospores originate terminally on a subtending hypha that forms a sporogenous cell on its tip; that structure is also called bulbous suspensor-like cell. After spore development, the subtending hyphae form several septa. The spore ontogeny in *Gigasporales* is unique in *Glomeromycota* (Oehl et al. 2011e). The spores are globose to subglobose, usually larger than 200 μm diam., with a smooth surface and a

single spore wall with a germinal layer ornamented with multiple warts. The spores are produced singly in the soil. However, Gadkar & Adholeya (2000) reported the formation of intraradical spores of *Gigaspora margarita* on carrot root organ culture. Root colonization with the absence of intraradical vesicles and the presence of auxiliary cells in extraradical mycelium. The auxiliary cells are white to pale white, 17–54 µm broad, apex echinulate with spines, formed in clusters on second or third-order branches from a runner hypha. The auxiliary cells are storage structures capable of supplying energy for spore development (Declerck et al. 2004) and hyphal healing (de Souza & Declerck 2003, de la Providencia 2005).

Genome and transcriptome available for *G. rosea* DAOM194757 and FL105, *G. margarita* BEG34 and NC121 (Salvioli et al. 2016, Tang et al. 2016, Morin et al. 2019, Venice et al. 2020, Montoliu-Nerin et al. 2021).

Family type – *Gigaspora* Gerd. & Trappe, Mycologia Memoir 5: 25 (1974)

Notes – *Gigasporaceae* was introduced by Morton & Benny (1990) with two genera, *Gigaspora*, and *Scutellospora*, which were proposed based on unique features of spore ontogenesis, root colonization pattern, and intra- and extraradical structures of mycelia. Later, based on molecular phylogenetic analysis, *Scutellospora* was shown to be polyphyletic (de Souza et al. 2005a, Oehl et al. 2008). Thus, *Scutellospora* species were transferred to four monophyletic families and nine genera (Oehl et al. 2008, Goto et al. 2012). Currently, *Gigasporaceae* includes only *Gigaspora*, with species distinguished by their unique mode of germination by hyphae arising from warts present on the inner surface of the third innermost spore wall layer and penetrating through the other layers of the spore wall, as well as producing spiny auxiliary cells. In contrast, in the other genera in *Gigasporales*, germination occurs from specialized structures called germination shields, and auxiliary cells are knobby. Germination shield-like structures are present in other genera, such as *Acaulospora*, *Pacispora* and *Ambispora*, the latter belonging to a basal clade – *Archaeosporales* – suggesting that the germination pattern of *Gigaspora* is an apomorphy unique within *Glomeromycota*. The characteristics of the root colonization with the absence of intraradical vesicles, and the extraradical mycelium with auxiliary cells only shared with *Pacispora*, led Morton (2000) to question the monophyly of arbuscular mycorrhizal fungi and to propose an independent origin for this group of fungi. Morton's proposition was rejected by the erection of the monophyletic phylum *Glomeromycota* based on molecular phylogenetic analyses (Schüßler et al. 2001). *Pacispora* species also produce auxiliary cells, but the relationship between *Pacisporaceae* and *Gigasporales* is unclear (Fig. 52).

Nine species are accepted in *Gigaspora*: *G. albida* N.C. Schenck & G.S. Sm., *G. candida* Bhattacharjee et al., *G. decipiens* I.R. Hall & L.K. Abbott, *G. gigantea*, *G. margarita* W.N. Becker & I.R. Hall, *G. polymorphira* L.M. Yao et al., *G. ramisporophora* Spain et al., *G. rosea* T.H. Nicolson & N.C. Schenck, and *G. siqueirae* F.A. de Souza et al. Bentivenga & Morton (1995) suggested synonymising *G. candida* under *G. rosea* and *G. ramisporophora* under *G. margarita* based on morphological characteristics (Schüßler & Walker 2010). However, molecular characteristics of these species do not support this hypothesis (de Souza et al. 2004, da Silva et al. 2013). *Gigaspora alboaurantiaca* W.N. Chou was placed later as a heterotypic synonym of *G. candida* by Schüßler & Walker (2010), which also is incongruent with the *G. alboaurantiaca* description that clearly states the sporogenous cell is pale brown (Chou et al. 1991), while it is always white in *G. candida*. *Gigaspora lazarri* Montecchi et al. and *G. tuberculata* Neeraj et al. are considered species pending additional analysis.

For most *Gigaspora* spp., living cultures of the type materials have been lost. Nevertheless, isolates of many of the described species are available in several culture collections such as BEG (https://i-beg.eu/), CICG (https://sites.google.com/site/cicgfma/home) and INVAM (https://invam.ku.edu/), among others.

The morphological distinctiveness between species usually requires examination of living cultures because it is based on the size and colour of spores and sporogenous cells, which are features that overlap between species. Besides, the bright colour of young mature spores usually turns pale brownish yellow to brown with age. Molecular methods based on Denaturing Gradient Gel Electrophoresis fingerprints (de Souza et al. 2004) and molecular signatures (Bago et al. 1998) targeting the V9 region of the 18S rRNA gene can be used to identify groups of species in this genus and discriminate between isolates. Bago et al. (1998) identified three *Gigaspora* groups based on a six nucleotide-long molecular signature: *Gigaspora rosea* group (*G. rosea* and *G. albida*), *Gigaspora margarita* group (*G. margarita* and *G. decipiens*) and *Gigaspora gigantea*, which constituted a group by itself. De Souza et al. (2004) enlarged the *Gigaspora rosea* group (*G. albida*, *G. candida*, *G. ramisporophora*, *G. rosea*). The extended barcode sequence for *Glomeromycota* (SSU–ITS–LSU) has been originally tested using sequences of two species only, *G. margarita* and *G. rosea* (Stockinger et al. 2010), which belong to distinct molecular groups (Bago et al. 1998, de Souza et al. 2004). *Gigaspora polymorphira* was recently described from China, and the phylogenetic inference based on the SSU–ITS–LSU segment placed its sequences in a monophyletic clade next to *G. margarita* (Long et al. 2022). *Gigaspora siqueirae* from Brazil was the last species described in the genus (Manawasinghe et al. 2025).

Phylogeny of *Gigaspora* has been based on nrRNA gene sequences (Oehl et al. 2008, de Souza et al. 2018, Wijayawardene et al. 2022), β-tubulin (Msiska & Morton 2009) and Cytochrome c Oxidase I (COI) genes (Borriello et al. 2014). Phylogeny based on partial nrDNA LSU sequences suggested *Gigaspora* as the most recent lineage of *Glomeromycota*, forming a sister clade to *Intraornatosporaceae* (Goto et al. 2012). This is also supported by phylogenetic reconstruction using the COI genes, which presents a low level of divergence reflecting either a slow rate of evolution or a more recent evolutionary divergence of this group (Borriello et al. 2014). However, Morton and colleagues made several phylogenetic propositions based on the evolution of morphological characters, which suggested *Gigaspora* to be a basal taxon in relation to other species in *Gigasporales* (Morton & Msiska 2010b, and references therein), even when the phylogenetic evidence based on nrRNA and β-tubulin genes has shown otherwise. Studies of the life history strategy of *Gigasporaceae* suggest they are K-strategists as compared with *Glomerales* (de Souza et al. 2005b). *Gigaspora* spp. were one of the first species of AMF cultured *in vitro* using root organ culture (Bécard & Fortin 1988), later used as a model system to study the AM symbiosis and the interaction with obligate endobacteria (Ruiz-Lozano & Bonfante 2001, Naumann et al. 2010, Salvioli et al. 2016, Venice et al. 2020).

The occurrence of Operational Taxonomic Units (OTU) related to *Gigaspora* has been recorded on all continents except Antarctica, supporting a worldwide distribution (Öpik et al. 2010, Rodríguez-Echeverría et al. 2017). The effectiveness of *G. margarita* inoculation significantly increased response in coffee plants under greenhouse and field trials (Siqueira et al. 1998, Cogo et al. 2017).

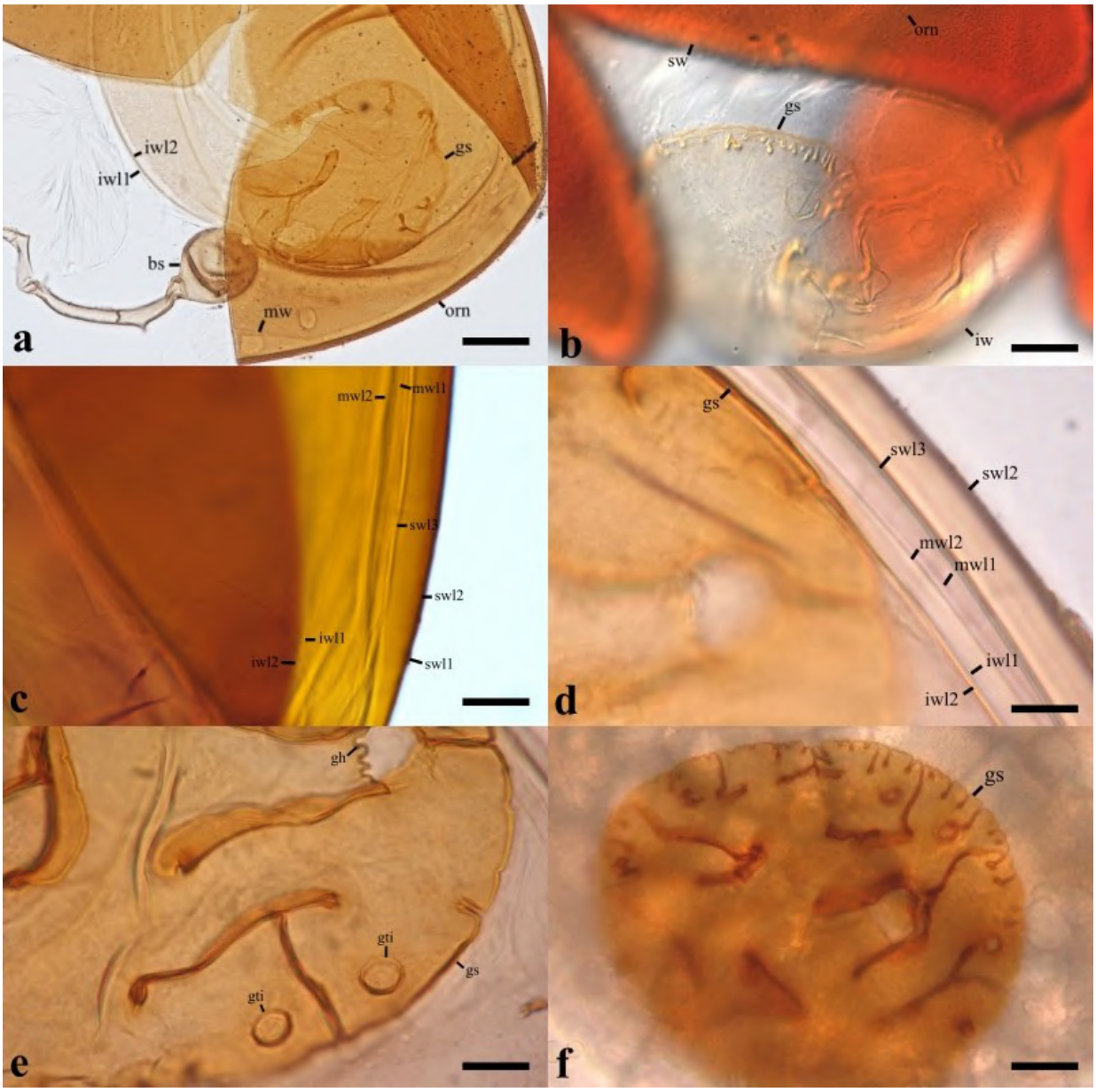


Figure 49 – *Dentiscutataceae.* a Spore of *Fuscutata aurea* with three walls and pigmented violin-shaped germinal shield (gs). b Germinal shield (gs) and spore wall ornamentation (orn) in *F. heterogama* (courtesy of E. Furrazola). c Spore wall of *Dentiscutata hawaiiensis* with three spore wall layers (swl1–3). d Spore wall of *D. scutata* with 3 walls (sw, mw, iw) e Germinal shield (gs) and germinal tube initiation (gti) in *D. scutata*. f General germination shield (gs) morphology in *Dentiscutata*. Scale bars: a–e = 10 μm.

Gigaspora Gerd. & Trappe emend. Oehl, F.A. de Souza & Sieverd.
Index Fungorum Identifier 20239

As in *Gigasporaceae* description.

Type species – *Gigaspora gigantea* (T.H. Nicolson & Gerd.) Gerd. & Trappe 1974

Basionym: *Endogone gigantea* T.H. Nicolson & Gerd. 1968

Notes – As in the *Gigasporaceae* notes.

Intraornatosporaceae B.T. Goto & Oehl, Mycotaxon 119: 121 (2012); Fig. 51
Index Fungorum Identifier 563599

The family represents a monophyletic lineage based on the LSU nrDNA marker (Fig. 4) - closely related with *Gigasporaceae*. Species of this family are characterized morphologically by the

introverted ornamentation in the spore wall and middle wall (Goto et al. 2012). Spores with 2–3 walls, the outer wall with 3–4 layers, and the inner wall with 2–3 layers. The middle wall of the 3-walled spores has introverted tuberculate ornamentation. Outer wall of 2-walled spores with introverted tuberculate ornamentation. Shield of 3-walled spores pigmented, yellow-brown to brown, with 5–8–10 wave-like projections. Shield in 2-walled spores is hyaline to light yellow, with 4–8 wave-like projections.

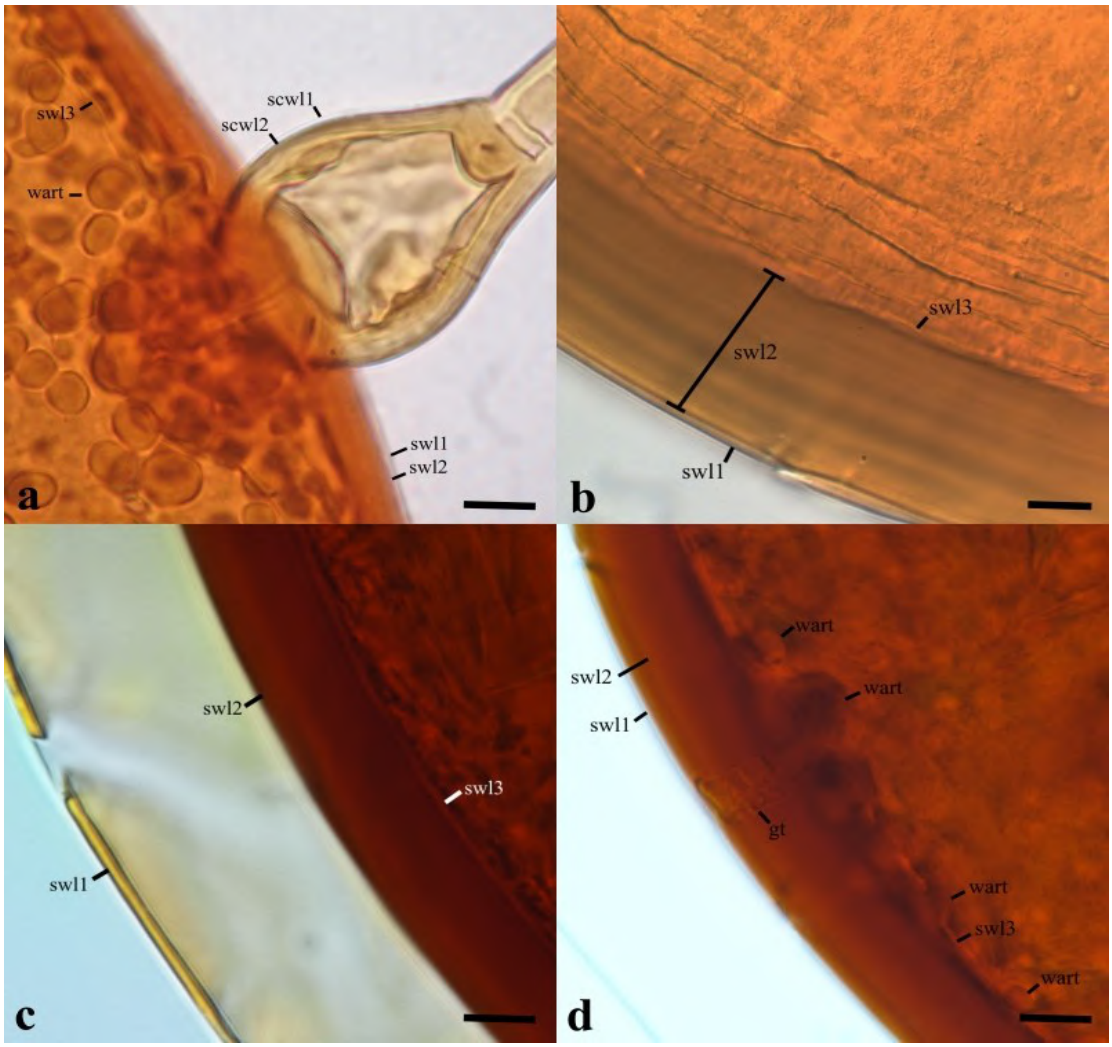


Figure 50 – *Gigasporaceae*. a Sporogenous cell with wall layers 1 and 2 (scwl1 and 2) attached to the spore base and warts on the inner surface of the spore wall. b Detail of spore wall layers (swl1–3) in the *Gigaspora* sp. (courtesy of E. Furrazola). c, d Typical spore wall with three layers (swl1–3) and the inner surface of swl3 ornamented with warts from which germ types (gt) arise in *G. siqueirae*. Scale bars: a–d = 10 µm.

Family type – *Intraornatospora* B.T. Goto, Oehl & G.A. Silva, Mycotaxon 119: 122 (2012)

Notes – Originally described by Goto et al. (2012) based on introverted ornamentation in the inner surface of the outer (*Intraornatospora*) and middle spore wall (*Paradentiscutata*), distinct from *Gigaspora* species in the sister clade. So far, only three species have been described for the family: *Intraornatospora intraornata* (basionym: *R. intraornata*), *Paradentiscutata maritima*, and *P. bahiana*. The most striking feature, observed in all species, is the presence of an introverted tuberculate ornamentation of the outer wall and middle wall (Goto et al. 2009, 2012). A similar pattern of ornamentation was observed only in another species described in the Brazilian Northeastern (*Dentiscutata colliculosa*), which presented the inner surface of the spore wall with large (hill-like) introverted projections (Goto et al. 2010a). However, in this species, the ornamentation was produced in the second layer of the outer wall, while in *I. intraornata* and

Paradentiscutata spp. it occurred in the third layer of the outer wall and the middle wall, respectively. Phylogenetic analysis also confirmed that *D. colliculosa* differed from the *Intraornatosporaceae* species. Both *Gigaspora*, *Intraornatospora*, and *Paradentiscutata* share introverted ornamentation on the inner surface of the spore wall, suggesting a recent common ancestor. Redecker et al. (2013) rejected *Intraornatosporaceae*, stating that the data used were fragile and represented an orphan clade requiring additional analysis. Subsequent papers, using the same data set, supported the close relationship of the species with *Gigaspora* (de Souza et al. 2018). Members of this family present a restricted distribution reported only in South America (Goto et al. 2012).

Intraornatospora B.T. Goto, Oehl & G.A. Silva, Mycotaxon 119: 122 (2012)
Index Fungorum Identifier 563600

Spores are produced singly in soil, from a sporogenous bulbous cell originating terminally from mycorrhizal hypha. Spores with two walls. The outer wall has three layers continuous with the wall of the bulbous suspensor cell. Inner surface of the outer wall with introverted tubercular ornamentations. Inner wall is hyaline, with 2–3 layers. The germinal shield produced on the outer surface of the inner wall is light yellow, with 4–8 wave-like projections. Differs from *Paradentiscutata* by the spore wall organization (2 walls vs. 3 walls) and from *Racocetra* by the introverted tuberculate ornamentation in the spore wall and the close phylogenetic relationship to the *Gigaspora* clade.

Type species – *Intraornatospora intraornata* (B.T. Goto & Oehl) B.T. Goto, Oehl & G.A. Silva, Mycotaxon 119: 122 (2012)

Basionym **–** *Racocetra intraornata* B.T. Goto & Oehl, Mycotaxon 109: 485 (2009)

Notes – The genus was introduced to accommodate *Racocetra intraornata* (Goto et al. 2009), a species described from Brazilian semiarid and sand dunes. The fungus was described only based on morphological analysis of spores obtained from field samples (Goto et al. 2009). Morphologically, *I. intraornata* differs from *Racocetra* (both with two walls) by the formation of a pigmented (yellowish) germination shield vs. a hyaline germination shield in *Racocetra* (Goto et al. 2012, de Souza et al. 2018). *Intraornatospora* is a monospecific genus with distribution restricted to Brazilian sand dunes, semiarid, rupestrian grassland, and Atlantic Rain Forest (Goto et al. 2012, Pereira et al. 2018, Vieira et al. 2019b, Queiroz et al. 2022). The description of mycorrhizal structures is still missing because the fungus is not available in single-species cultures yet.

Other genera in *Intraornatosporaceae*

Paradentiscutata B.T. Goto, Oehl & G.A. Silva, Mycotaxon 119: 122 (2012)
Index Fungorum Identifier 563602; Index Fungorum (2025) and Species Fungorum (2025) list two species; DNA sequences available.

Type species – *Paradentiscutata bahiana* Oehl, Magna, B.T. Goto & G.A. Silva 2012

Racocetraceae Oehl, Sieverd. & F.A. Souza, Mycotaxon 106: 333 (2009); Fig. 52
Index Fungorum Identifier 511946

Glomerospores are formed singly in soil, terminally on a subterminal bulbous sporogenous cell. Spores globose, subglobose or ellipsoidal, hyaline or coloured, with two to three walls. Each wall has one or several layers that can be laminated, membranous, flexible to rigid, or semi-persistent to persistent. Spore wall components are ornamented (with spines, warts and pits) or smooth. The distinguishing feature of *Racocetraceae* is the germination shield arising on the outer surface or beneath a thin outer layer of the inner wall. The shield is hyaline to sub-hyaline, sometimes light yellow, generally oval to ovoid, ellipsoid or subglobose. This structure is multiple-lobed with four or more compartments, each with one germ tube initiation. Often, several septa are formed distally from the pore of the sporogenous cell subtending the hypha. Spores of some species stain in Melzer's reagent. Species forming auxiliary cells with a knobby appearance. Formation of intraradical vesicles is unknown.

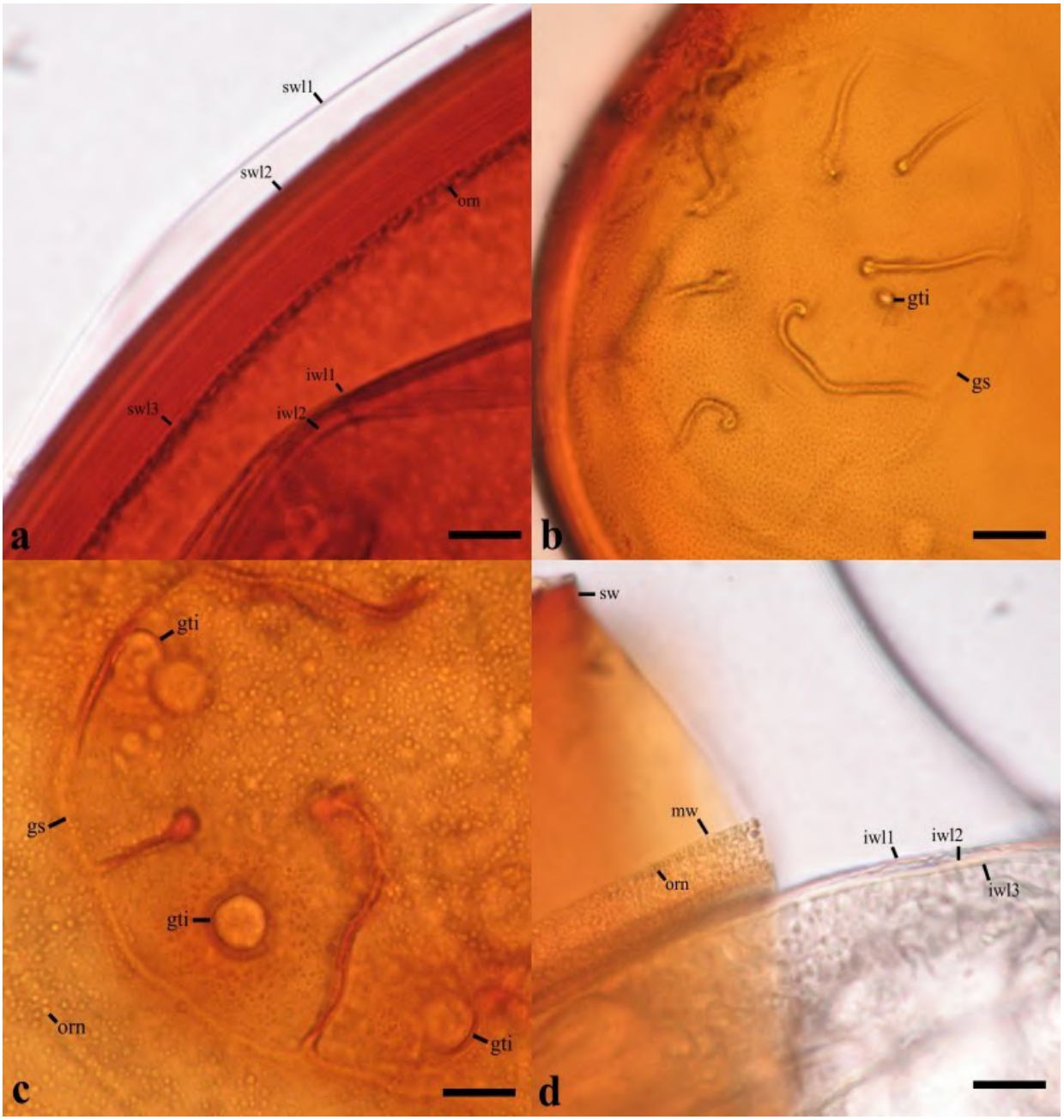


Figure 51 – *Intraornatosporaceae.* a,b Spore wall (sw) and inner wall (iw) with introverted ornamentation (orn) and germinal shield (gs) in *Intraornatospora intraornata*. c–d Three walls of *Paradentiscutata maritima* (sw, mw, iw) with introverted ornamentation (orn) in the middle wall and germinal shield (gs). Scale bars: a–d = 10 μm.

Family type – *Racocetra* Oehl, F.A. Souza & Sieverd., Mycotaxon 106: 334 (2009)

Notes – *Racocetraceae* was introduced by Oehl et al. (2008) based on molecular phylogeny of the LSU nrDNA, indicating a monophyletic lineage at the family level as well as diagnostic morphology of germination shields and the number of spore walls among *Scutellospora* species. Consequently, members of *Scutellospora* were placed in three new families, including *Racocetraceae* with two new genera, *Cetraspora* and *Racocetra*. Phylogenetic analyses of the same study showed that *Racocetraceae* and *Scutellosporaceae* are not sister clades. Goto et al. (2011) and Krüger et al. (2012) provided further support for the two genera in *Racocetraceae.* Currently, the family has 22 species, 14 within *Racocetra* and eight in *Cetraspora* (https://biologiademicorrizas.wixsite.com/glomeromycota/gigasporales). *Racocetra cromosomica* Chim-Sánch. et al. and *Cetraspora huaxica* D.Y. Chen et al. are the most recent species described

and they were originally found in Mexico and China, respectively (Chimal-Sánchez et al. 2021, Chen et al. 2023). Members of *Racocetraceae* are distributed worldwide, including countries in tropical and temperate regions.

Genome available for *R. fulgida* IN212, *R. persica* MA461A and *C. pellucida* FL966 (Montoliu-Nerin et al. 2021); transcriptome available for *R. castanea* BEG 1 (Beaudet et al. 2018).

Racocetra Oehl, Sieverd. & F.A. Souza, Mycotaxon 106: 333 (2009)
Index Fungorum Identifier 511947

As in the *Racocetraceae* description. Distinct from *Cetraspora* due to the number of spore walls– two in *Racocetra* vs three in *Cetraspora* – and in the nucleotide sequences of the LSU nrDNA region.

Type species – *Racocetra coralloidea* (Trappe, Gerd. & I. Ho) Oehl, F.A. Souza & Sieverd., Mycotaxon 106: 336 (2009)

Notes – This genus is distributed among more than 20 countries in tropical and temperate regions.

Other genera in *Racocetraceae*

Cetraspora Oehl, F.A. Souza & Sieverd., Mycotaxon 106: 337 (2009)
Index Fungorum Identifier 511957; Index Fungorum (2025) and Species Fungorum (2025) list nine species; DNA sequences available for six of them.

Type species – *Cetraspora gilmorei* (Trappe & Gerd.) Oehl, F.A. Souza & Sieverd. 2009

Scutellosporaceae Sieverd., F.A. Souza & Oehl, Mycotaxon 106: 330 (2009); Fig. 53
Index Fungorum Identifier 511945

Species are characterized by formation of (i) spores singly from bulbous sporogenous cells, (ii) three spore walls, (iii) germination shields which are hyaline to sub-hyaline, seldom light yellow, generally bi-lobed, rarely mono-lobed, often violin-shaped or oval to ovoid, with only a few folds covering the shield surface and two germ tube initiations, (iv) knobby auxiliary cells, and (v) arbuscular mycorrhiza without vesicles. Both *Bulbospora* and *Orbispora* species share three spore walls and an orbital germinal shield (considered morphologically simplest), producing only one germ tube (Oehl et al. 2011a, Marinho et al. 2014). However, the genus *Bulbospora* was accommodated in a distinct family, introduced here as *Bulbosporaceae* (see the *Bulbosporaceae* section), due to a revised interpretation of phylogenetic analysis (Oehl et al. 2011a, Marinho et al. 2014).

Family type – *Scutellospora* C. Walker & F.E. Sanders. emend. Oehl, F.A. Souza & Sieverd., Mycotaxon 106: 330 (2008)

Notes – Sixteen species are recognized in *Scutellosporaceae*, 14 in *Scutellospora*, and two in *Orbispora* (https://biologiademicorrizas.wixsite.com/glomeromycota/gigasporales). The relationships in *Gigasporales* were reconstructed from analyses of sequences of a partial nrDNA, mainly the larger subunit (LSU) (Oehl et al. 2011e). The *Scutellosporaceae* clade with three genera was supported following analyses of sequences of ten species (Oehl et al. 2008, 2011d, Marinho et al. 2014, Crossay et al. 2018, Guillén et al. 2021). The erection of *Bulbosporaceae* as a separate family does not require any emendation of *Scutellosporaceae* because the morphological features of spore walls and germinal shields are still valid.

Members of the family have a worldwide distribution, occurring in both temperate and tropical regions in terrestrial and aquatic ecosystems. Genome and transcriptome available for

Scutellospora calospora AU212A and IL209, respectively (Beaudet et al. 2018, Montoliu-Nerin et al. 2021).

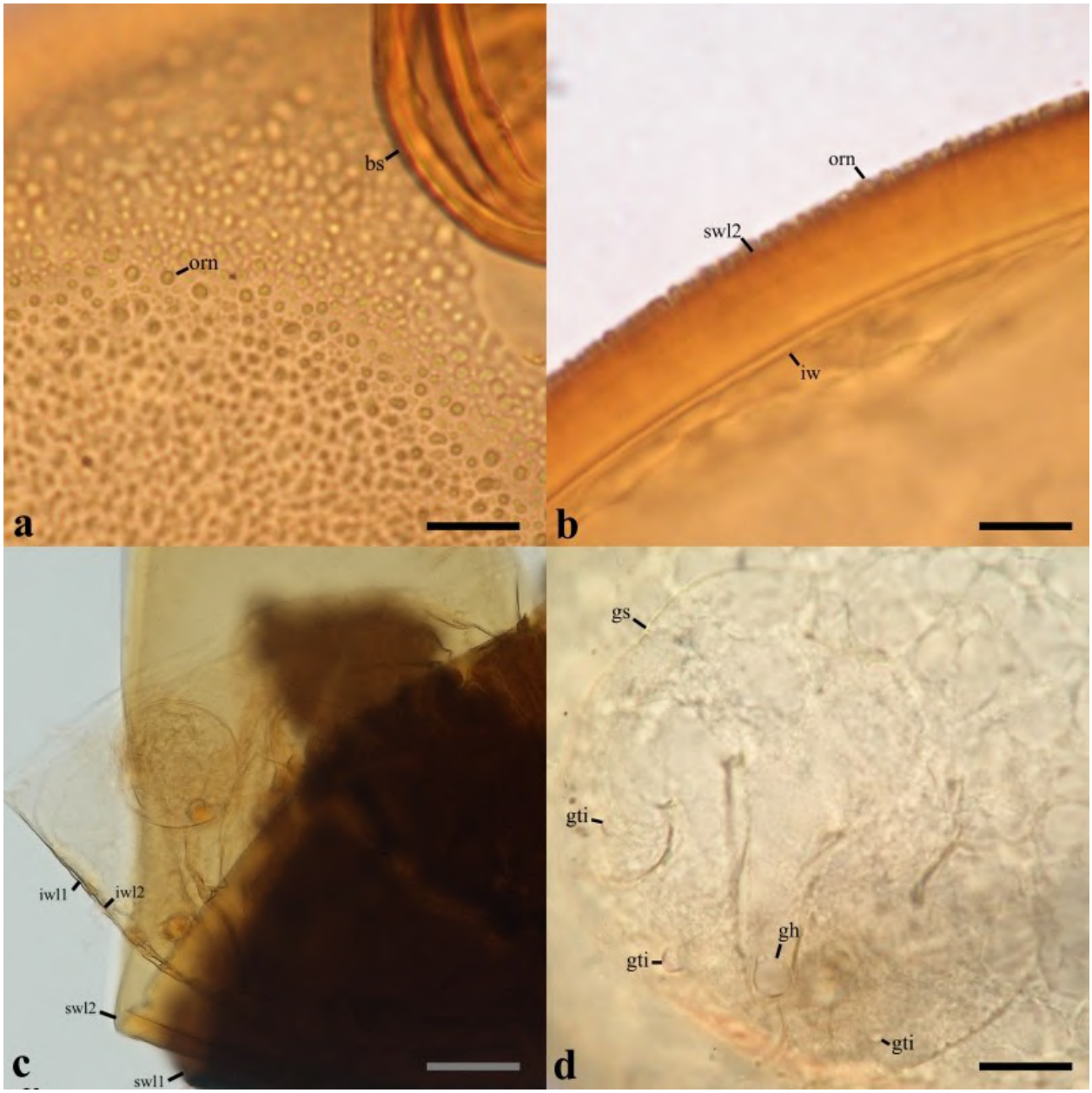


Figure 52 – *Racocetraceae*. a, b Spore ornamentation and two walls in *Racocetra verrucosa* (sw, iw). c *R. gregaria* with two walls (sw, iw). d *R. tropicana* with a hyaline germinal shield (gs) and several germinal tube initiations (gti). Scale bars: a–b = 5 µm, c = 20 µm d = 10 µm.

Scutellospora C. Walker & F.E. Sanders. emend. Oehl, F.A. Souza & Sieverd. emend. Oehl, F.A. Souza & Sieverd., Mycotaxon 106: 330 (2008)
Index Fungorum Identifier 561646

Spore with three walls, outer wall, continuous with the sporogenous cell wall, consisting of a rigid outer layer, a laminate middle layer and a thin, often membranous third layer, tightly adherent to the laminate layer; 1–2-layered and 2–3-layered hyaline middle and inner walls, respectively, formed *de novo*, and (ii) hyaline to sub-hyaline, seldom light yellow, bi-lobed, often violin-shaped to oval to ovoid to more rarely cardioid germination shields associated with the inner spore wall. *Scutellospora* differs from *Orbispora* and *Bulbospora* in having bi-lobed germinal shields rather than single-lobed.

Type species – *Scutellospora calospora* (T.H. Nicolson & Gerd.) C. Walker & F.E. Sanders, Mycotaxon 27: 180 (1986)

Notes – Oehl et al. (2008) emended the genus described by Walker & Sanders (1986). Currently, *Scutellospora* has 14 described species (https://biologiademicorrizas.wixsite.com/glomeromycota/gigasporales). Only eight have their phylogenetic position confirmed by molecular sequence analysis. The species are distributed among countries in tropical and temperate regions: Brazil, EUA, Mexico, Venezuela, Spain and Poland.

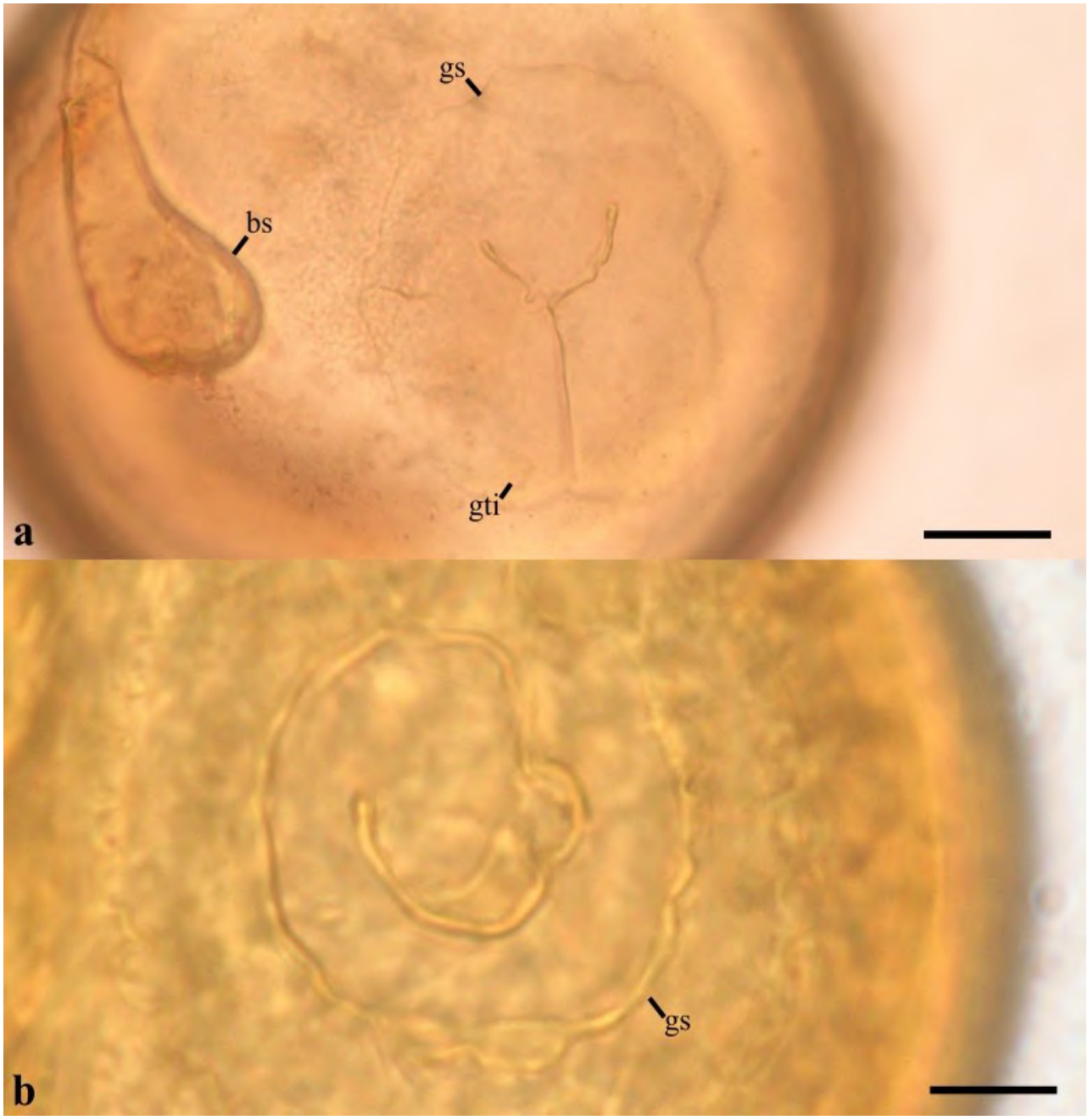


Figure 53 – *Scutellosporaceae.* a Bi–lobed germinal shield produced in *Scutellospora* spp. b Orbital germinal shield (gs) produced by *Orbispora pernambucana*. Scale bars: a,b = 10 μm.

Other genera in *Scutellosporaceae*

Orbispora Oehl, G.A. Silva & D.K. Silva, Mycotaxon 116: 163 (2011)

Index Fungorum Identifier 519533; Index Fungorum (2025) lists two epithets also listed in Species Fungorum (2025); DNA sequences available.

Type species – *Orbispora pernambucana* (Oehl et al.) Oehl, G.A. Silva & D.K. Silva 2011

Glomerales J.B. Morton and Benny, emend. Błaszk., B.T. Goto, & Magurno.
Glomeraceae Piroz. & Dalpé emend. Oehl, G.A. Silva & Sieverd., [as '*Glomaceae*'] Symbiosis 7: 19 (1989); Fig. 54
Index Fungorum Identifier 82026

Glomerospores formed at the tip of sporogenous hyphae, occasionally intercalary (inside hyphae), in soil or inside roots. Spores globose, subglobose, irregular or ellipsoid, hyaline to pigmented. Extraradical glomerospores can be produced singly, in clusters with few to many spores, in compact, unorganized glomerocarps, with or without a peridium. Glomerospores have one spore wall consisting of one or more layers, which may be evanescent or permanent, flexible, semi-flexible, laminate, or mucilaginous, staining or not in Melzer's reagent. Layers can be smooth or ornamented. Subtending hyphae are cylindrical or slightly funnel-shaped or constricted at the spore base; subtending hyphal wall concolourous or slightly lighter than the spore and composed of layers continuous with the spore wall layers. Pore open or closed by thickening of the spore wall and hyphal wall towards the center of the lumen of the subtending hypha. This septum is formed from the inner surfaces of the subtending hyphal wall, slightly below the spore base or the innermost layer of the spore wall at or slightly above the spore base. Mycorrhizae with arbuscles, vesicles, as well as intra- and extra-radical hyphae, staining in Trypan blue.

Family type – *Glomus* Tul. & C. Tul., Giornale Botanico Italiano 1 (2): 63 (1845)

Notes – Based on analysis of fossil records of spores with glomoid development, Pirozynski & Dalpé (1989) proposed the family *Glomaceae* (= *Glomeraceae*) with two genera, *Glomus* and *Sclerocystis*. Along with new studies, several genera joined the family due to the similar mode of glomerospore formation. Up to 2024, *Glomeraceae* was considered a family with the highest number of genera (23) and species (ca. 150) described for *Glomeromycota* (Wijayawardene et al. 2022, Błaszkowski et al. 2023, 2024, Tedersoo et al. 2024). Da Silva et al. (2024) proposed a new organization of *Glomeraceae* based on the highly supported clades resulting from the analysis of partial 45S nrDNA. As a result, *Glomeraceae* was split into five families: *Glomeraceae* (*Glomus, Sclerocarpum, Complexispora* and *Simiglomus* whose validity is uncertain due to the lack of molecular phylogeny), *Sclerocystaceae* (*Sclerocystis, Oehlia, Rhizoglomus, Halonatospora, Silvaspora, Parvocarpum*), *Kamienskiaceae* (*Kamienskia, Microkamienskia, Epigeocarpum*), *Septoglomeraceae* (*Septoglomus, Funneliformis, Funneliglomus, Viscospora, Blaszkowskia*), and *Dominikiaceae* (*Dominikia, Macrodominikia, Microdominikia, Nanoglomus, Orientoglomus*). According to the new taxonomic arrangement, *Glomeraceae* gathers 60 morphologically described species distributed in three accepted genera: *Complexispora* (2), *Glomus* (57), and *Sclerocarpum* (4). Many species, mostly identified in the genus *Glomus*, still need molecular and phylogenetic confirmation about their taxonomic status. Only ca. 18% of species of *Glomeraceae* have been identified based on molecular phylogeny. Furthermore, an increasing number of environmental molecular studies are showing a high number of Operational Taxonomic Units (OTUs) that might be affiliated to taxa (at species and genus level) not yet described in *Glomeraceae* (Öpik et al. 2013, Wang et al. 2020a, Tedersoo et al. 2024). According to the phylogeny of Tedersoo et al. (2024), nine potential undescribed genera have been detected in the clade representing now the family *Glomeraceae*.

Glomus Tul. & C. Tul., Giornale Botanico Italiano 1 (2): 63 (1845)
Index Fungorum Identifier 20244

Glomerospores formed at the tip of sporogenous hyphae, occasionally interspersed inside roots. They can be globose, subglobose, irregular, or ellipsoid, hyaline to pigmented, with thick or thin walls that can have smooth or ornamented layers. Spores are formed singly in the soil, in small and large clusters, in compact, organised and unorganized epigeous, sub-hypogeous or hypogeous glomerocarps, with or without peridium. Spores present one spore wall and several layers: evanescent, laminate, permanent, semiflexible, smooth, mucilaginous, and semi-persistent. Some

species react with Melzer's reagent. Subtending hyphae can be straight or curved, cylindrical to flared, or rarely constricted at the spore base. The wall of the subtending hypha is continuous with the spore wall layers. Pore open or closed by a curved septum.

Type species – *Glomus macrocarpum* Tul. & C. Tul., Giornale Botanico Italiano 1 (2): 63 (1845)

Notes – Initially, the genus was described with two species, *G. macrocarpum* and *G. microcarpum*, but today there are 57 species (Wijayawardene et al. 2022, 2024, Hyde et al. 2024). Most of these species have to be considered as *Glomus sensu lato*, whose correct taxonomic status needs molecular and phylogenetic confirmation. Despite the genus having the putative highest number of species, only eight have molecular data and a determined phylogenetic position: *G. macrocarpum*, *G. ibericum*, *G. atlanticum*, *G. chinense*, *G. rugosae*, *G. mongioiense*, *G. bareae* and *G. tetrastratosum* (Magurno et al. 2024). It is also worth noting that when *Glomus* was described, the term "mycorrhiza" did not exist. It was coined, 41 years later, by Frank (1885). Another issue that needs to be addressed is related to the molecular epitype of *G. macrocarpum* used to establish the *Glomus* clade. The isolate used by Schüßler & Walker (2010) presented spores produced singly in the soil (not in sporocarps), thus not showing all the characteristics of the specimen used to define the species. Large sporocarps of *G. macrocarpum* have been reported from various regions of the world, both temperate and tropical. Obtaining specimens from the type location (in France or its vicinity), where the Tulasne brothers discovered *G. macrocarpum*, revisited by Berch & Fortin (1983), would allow us to verify the sequences assigned to this species.

Representatives of the genus are commonly found in tropical, subtropical, and temperate terrestrial ecosystems (Davison et al. 2015, Barbosa et al. 2017, Rodríguez-Echeverría et al. 2017), but were also found in aquatic environments (Gomes et al. 2022) and decomposing plant organic matter, such as leaves and branches (Bunn et al. 2019, Díaz-Ariza et al. 2021, Lima et al. 2023, 2024). The occurrence of *Glomus* spp. is documented in at least 85 countries. However, several occurrences might refer to taxa currently considered as *Glomus sensu lato*, whose correct taxonomic status needs molecular and phylogenetic confirmation.

Other genera in *Glomeraceae*

Complexispora Błaszk., B.T. Goto, Niezgoda & Magurno, Mycol. Prog. 22(5, no. 34): 4 (2023)
Index Fungorum Identifier 847607; Index Fungorum (2025) and Species Fungorum (2025) lists two epithets; DNA sequences available.

Type species – *Complexispora multistratosa* Błaszk., B.T. Goto, Niezgoda & Magurno

Sclerocarpum B.T. Goto, Błaszk., Niezgoda, A. Kozłowska & Jobim, Mycol. Prog. 18(3): 375 (2019)
Index Fungorum Identifier 828316; Index Fungorum (2025) lists four epithets, while Species Fungorum (2025) lists one; DNA sequences are available for one species.

Type species – *Sclerocarpum amazonicum* Jobim, Błaszk., Niezgoda, A. Kozłowska & B.T. Goto 2019

Dominikiaceae G.A. Silva, Sieverd. & Oehl, Microfossils of the Precambrian of the USSR (Leningrad) 4(4): 773 (2024); Fig. 55
Index Fungorum Identifier 855469

Spores hypogeous and/or intraradical, produced singly, in loose clusters to compact sporocarps, terminally or intercalary on subtending hyphae, hyaline to sub-hyaline or yellow to yellow brown, globose to subglobose or rarely obovoid, ranging from 10 to 100 µm diam., presenting one wall with one to four layers. Subtending hyphae are straight or recurved, generally cylindrical or funnel-shaped, with the wall continuous with the spore wall, and for a certain distance, concolourous with the spore wall, or slightly lighter in colour. Pore often closed at the spore base by a thin, straight or curved septum, sometimes supported by a certain degree of

introverted wall thickening. Melzer's reaction to the spore wall in representatives of all genera, except for the monospecific genus *Macrodominikia*. Forming vesicular-arbuscular mycorrhizae.

Family type – *Dominikia* Błaszk., Chwat & Kovács, in Błaszkowski, Chwat, Góralska & Ryszka, Kovács, Nova Hedwigia 100(1-2): 228 (2014)

Notes – *Dominikiaceae* is one of the new families introduced by da Silva et al. (2024) according to a new organization of *Glomerales*, resulting from partial 45S nrDNA phylogeny. The same study transferred *Dominikia compressa* to *Macrodominikia*, solving the issue of low support for the *Domikia* clade. Błaszkowski et al. (2024) introduced *Delicatispora*, based on a new combination of *D. indica*, and also a new species *Dominikia paraminuta*, in *Dominikiaceae*. According to Tedersoo et al. (2024), at least one potential new genus could be described in *Dominikiaceae*. Interestingly, *Nanoglomus*, despite having only one species described, showed a very high number of environmental occurrences characterized by high genetic diversity, depicting a potentially high number of undescribed species.

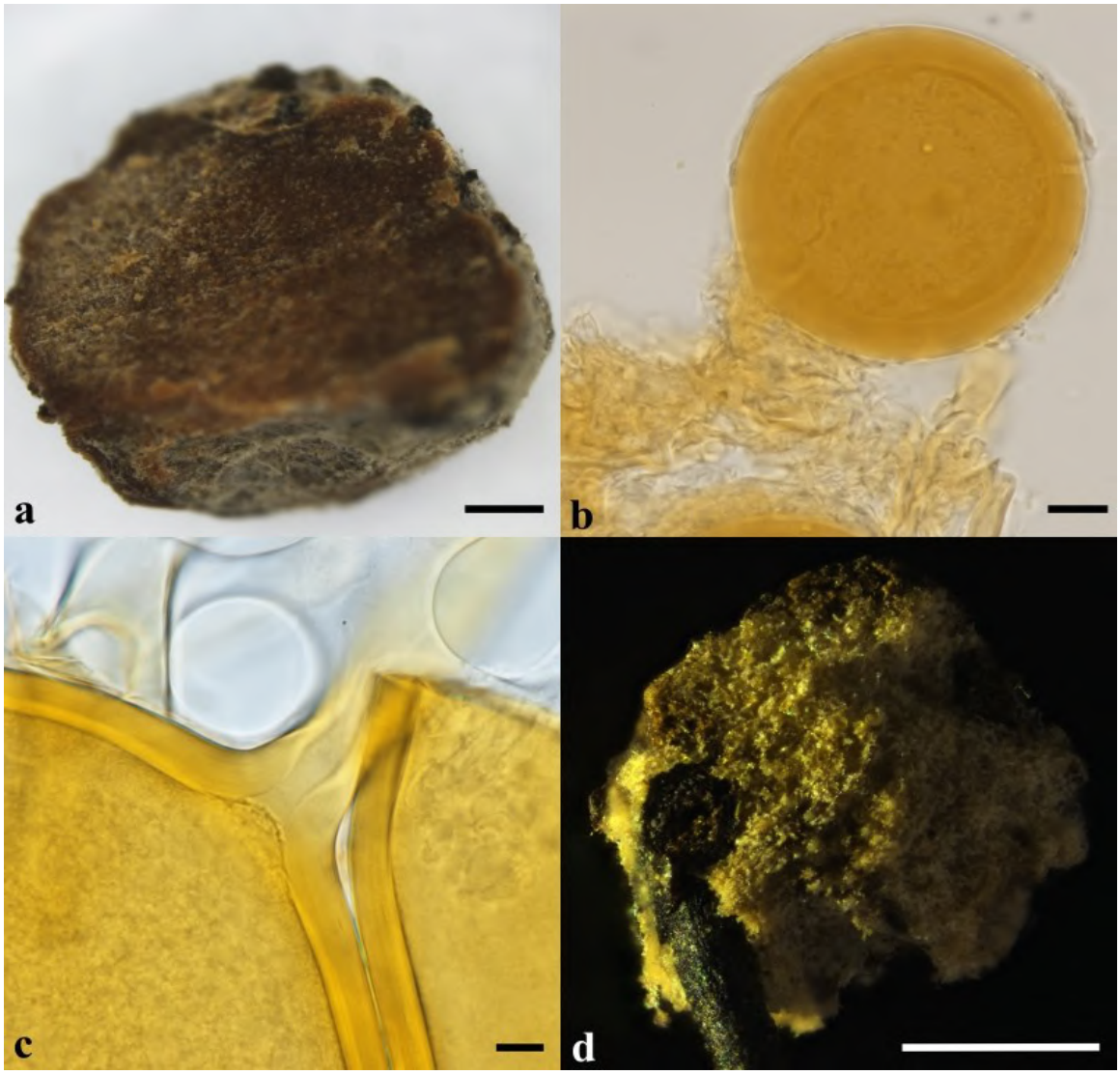


Figure 54 – *Glomeraceae*. a Glomerocarps of *Glomus microcarpum*. b Spores in glomerocarps of *G. microcarpum*. c Spores in sporocarps of *Glomus macrocarpum*. d Glomerocarps of *Sclerocarpum amazonicum*. Scale bars: a = 0.5 mm, b, c = 10 μm, d = 1mm.

Dominikia Błaszk., Chwat & Kovács, in Błaszkowski, Chwat, Góralska & Ryszka, Kovács, Nova Hedwigia 100(1-2): 228 (2014)
Index Fungorum Identifier 808255

Spores formed in loose or compact clusters, rarely singly; usually hypogeous, although epigeous glomerocarps have also been described. Spores develop blastically at the tip of sporogenous hyphae branched from a parent hypha, continuous with an extraradical hyphae. Spores are small, less than 70 µm in diameter, globose to subglobose, sometimes irregular, and glomoid, consisting of two to three layers in the spore wall. Subtending hyphae straight or recurved, cylindrical to funnel-shaped, rarely constricted at the spore base. The wall of the subtending hypha is continuous with the spore wall layers. Pore open or generally closed by a septum continuous with the second or third layer of the spore wall. Forming mycorrhiza with arbuscules, vesicles, and intra- and extraradical hyphae.

Type species – *Dominikia minuta* (Błaszk., Tadych & Madej) Błaszk., Chwat & Kovács 2015

Notes – *Dominikia* was described to accommodate *Glomus achrum* Błaszk. et al. *G. iranicum* Błaszk. et al. *G. minutum* Błaszk. et al. and *Dominikia disticha* Błaszk. et al. that form an independent clade sister to *Kamienskia* and *Rhizoglomus* (Błaszkowski et al. 2015b). Currently, 14 species belong to *Dominikia*, including mainly species producing spores in clusters and glomerocarps, but also singly in the soil as *D. difficilevidera* (Yu et al. 2022, Błaszkowski et al. 2024).

Other genera in *Dominikiaceae*

Macrodominikia Oehl, Sieverd. & G.A. Silva, Taxonomy 4(4): 774 (2024)
Index Fungorum Identifier 855470; Index Fungorum (2025) lists one epithet, not listed in Species Fungorum (2025); DNA sequences available.

Type species – *Macrodominikia compressa* (Sieverd. et al.) Oehl, Siev. & G.A. Silva, Taxonomy 4(4): 774 (2024)

Microdominikia Oehl, Corazon-Guivin & G.A. Silva, Mycol. Prog. 18(12): 1400 (2019)
Index Fungorum Identifier 831098; Index Fungorum (2025) and Species Fungorum (2025) list one epithet; DNA sequences available.

Type species – *Microdominikia litorea* (Błaszk. & Kozłowska) Oehl, Corazon-Guivin & G.A. Silva 2019

Nanoglomus Corazon-Guivin, G.A. Silva & Oehl, Mycol. Prog. 18(12): 1398 (2019)
Index Fungorum Identifier 831096; Index Fungorum (2025) and Species Fungorum (2025) list one epithet; DNA sequences available.

Type species – *Nanoglomus plukenetiae* Corazon-Guivin, G.A. Silva & Oehl 2019

Orientoglomus G.A. Silva, Oehl & Corazon-Guivin, Mycol. Prog. 18(12): 1400 (2019)
Index Fungorum Identifier 831100; Index Fungorum (2025) and Species Fungorum (2025) list one epithet; DNA sequences available.

Type species – *Orientoglomus emiratium* (Błaszkowski et al.) G.A. Silva, Oehl & Corazon-Guivin 2019

Kamienskiaceae G.A. Silva, Sieverd. & Oehl, Microfossils of the Precambrian of the USSR (Leningrad) 4(4): 772 (2024); Fig. 56
Index Fungorum Identifier 855468

Spores hypogeous and/or intraradical, in loose clusters to compact sporocarps, not organized around a central plexus of hyphae, hyaline, up to 50 µm diam. Spore wall with permanent layers, of which one may stain in Melzer's reagent. Subtending hyphae cylindrical to slightly funnel-shaped with an open pore. Forming vesicular-arbuscular mycorrhizae.

Family type – *Kamienskia* Błaszk., Chwat & Kovács, Nova Hedwigia 100(1-2): 230 (2014)

Notes – *Kamienskiaceae* is one of the new families introduced by Silva et al. (2024) according to a new organization of *Glomerales*, resulting from partial 45S nrDNA phylogeny.

According to Tedersoo et al. (2024), the clade representing the family *Kamienskiaceae* would be embedded in a larger clade representing *Sclerocystaceae*. The same analysis of Tedersoo et al. (2024) predicted at least one potential undescribed genus belonging to *Kamienskiaceae.* In our phylogenetic analysis, where eDNA sequences were not included, the clade presented high support (Fig. 4), but the sister clade *Sclerocystaceae* showed only moderate ML support.

Kamienskia Błaszk., Chwat & Kovács, Nova Hedwigia 100(1-2): 230 (2014)
Index Fungorum Identifier 808260; Index Fungorum (2025) and Species Fungorum (2025) list three epithets, though 2 are representative of the genus *Microkamienskia*; DNA sequences available.

Spores formed in loose to compact aggregates in soils, rarely inside roots, small (<50 µm diam), globose to subglobose, glomoid, composed of two permanent, hyaline layers, with Melzer's reaction in layer 2. Subtending hyphae hyaline, straight or recurved, flared to funnel-shaped, composed of two layers continuous with spore wall layers 1 and 2. Pore open.

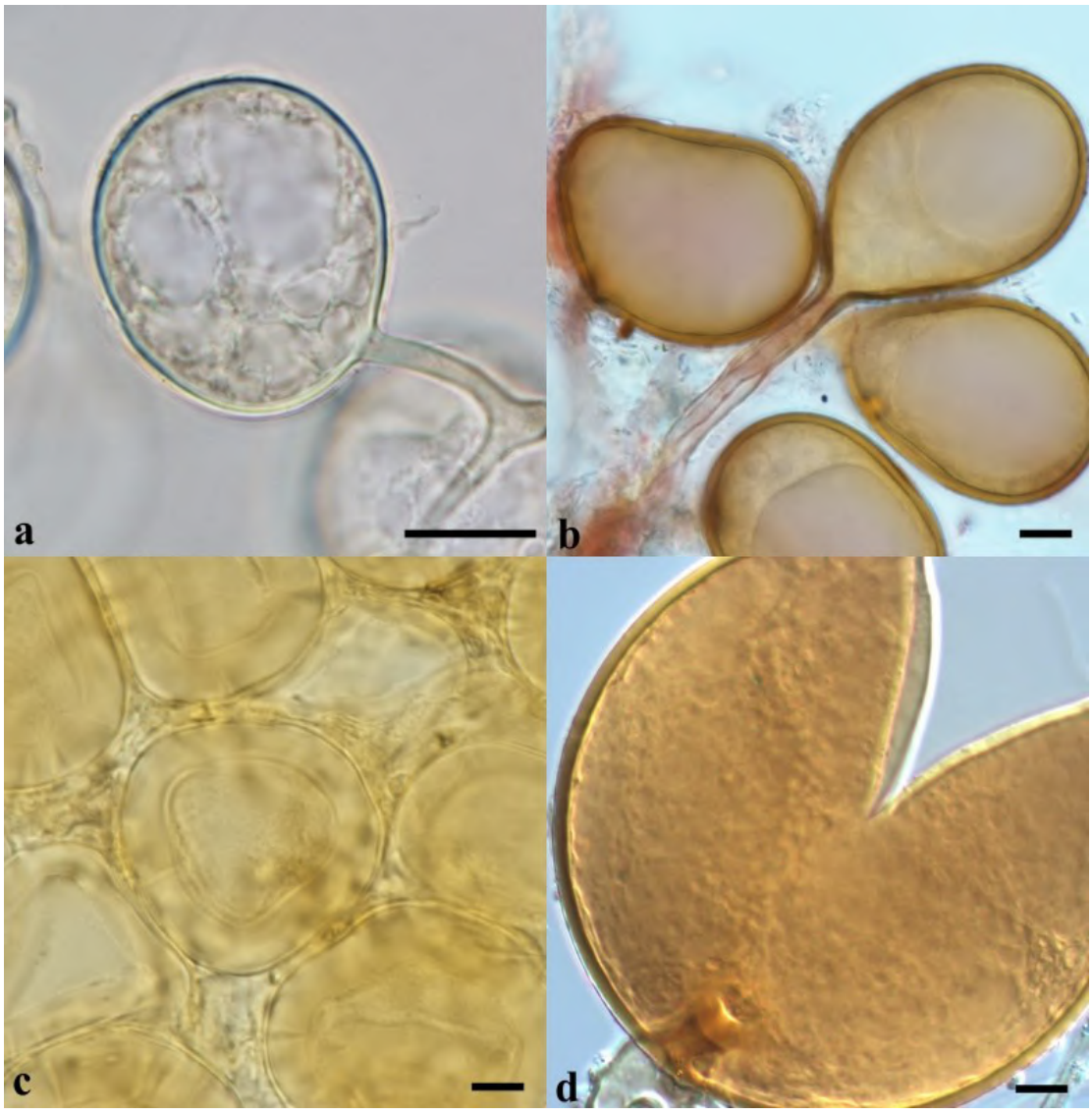


Figure 55 – *Dominikiaceae*. a Spores of the *Dominikia minuta.* b Cluster of spores of *Dominikia gansuensis*. c Spores in sporocarps of *Dominikia glomerocarpica*. d Spore wall of *Macrodominikia. compressa*. Scale bars: a–d = 10 µm, c = 5 µm.

Type species – *Kamienskia bistrata* (Błaszk., D. Redecker, Koegel, Symanczik, Oehl & Kovács) Błaszk., Chwat & Kovács 2015

Notes – The genus was described to accommodate only *Glomus bistratum* Błaszk. et al. and *Glomus perpusillum* Błaszk. & Kovács (Błaszkowski et al. 2015b). *Kamienskia* is a monospecific genus since *G. perpusillum* was designated as the type species for the new genus *Microkamienskia* (Corazon-Guivin et al. 2019a).

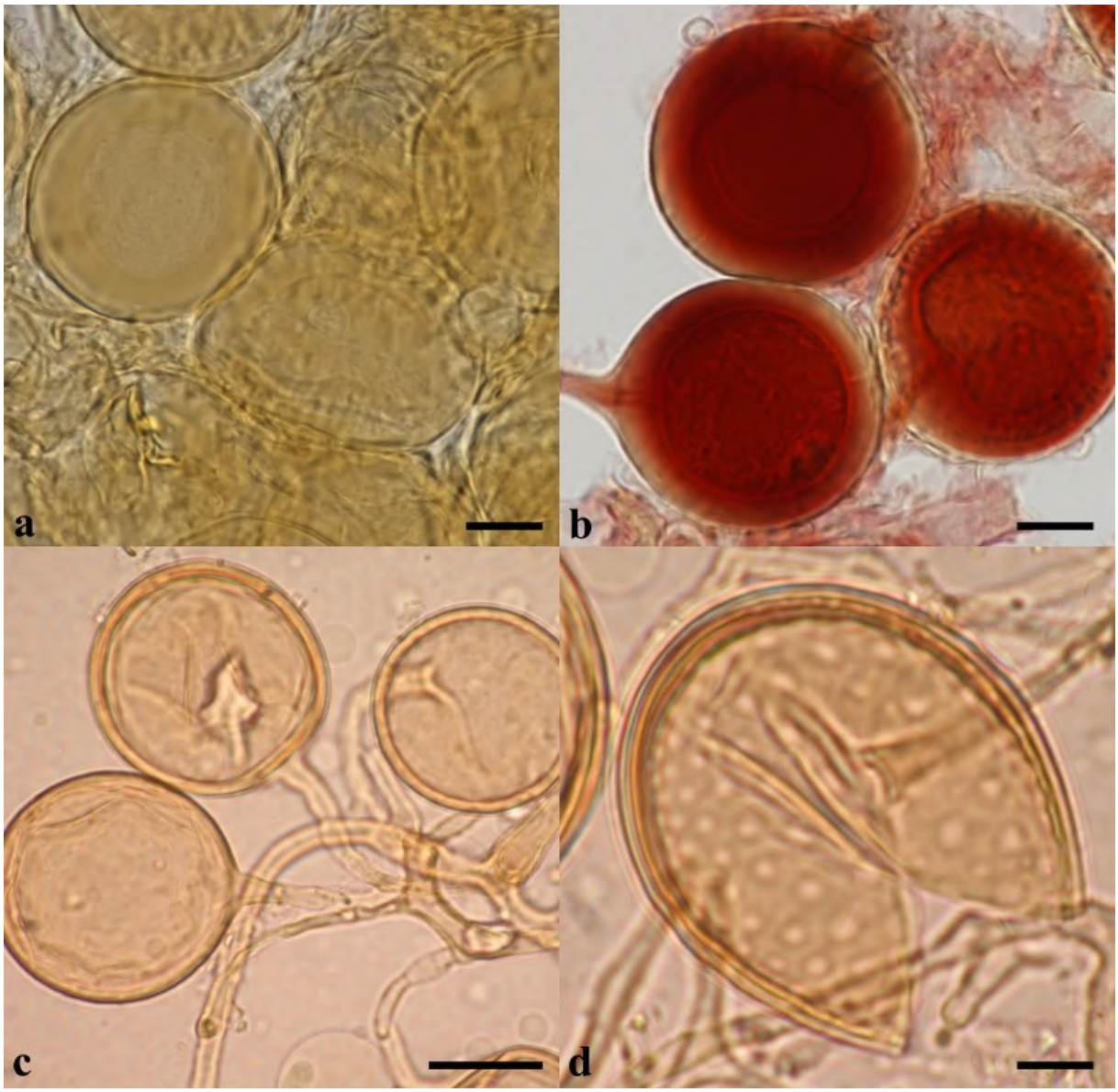


Figure 56 –. *Kamieskiaceae*. a Spores of the *Epigeocarpum crypticum* obtained from glomerocarp. b Cluster of *E. crypticum* with three spore wall layers (swl1–3) in Melzer reaction. c Cluster with spores of *Kamieskia bistrata* in PVLG. d Spore wall of *K. bistrata* with two spore wall layers (swl1–2) in Melzer reaction and inter interlayer collapsed. Scale bars: a, b, d = 10 µm, c = 20 µm.

Other genera in *Kamienskiaceae*

Epigeocarpum Błaszk., B.T. Goto, Jobim, Niezgoda & Magurno, Frontiers in Microbiology 12 (no. 655910): 10 (2021)

Index Fungorum Identifier 838879; Index Fungorum (2025) and Species Fungorum (2025) list two epithets for the genus; DNA sequences available.

Type species – *Epigeocarpum crypticum* Jobim, Błaszk., Niezgoda, Magurno & B.T. Goto 2021

Microkamienskia Corazon-Guivin, G.A. Silva & Oehl, Nova Hedwigia 109(3-4): 359 (2019)

Index Fungorum Identifier 830814; Index Fungorum (2025) lists three epithets as well as Species Fungorum (2025); DNA sequences available.

Type species – *Microkamienskia perpusilla* (Błaszk. & Kovács) Corazon-Guivin, G.A. Silva & Oehl 2019

Sclerocystaceae Oehl, G.A. Silva, & Sieverd, Microfossils of the Precambrian of the USSR (Leningrad) 4(4): 770 (2024); Fig. 57
Index Fungorum Identifier 855467

Glomoid spores are produced terminally or intercalary from subtending hyphae or arising radially from a central plexus of hyphae. Spores are produced singly, in loose or compact aggregates (clusters) with or without a peridium, either in soil or within roots. Spores globose, subglobose, ovoid or ellipsoid, with one wall typically consisting of two to three layers, occasionally up to five. Subtending hypha straight or slightly curved, cylindrical or slightly flared, sometimes slightly constricted at the spore base. Wall of the subtending hypha continuous with spore wall layers and for a certain distance concolourous with the spore wall, or slightly lighter in colour. Pore at the spore base open, or closed by a septum. Forming vesicular-arbuscular mycorrhizae, whose fungal structures stain blue to dark blue in trypan blue.

Family type – *Sclerocystis* Berk. & Broome, J. Linn. Soc., Bot. 14(no. 74): 137 (1873)

Notes – *Sclerocystaceae* is one of the new families introduced by da Silva et al. (2024) according to a new organization of *Glomerales*, resulting from partial 45S nrDNA phylogeny. Analysis of Tedersoo et al. (2024) predicted 17 potential undescribed genera belonging to *Sclerocystaceae*, making it the most taxonomically diverse family in *Glomeromycota*.

Genome available for several species, including *Rhizoglomus irregulare* DAOM197198 (Tisserant et al. 2013, Lin et al. 2014), *R. irregulare* MUCL 43196 (originally ascribed to *Glomus diaphanum* Błaszkowski et al. 2018b) (Chen et al. 2018, Morin et al. 2019), and several other isolates of the species; *Rhizoglomus clarum* (Kobayashi et al. 2018), *Rhizoglomus proliferum* (Singh et al. 2021a), *Oehlia diaphana* DAOM 227022 (erroneously identified as *Rhizophagus cerebriforme;* Błaszkowski et al. 2018b) (Chen et al. 2018, Morin et al. 2019). Transcriptome available for *Rhizoglomus irregulare* DAOM234181 (Beaudet et al. 2018).

Moreover, the family harbours a wealth of species with a broad biotechnological role, commonly used in agronomy and the restoration of degraded areas (Igiehon et al. 2017, Pedroso et al. 2018, Medeiros et al. 2021). Species of *Rhizoglomus*, particularly *R. irregulare*, are largely applied in commercial formulations of arbuscular mycorrhizal fungal inoculants (Basiru et al. 2021), representing the 100 most cited fungi (Bhunjun et al. 2024).

Sclerocystis Berk. & Broome, J. Linn. Soc., Bot. 14(no. 74): 137 (1873)
Index Fungorum Identifier 20512; Index Fungorum (2025) and Species Fungorum (2025) list 15 and 13 epithets, respectively; DNA sequences available.

Spores formed in compact sporocarps, in soils or within roots, arising radially from a central plexus of hyphae. Sporocarps whitish to brownish orange, covered by a dense peridium with sinuous hyphae or with hemispherical arrangements connecting glomerospores in columns. Spores pale yellow to reddish yellow, globose to subglobose, often pulvinate, elliptical to clavate, with a wall consisting of one to two layers. Subtending hyphae straight or recurved, cylindrical to funnel-shaped, continuous and concolours with the spore wall. Pore at the spore base is open or closed by a thin, curved septum. Mycorrhizal structures stain intensely in trypan blue.

Type species – *Sclerocystis coremioides* Berk. & Broome 1873

Notes – Silva et al. (2024) anchored the new family with *Sclerocystis coremioides*, as the type species. The only SSU sequence (ca. 1,700 bp) available for this species, when employed in phylogeny, formed a clade with a consensus sequence obtained from *S. sinuosa* (Krüger et al. 2012). Another taxon in possession of molecular data is *S.* cf. *pubescens* (*S. pubescens* is now recognized as non *Glomeromycota*), utilized together with *S. sinuosa* in the first published *rpb1*-based phylogeny of *Glomeromycota* (Stockinger et al. 2014). Currently, long SSU-ITS-LSU

sequences (as those used in our phylogeny) are available for *S. sinuosa*, significantly improving the reliability of phylogenetic support of *Sclerocystis* in *Sclerocystaceae.*

Other genera in *Sclerocystaceae*

Halonatospora Błaszk., Niezgoda, B.T. Goto & Kozłowska, Canadian Journal of Botany 96(11): 743 (2018)

Index Fungorum Identifier 826963; Index Fungorum (2025) lists only one epithet also listed in Species Fungorum (2025); DNA sequences available.

Type species – *Halonatospora pansihalos* (S.M. Berch & Koske) Błaszk., Niezgoda, B.T. Goto & Kozłowska 2018

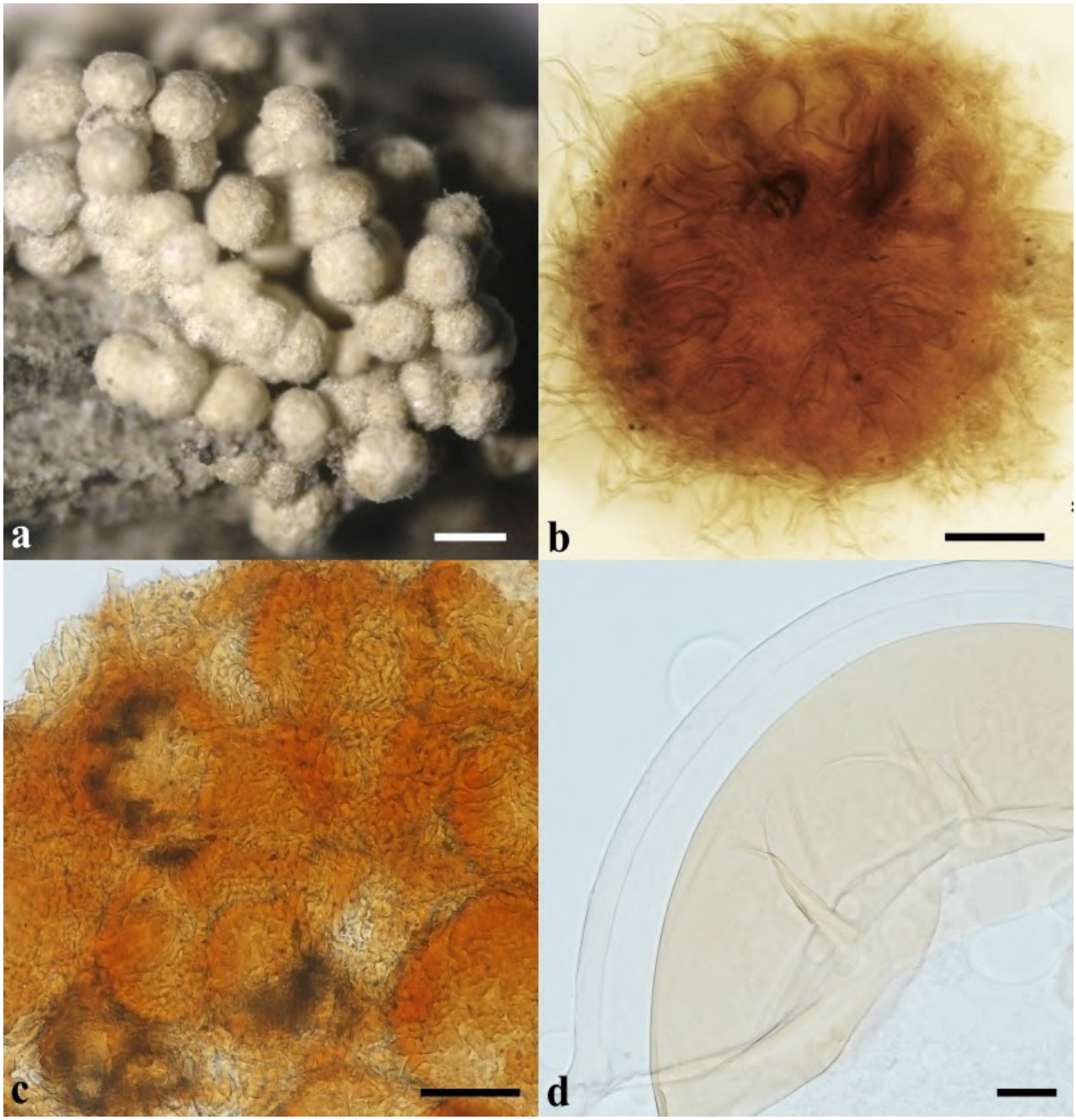


Figure 57 – *Sclerocystaceae*. a Glomerocarps of the *Sclerocystis coremioides.* b Peridium of the *S. coremioides*. c Peridium with sinuous hyphae in *S. sinuosa*. d Spore wall of *R. clarum*. Scale bars: a = 400 µm, b = 50 µm, c = 25 µm, d = 10 µm.

Oehlia Błaszk., Kozłowska, Niezgoda, B.T. Goto & Dalpé, Nova Hedwigia 107(3-4): 507 (2018)
Index Fungorum Identifier 824689; Index Fungorum (2025) lists only one epithet also listed in Species Fungorum (2025); DNA sequences available.

Type species – *Oehlia diaphana* (J.B. Morton & C. Walker) Błaszk., Kozłowska, Niezgoda, B.T. Goto & Dalpé 2018

Parvocarpum Magurno, MycoKeys 107: 283 (2024)
Index Fungorum Identifier 853558; Index Fungorum (2025) lists only one epithet also listed in Species Fungorum (2025); DNA sequences available.

Type species – *Parvocarpum badium* (Oehl, Redecker & Sieverd.) Magurno 2024

Rhizoglomus Sieverd., G.A. Silva & Oehl, Mycotaxon 129(2): 377 (2015)
Index Fungorum Identifier 803191; Index Fungorum (2025) lists 23 epithets as well as Species Fungorum (2025), still including *R. neocaledonicum* (now *Silvaspora neocaledonica*); DNA sequences available for most of the species.

Type species – *Rhizoglomus intraradices* (N.C. Schenck & G.S. Sm.) Sieverd., G.A. Silva & Oehl 2015

Silvaspora Błaszk., Niezgoda, B.T. Goto, Crossay & Magurno, Frontiers in Microbiology 12 (no. 655910): 10 (2021)
Index Fungorum Identifier 838881; Index Fungorum (2025) lists only one epithet also listed in Species Fungorum (2025); DNA sequences available.

Type species – *Silvaspora neocaledonica* (D. Redecker et al.) Błaszk., Niezgoda, B.T. Goto, Crossay & Magurno 2021

Septoglomeraceae Oehl, G.A. Silva & Sieverd., Microfossils of the Precambrian of the USSR (Leningrad) 4(4): 768 (2024); Fig. 58
Index Fungorum Identifier 855466

Spores formed in soil singly or in loose clusters, occasionally inside roots; develop terminally or intercalary on funnel-shaped to rarely cylindrical or straight subtending hyphae. Spores globose to subglobose, sometimes irregular, ovoid to oblong, consisting of a mono- to multilayered wall. Subtending hypha wall is conspicuously continuous and concolourous with the spore wall, or slightly lighter in colour than the spore wall. Pore open or closed by one to several, straight to curved septa. Forming typical vesicular-arbuscular mycorrhiza, with mycorrhizal structures that stain intensely in trypan blue.

Family type – *Septoglomus* Sieverd., G.A. Silva & Oehl, Mycotaxon 116: 105 (2011)

Notes – Oehl et al. (2011b) described *Septoglomus* based on the morphology of subtending hyphae and phylogenetic analysis of rDNA that clearly separates into an independent, highly supported clade in *Glomeraceae* species forming glomoid pigmented spores with constricted and/or cylindrical subtending hyphae. The genus became type of *Septoglomeraceae*, originating from the new organization of *Glomerales* as proposed by Silva et al. (2024). The new family accounts for five genera and more than 20 species confirmed by phylogenetic placement, most of which belong to *Septoglomus*.

In the analysis of Tedersoo et al. (2024), the recently described genus *Blaszkowskia* G.A. Silva & Oehl was nested within *Viscospora*. The choice was dictated by a conservative approach aimed at preventing a proliferation of genera. Nevertheless, the same analysis predicted the possibility of two potential new genera outside the *Viscospora-Blaszkowskia* clade in *Septoglomeraceae*.

However, the phylogenetic analysis presented in this paper, using only sequences from described species, does not support the synonymization, with *B. deserticola* forming an independent clade sister to *Viscospora*. Thus, awaiting more taxa described in the *Viscospora-Blaszkowskia* clade and more clarification about their relationship, the latter is revalidated as an

independent genus in *Septoglomeraceae* based on available sequences. *Septoglomus titan*, described from Brazil (Goto et al. 2013), whose morphology differs from *Viscospora* spp., is affiliated to the *Viscospora* clade, suggesting a future emendation of the genus or a new genus clade.

Genome available for *Funneliformis mosseae* (Montoliu-Nerin et al. 2021) and *Funneliformis geosporum* (Sahraei et al. 2022). Transcriptome available for *Funneliformis mosseae* DAOM 236685 (Beaudet et al. 2018).

Species of *Funneliformis* are largely applied in commercial formulations of arbuscular mycorrhizal fungal inoculants (Basiru et al. 2021), representing one of the 100 most cited fungal genera (Bhunjun et al. 2024).

Septoglomus Sieverd., G.A. Silva & Oehl, Mycotaxon 116: 105 (2011)
Index Fungorum Identifier 518436; Index Fungorum (2025) lists 16 epithets and 15 are listed in Species Fungorum (2025), both databases including two species belonging to other genera in *Septoglomeraceae*; DNA sequences available.

Septoglomus species typically produce spores in loose clusters or singly in soils, rarely in roots. Spores globose to subglobose, rarely ovoid, with one or, less commonly, two subtending hyphae. The subcellular structure of spores consists of a single wall containing up to four layers. Melzer's reaction of the spore wall layers is not observed in most species. Subtending hyphae are straight or curved, cylindrical or flared to funnel-shaped, usually distinctly constricted at the spore base. The subtending hyphae wall is continuous with the spore wall layers. Pores are usually closed by a septum at the spore base, or at a short distance to the base in the subtending hyphae.

Type species – *Septoglomus constrictum* (Trappe) Sieverd., G.A. Silva & Oehl 2011

Notes – The type species of *Septoglomus*, *S. constrictum* (basionym *Glomus constrictum* Trappe) was originally isolated from Mexico (Trappe 1977). Since the original material for the description of the species was preserved in lactophenol and, therefore, not suitable for molecular analysis, a new epitype was designed using W3809 from C. Walker collection, and the species was moved to the new genus *Funneliformis* (Walker & Schüßler 2010). However, new evidence based on both morphological and phylogenetic analysis suggested that *G. constrictum* belonged to a new independent genus, *Septoglomus* (Oehl et al. 2011b). Because the newly designated epitype was derived from a culture isolated from Germany, obtaining sequences of *S. constrictum* from the type location will clarify the true phylogenetic position of the species.

Other genera in *Septoglomeraceae*

Blaszkowskia G.A. Silva & Oehl, Mycol. Prog. 22(74): 5 (2023)
Index Fungorum Identifier 847414; Index Fungorum (2025) and Species Fungorum (2025) list one epithet; DNA sequences available.

Type species – *Blaszkowskia deserticola* (Trappe, Bloss & J.A. Menge) Oehl & G.A. Silva, Mycol. Prog. 22(74): 5 (2023).

Funneliformis C. Walker & A. Schüßler, The *Glomeromycota*, A species list with new families and new genera (Gloucester): 13 (2010)
Index Fungorum Identifier 542894; Index Fungorum (2025) lists 18 epithets, Species Fungorum (2025) nine species, both databases include several species belonging to other genera in *Glomerales.* Among the species with molecular data, five are correctly affiliated with *Funneliformis*; DNA sequences are available.

Type species – *Funneliformis mosseae* (T.H. Nicolson & Gerd.) C. Walker & A. Schüßler 2010

Funneliglomus Corazon-Guivin, G.A. Silva & Oehl, Sydowia 71: 19 (2019)

Index Fungorum Identifier 829266; Index Fungorum (2025) lists only one epithet also listed in Species Fungorum (2025); DNA sequences available.

Type species – *Funneliglomus sanmartinensis* Corazon-Guivin, G.A. Silva & Oehl 2019

Viscospora Sieverd., G.A. Silva & Oehl, Mycotaxon 116: 108 (2011)
Index Fungorum Identifier 518439; Index Fungorum (2025) and Species Fungorum (2025) list three species, both datasets including *Blaszkowskia deserticola* as *Viscospora deserticola*; DNA sequences available.

Type species – *Viscospora viscosa* (T.H. Nicolson) Sieverd., Oehl & G.A. Silva 2011

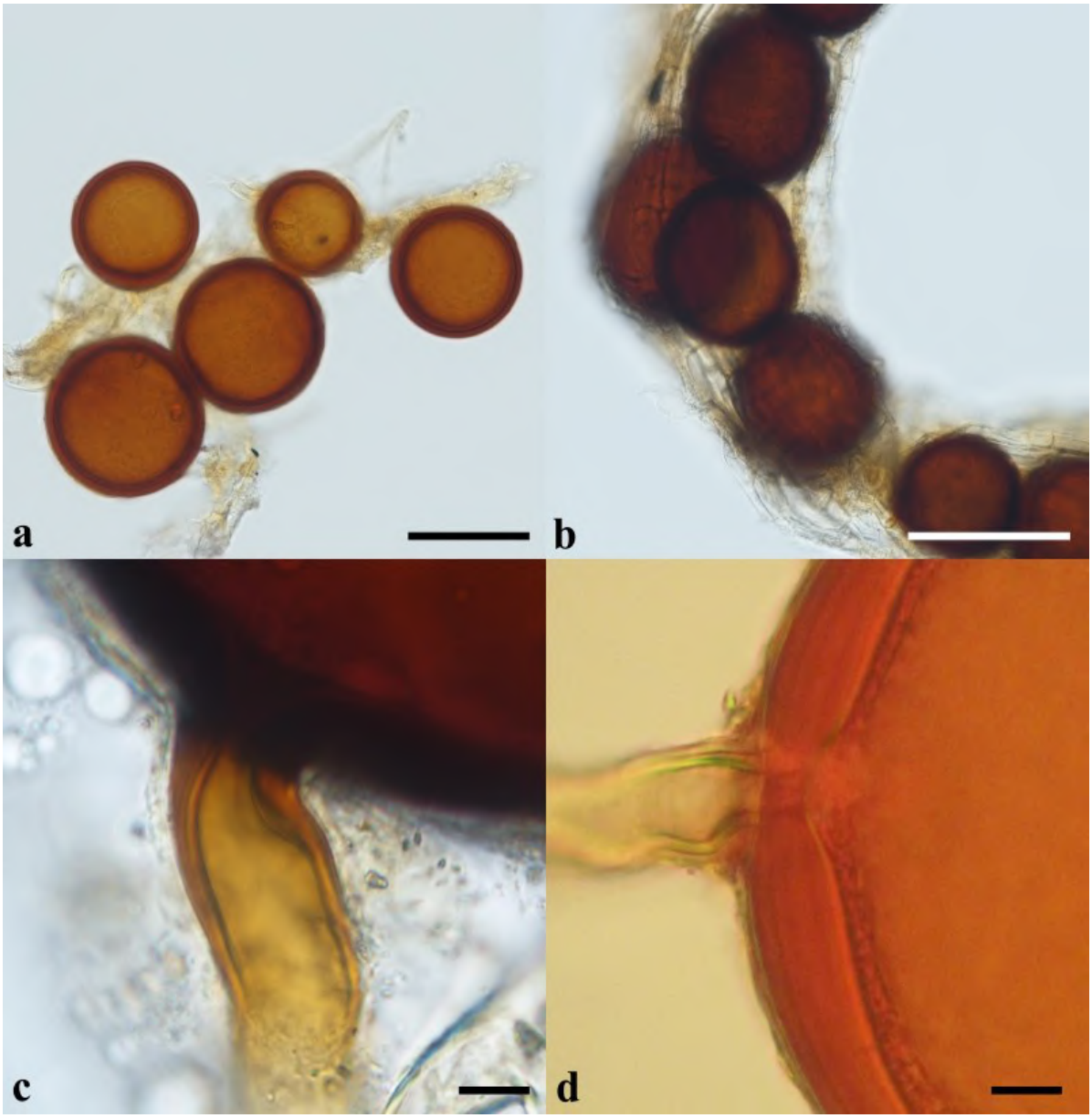


Figure 58 – *Septoglomeraceae*. a Cluster of *Septoglomus* sp. attached to the root. b Spores of *Septoglomus* sp. inside the root. c Constrict subtending hypha attached to the spore of *S. constrictum*. d Subtending hypha attached to the spore of *S. titan*. Scale bars: a = 100 μm, b = 150 μm, c = 10 μm, d = 5 μm.

Paraglomeromycetes Oehl, G.A. Silva, B.T. Goto & Sieverd.
Paraglomerales C. Walker & A. Schüßler

Paraglomeraceae J.B. Morton & D. Redecker, Mycologia 93 (1): 188 (2001); Fig. 59
= *Paraglomaceae* J.B. Morton & D. Redecker
Index Fungorum Identifier 82113

Glomerospores develop blastically at the tip of sporogenous hyphae; they are formed singly in the soil or in loose clusters in the soil or in the roots; they are rarely formed inside empty spores of other AMF. Glomerospores globose to subglobose, sometimes ovoid to obovoid or irregular, and generally unpigmented and small (50–130 µm). Spore structure consists of one wall with three hyaline layers (e.g., *Innospora*) or two multi-layered walls (e.g., *Paraglomus*). Reaction in Melzer's reagent is species-specific, usually staining orange to pinkish-yellow in the outermost spore wall layers. The subtending hypha is hyaline, straight or curved, cylindrical to slightly funnel-shaped, or rarely flared or inflated. The wall of the subtending hypha is continuous with the spore wall layers and presents the same colour. Pores usually open at the spore base or are sometimes closed distally by a septum. Mycorrhizal structures stain faintly in the Trypan blue. Vesicles are rarely found.

Family type – *Paraglomus* J.B. Morton & D. Redecker, Mycologia 93 (1): 188 (2001)

Notes – Based on nrDNA phylogenetic evidence, Morton & Redecker (2001) introduced *Paraglomeraceae* in *Glomerales*, in *Zygomycota* (Morton & Benny 1990), to accommodate the new ancestral genus *Paraglomus* with two glomoid species (*P. brasilianum*, *P. occultum*). Schüßler et al. (2001) proposed to include *Paraglomerales* in *Glomeromycota* with the newly introduced family *Paraglomeraceae*. Afterward, the new class *Paraglomeromycetes* was erected to accommodate the order (Oehl et al. 2011f). Although some species placed in *Paraglomus* were originally described as forming a single spore wall, Mello et al. (2013) suggested that only *P. majewskii* (Błaszkowski et al. 2012) produced a single wall. This morphological feature agreed with subsequent phylogenetic analyses, suggesting that this species represents a separate genus in *Paraglomeraceae*, leading to the erection of the monospecific *Innopora* (Błaszkowski et al. 2017). More *Paraglomus* species were described or recognized in the last decade through morphological, molecular, and ecological studies (Mello et al. 2013, Oehl et al. 2016, Corazon-Guivin et al. 2020, Lebeuf et al. 2021). Environmental sequence data suggest that *Paraglomeraceae* harbours a much larger richness than the 11 species currently known (Mello et al. 2013, Yang et al. 2018). Tedersoo et al. (2024) enlarged the family with one potential new genus. *Paraglomeraceae* are documented in at least 50 countries from different climate zones.

Paraglomus J.B. Morton & D. Redecker, Mycologia 93 (1): 188 (2001)
Index Fungorum Identifier 28458

Description as in *Paraglomeraceae*. *Paraglomus* differs from *Innospora* in having two spore walls. Some species might have at least one ornamented spore wall layer with shallow, pentagonal pits (e.g., *P. bolivianum*, *P. pernambucanum*) or labyrinthiformis ornamentation (e.g. *P. brasilianum*).

Type species – *Paraglomus occultum* (C. Walker) J.B. Morton & D. Redecker, Mycologia 93(1): 190 (2001)

Notes – Relying mainly on 18S nrDNA phylogenies, Morton & Redecker (2001) introduced *Paraglomus* to categorize the species *P. occultum* and *P. brasilianum*, previously recognized in *Glomus*. Morphologically, these species differed from other *Glomus* species only by the faint colouration of the intraradical hyphae in Trypan blue solution. However, phylogenetically, they were shown to be close to *Archaeospora* and to represent the most basal lineage of the glomeromycotan fungi. According to the analysis of ITS, SSU and LSU sequences, Renker et al. (2007) placed *G. laccatum* (Błaszkowski 1988b) in the genus *Paraglomus*. Oehl et al. (2011e) transferred two more *Glomus* species to *Paraglomus* only based on morphological similarity of their spores (*P. albidum*, *P. lacteum*). Using partial SSU and LSU sequences, Błaszkowski et al. (2012) described *P. majewskii*, later transferred to the new monospecific genus *Innospora* in *Paraglomeraceae* based on new phylogenies and the one-walled spores (vs. *Paraglomus* spp. with two-walled spores) (Błaszkowski et al. 2017). Mello et al. (2013) described *P. pernambucanum* and transferred *Pacispora boliviana* (Sieverding & Oehl 2004) to *Paraglomus*. Based on spore

morphology and mycorrhizal colonization characteristics, Oehl et al. (2016) described *P. turpe*. Finally, two new *Paraglomus* species from Peruvian Amazonia (*P. occidentale*, *P. peruvianum*) were introduced by using concomitant morphological and molecular evidence (Corazon-Guivin et al. 2020, Lebeuf et al. 2021). Currently, *Paraglomus* groups seven species supported by molecular phylogeny and three species whose phylogenetic evidence is still missing.

Paraglomus spp. occur in alpine, temperate, Mediterranean to tropical, subtropical, arid and humid areas (Mello et al. 2013) across nearly 50 countries, and are very common in agricultural soils (Gosling et al. 2013, Oehl et al. 2017).

Inoculation with *P. occultum* was shown to confer salt tolerance in tomato plants by improving nutritional status and regulating expressions of stress-responsive genes (aquaporins and SOS1) (Liang et al. 2022). In orange trees, it assisted in the osmotic adjustment, altering the sugar metabolism and ensuring a greater concentration of fructose, glucose and sucrose in the leaves (Wu et al. 2017). Furthermore, *Paraglomus* was proven to modulate the activity of salicylic acid, an important phytohormone in citrus canker resistance (Zhang et al. 2018a).

There are two genome assemblies and one transcriptome available in GenBank from *P. brasilianum* (Beaudet et al. 2018, Montoliu-Nerin et al. 2021) and *P. occultum* (Montoliu-Nerin et al. 2021, Malar et al. 2022). They demonstrate that these two early branching species keep a reduced genome size compared to other AMF taxa such as *Scutellospora* and *Rhizoglomus* (Tisserant et al. 2013, Montoliu-Nerin et al. 2021).

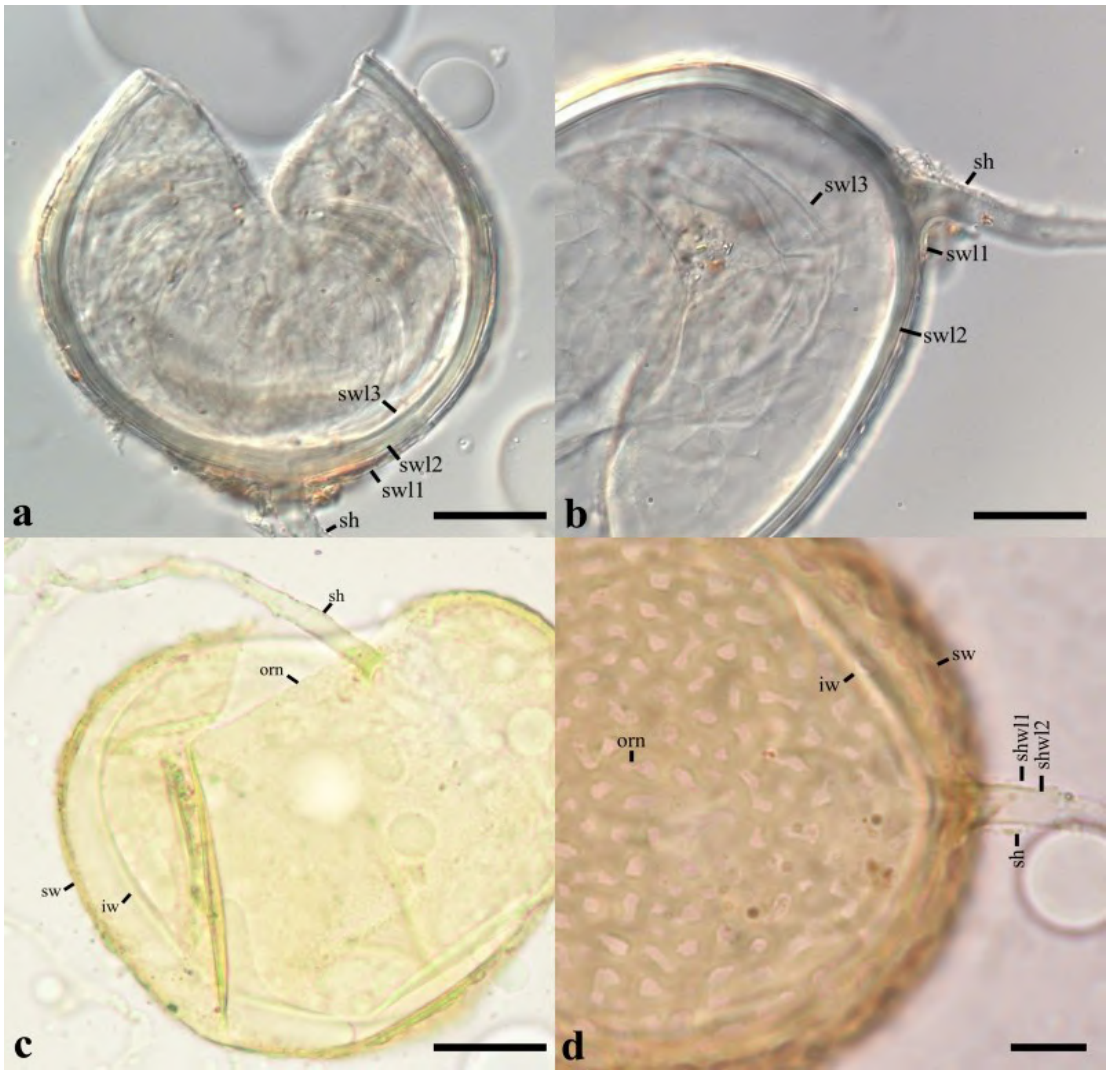


Figure 59 – *Paraglomeraceae.* a, b *Paraglomus occultum* spores with a 3–layered (swl1–3) spore wall and the subtending hyphae (sh) (courtesy of E. Furrazola). c *P. brasilianum* with spore wall

(sw and iw) and ornamentation (orn). d *P. pernambucanum* with a pigmented and ornamented (orn) spore wall. Scale bars: a–c = 20 µm, d = 10 µm.

Other genus in *Paraglomeraceae*

Innospora Błaszk., Kovács, Chwat & A. Kozłowska, Nova Hedwigia 105(3-4): 401 (2017)
Index Fungorum Identifier 820124; Index Fungorum (2025) lists only one epithet also listed in Species Fungorum (2025); DNA sequences available.

Type species – *Innospora majewskii* (Błaszk. & Kovács) Błaszk., Kovács, Chwat & Kozłowska 2017

Pervetustaceae Błaszk., Chwat, Kozłowska, Symanczik & Al-Yahya'ei, Nova Hedwigia 105(3–4): 403 (2017); Fig. 60
Index Fungorum Identifier 820126

Spores are glomoid, hyaline or colourless, very small, globose to subglobose and very rarely ovoid, with one spore wall. Mode of spore germination unknown. Spores are produced blastically at the tip of sporogenous hyphae, singly in soil and have a simple spore wall structure with two hyaline layers. Layer 1, forming the spore surface, evanescent and short-lived, usually highly deteriorated or completely sloughed in most spores. Layer 2 laminate, smooth, consisting of very thin, <0.5 µm thick, laminae, tightly adherent to each other. None of these layers shows amyloid or dextrinoid reactions in Melzer's reagent. Subtending hyphae hyaline, with a pore open or occluded by a straight or curved septum connecting the inner surfaces of subtending hyphal wall layer 2. Mycorrhiza with arbuscules staining variably in Trypan blue. nrDNA sequences are highly divergent from those of *Innospora* and *Paraglomus* spp., which represent *Paraglomeraceae*, the sister family to *Pervetustaceae*.

Family type – *Pervetustus* Błaszk., Chwat, Kozłowska, Symanczik & Al-Yahya'ei, Nova Hedwigia 105 (3–4): 404 (2017)

Notes – *Pervetustaceae* has only one genus (*Pervetustus*) and one species (*P. simplex*). The Latin name, *Pervetustus*, refers to the molecular phylogeny of the type species of the family, suggesting its very ancient divergence in the *Paraglomerales* clade. Analysis of Tedersoo et al. (2024, Fig S1) revealed several clades within the genus that may represent yet-to-be-described species. Originally described from an undisturbed natural field located in Oman, two maritime sand dune sites belonging to Greece and Tunisia, and soil of a nickel mine in New Caledonia. The geographic distribution of *Pervetustaceae* is very restricted, being reported, in addition to the countries of origin, only in Brazil, Canada, Morocco and the USA (Błaszkowski et al. 2017, Vieira et al. 2019b, Dirks & Jackson 2020, El Hilali et al. 2022, Pawuluwage et al. 2022).

Pervetustus Błaszk., Chwat, Kozłowska, Symanczik & Al-Yahya'ei, Nova Hedwigia 105 (3–4): 404 (2017)
Index Fungorum Identifier 820127

As in the description of *Pervetustaceae*.

Type species – *Pervetustus simplex* Błaszk., Chwat, A. Kozłowska, Crossay, Symanczik & Al-Yahya'ei, Nova Hedwigia 105(3–4): 404 (2017)

Notes – As in *Pervetustaceae* notes.

KICKXELLOMYCOTA Tedersoo, Sanchez-Ramirez, Kõljalg, Bahram, M. Döring, Schigel, T.W. May, M. Ryberg & Abarenkov
Asellariomycetes Tedersoo, Sanchez-Ramirez, Kõljalg, Bahram, M. Döring, Schigel, T.W. May, M. Ryberg & Abarenkov
Asellariales Manier ex Manier & Lichtw.
Asellariaceae Manier ex Manier & Lichtw., Annls Sci. Nat., Bot. Biol. Vég., sér. 12 9: 526 (1968)
Index Fungorum Identifier 80487

Thalli branched, holdfasts elaborate, plugged septum, generative cells disarticulate and function as propagules, do not produce external and deciduous trichospores Sexual reproduction absent or extremely uncommon (Benjamin 1979, Lichtwardt 1986).

Family type – *Asellaria* R.A. Poiss., Bull. biol. Fr. Belg. 66: 232 (1932)

Ecology & life modes – Members of *Asellariaceae* have adapted to semi-terrestrial insects (*Collembola*) and isopods dwelling in freshwater, marine, and terrestrial environments.

Notes – Manier & Lichtwardt (1969) introduced *Asellariaceae* to accommodate *Asellaria.*The type genus *Asellaria* comprises nine species (Species Fungorum 2025). Lichtwardt & Manier (1978) upgraded *Asellariaceae* to an ordinal level and introduced *Asellariales.* Tedersoo et al. (2018) showed that *Asellariales* has a distinct phylogenetic lineage in Phylum *Kickxellomycota*. *Asellariaceae* is the only family in *Asellariales* that has had the least amount of research in *Trichomycetes* (as an ecological group) and as few as twelve species have been described. Tretter et al. (2014) provided phylogenetic analyses based on eight loci and confirmed the position of *Asellariaceae* within the *Kickxellomycotina*. Based on DNA sequence analyses, Tedersoo et al. (2018) introduced a new class, *Asellariomycetes,* to accommodate *Asellariaceae* under *Kickxellomycota,* which is followed in this study.

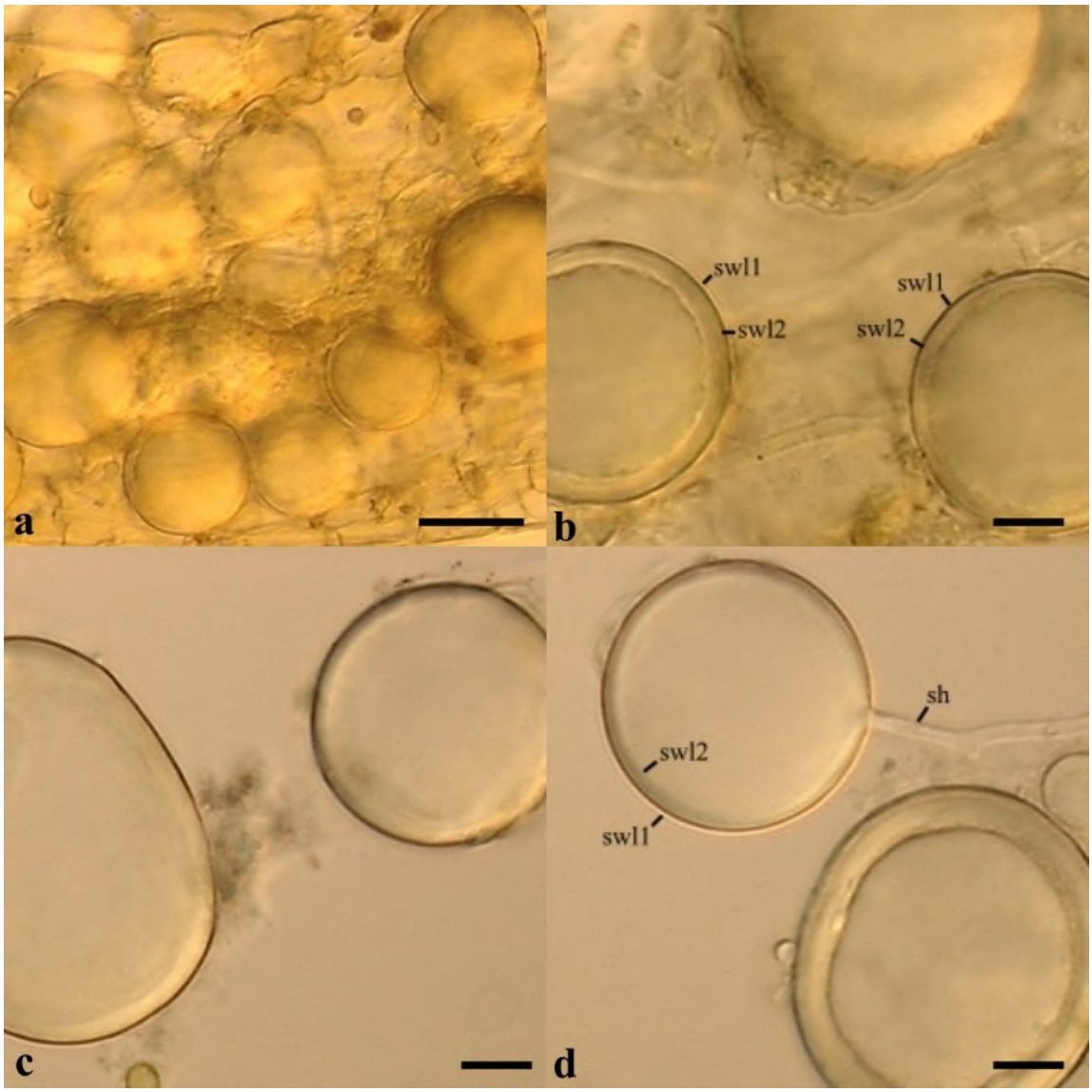


Figure 60 – *Pervetustaceae.* a *Pervetustus simplex* spores produced inside the roots of the host plant. b–d Spore wall layers (swl1 and 2) and subtending hypha (sh) attached. Scale bars: a = 20 μm, b–d = 10 μm.

Asellaria R.A. Poiss., Bull. biol. Fr. Belg. 66: 232 (1932); Fig. 61
Index Fungorum Identifier 20058

Thalli branched, long and main hyphal filaments with verticillate projections and secondary branching. Basal cell elongated or pyriform or globular or spherical, branched. The holdfast involves part of the hindgut lining in the central furrow. Profuse verticillate branches arise laterally from the basal cell. Arthrospores, slightly bent and with a truncate apex (Valle 2006).

Type species – *Asellaria caulleryi* R.A. Poiss., Bull. biol. Fr. Belg. 66: 233 (1932)

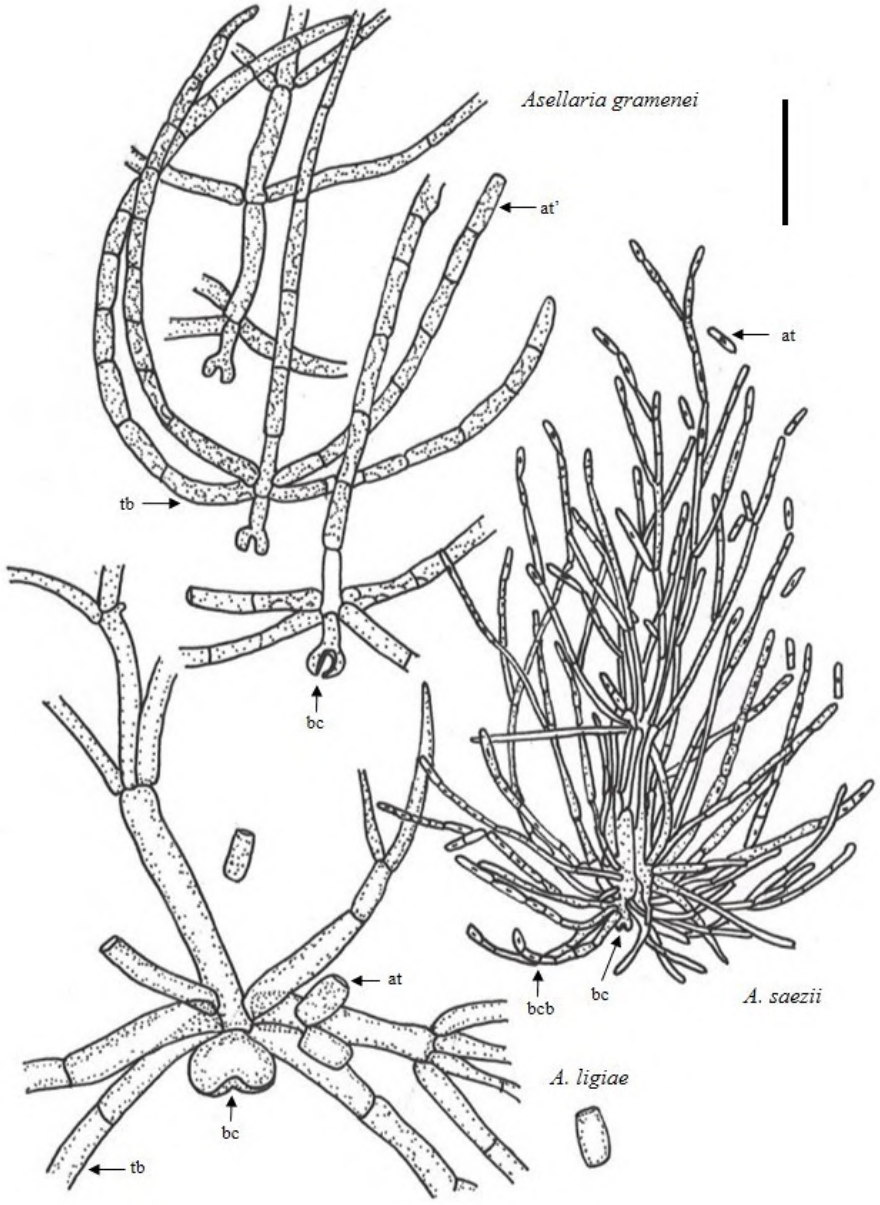


Figure 61 – *Asellaria gramenei*, *A. saezii* and *A. ligiae.* The species of *Asellaria* are here represented to easily compare shapes and sizes. Indicated here are: bc, basal cell; bcb, basal cell branches, at, arthrospores, at, arthrospores not disarticulated from the thallus: tb, thallial branches, Scale bar = 50 μm for all the figures (Redrawn from Valle 2006).

Barbatosporomycetes Tedersoo, Sanchez-Ramirez, Kõljalg, Bahram, M. Döring, Schigel, T.W. May, M. Ryberg & Abarenkov, Fungal Diversity 90: 151 (2018)
Barbatosporales Doweld

Barbatosporaceae Doweld, Index Fungorum 87: 1 (2014)
Index Fungorum Identifier 550396

With a basal cell harbouring a cup-shaped holdfast, the thalli branched. Trichospores are cylindrical, lack a collar, have numerous little appendages at their base, and may have a cylindrical wall or sleeve at their terminal end that, upon dehiscence, may disclose filaments that resemble appendages (White et al. 2006).

Family type – *Barbatospora* M.M. White, Siri & Lichtw.

Ecology and life modes – Entomopathogenic fungi (Hussain et al. 2014)

Notes – Tretter et al. (2013) confirmed the phylogenetic placement of *Barbatospora* in *Kickxellomycota.* Index Fungorum (2014) introduced *Barbatosporaceae* and *Barbatosporales* which comprise only one genus, *Barbatospora.* The genus is also monotypic thus the family is represented by the type species of *Barbatospora.* Tedersoo et al. (2018) introduced Class *Barbatosporomycetes* in Phylum *Kickxellomycota.* The *Ramicandelaber* clade, the *Mycomilia* together with *Spiromyces* clade, and two additional groupings (the *Barbatospora* clade and the *Orphella* clade) were recovered by Tretter et al. (2013, 2014) using a phylogenetic reconstruction. *Barbatospora* consistently lies under the branch which consists of *Harpellales*, *Kickxellales*, *Orphella*, and *Spiromyces*. This placement is present (but not entirely supported) in the rDNA study as well as in the MCM7, TSR1, 3-gene, and 4-gene analyses. One of the most consistent and well-supported evolutionary theories offered by this study is that *Barbatospora* is an 'offshoot' of an ancestral clade that split to produce the *Kickxellales* and *Harpellales*. This is based on the species' location in the study. *Barbatospora* may therefore provide important information about the early evolution of this group (Corsaro et al. 2018, Tretter et al. 2013).

Barbatospora M.M. White, Siri & Lichtw., Mycologia 98(2): 335 (2006)
Index Fungorum Identifier 29016

Branching thalli produce cylindrical trichospores that lack a collar but have several little appendages at their base. Trichospores may also have a cylindrical wall or sleeve which is sometimes called as the ‘cap-like’ structure at their terminal end, which, upon dehiscence, may show filaments that resemble appendages. Thallus has a cup-shaped holdfast and a basal cell (8–12 µm in diameter) that is branched close to the base. Branchlets with non-persistent fine numerous appendages at their base produce one to four cylindrical trichospores with dimensions ranging from 38–42 x 3–4 µm. Trichospores occasionally feature filaments that resemble appendages at their terminal end, which are initially hidden by a cylindrical sleeve or wall with dimensions of 6–13 x 2.5–4 µm (White et al. 2006).

Type species – *Barbatospora ambicaudata*; Fig. 62

Notes – Only one species of *Barbatospora* has been recorded (Wijayawardene et al. 2018). The genus is typically made up of fungi with underdeveloped thalli that are discovered in conjunction with the guts of various arthropod species. These fungi are generally reported to be associated with aquatic Simuliidae larvae (Naranjo-Ortiz & Gabaldón, 2019). Tretter et al. (2013) with eight loci phylogeny showed that *Barbatospora* has a unique position in the tree and is of particular significance.

Dimargaritomycetes Tedersoo, Sanchez-Ramirez, Kõljalg, Bahram, M. Döring, Schigel, T.W. May, M. Ryberg & Abarenkov
Dimargaritales R.K. Benj.
Dimargaritaceae R.K. Benj., Aliso 4(2): 364 (1959)
Index Fungorum Identifier 80703

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 coloured, 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, colourless, more or less biconvex plugs bearing small, usually globose enlargements at their poles; zygospores globoid, thick-walled, hyaline, formed from the fusion of similar, undifferentiated hyphae, usually containing one or more refractive globules at maturity. Parasites or facultative parasites of other *Mucorales* (Benjamin 1959).

Family type – *Dimargaris* Tiegh., Annls Sci. Nat., Bot., sér. 6 1: 154 (1875)

Ecology & life modes – Cosmopolitan; Haustorial mycoparasites of *Mucorales* and *Ascomycota*; Typically isolated from dung and rarely from soil.

Notes – Benjamin (1959) defined *Dimargaritaceae*, which then includes four genera (Zycha et al. 1969). However, according to Tanabe et al. (2000), *Dimargaritaceae* is the only family in *Dimargaritales* and it contains three genera that are obligately mycoparasitic primarily on mucoralean hosts. Tretter et al. (2013) amplified the MCM7 of a single representative *Dimargaris bacillosporus* and placed it as a monophyletic clade under *Kickxellomycotina*. Voigt & Kirk (2012) stated that there are only 18 species in four genera: *Dimargaris*, *Dispira*, *Spinalia* and *Tieghemiomyces*, in *Dimargaritales*.

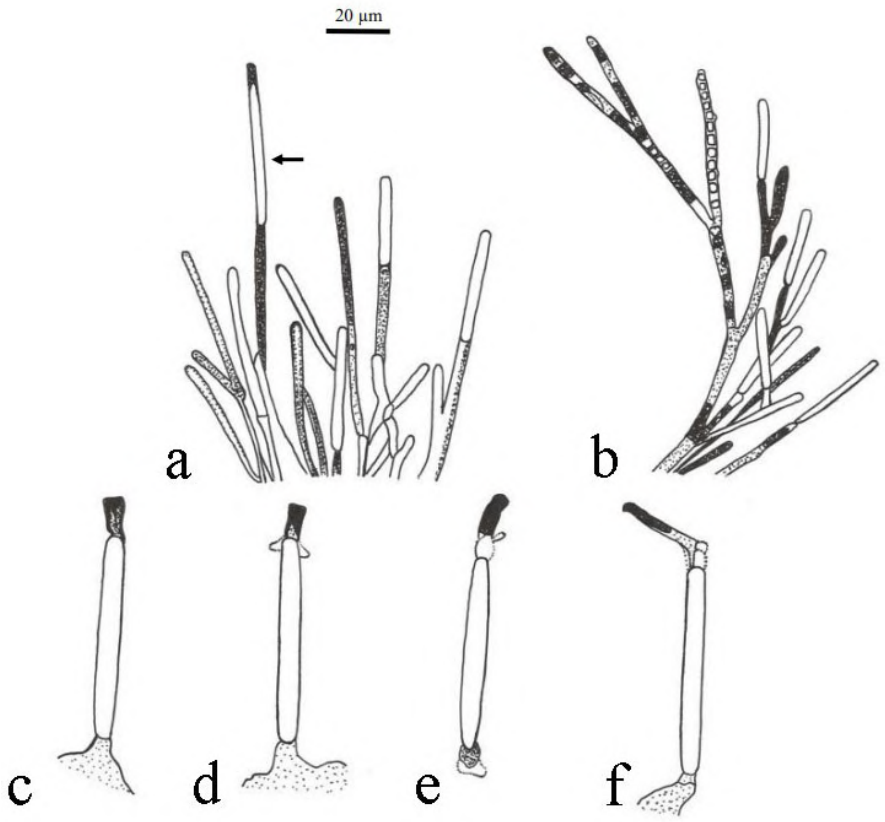


Figure 62 – *Barbatospora ambicaudata.* a Detaching with a cylindrical wall that resembles a cap at the terminal end. b Sporulating branchlets removed from a simuliid larva. c-f reconstruction of a sequence of development in released trichospores, following dehiscence of the cap-like structure at the terminal end, displaying numerous appendages basally and appendage-like filaments distally (modified drawing from White et al. 2006).

Dimargaris Tiegh., Annls Sci. Nat., Bot., sér. 6 1: 154 (1875); Fig. 63
Index Fungorum Identifier 20178

Sporangiophores erect, septate, at first simple, becoming irregularly cymosely or verticillately branched and producing fertile heads terminally; sterile branches absent; spore-heads composed of

few or many sporiferous branchlets subtended or not subtended by vesicular enlargements; sporiferous branchlets simple or ramiform, consisting of several superposed cells produced by apical and lateral budding, each cell giving rise to distal whorls of two-spored merosporangia; spores smooth, ellipsoidal or bacilliform, immersed in liquid at maturity; zygospores thick-walled, hyaline, smooth or delicately punctate (Benjamin 1959).

Type species – *Dimargaris cristalligena* Tiegh., *Annls Sci. Nat.*, Bot., sér. 6(1): 154 (1875)

Other genera in *Dimargaritaceae*

Dispira Tiegh., Annls Sci. Nat., Bot., sér. 6 1: 160 (1875)

Index Fungorum Identifier 20186; Index Fungorum (2025) and Species Fungorum (2025) accepted four species.

Type species – *Dispira cornuta* Tiegh. 1875

Tieghemiomyces R.K. Benj., Aliso 4(2): 390 (1959)

Index Fungorum Identifier 20577; Index Fungorum (2025) and Species Fungorum (2025) accepted two species.

Type species – *Tieghemiomyces californicus* R.K. Benj. 1959

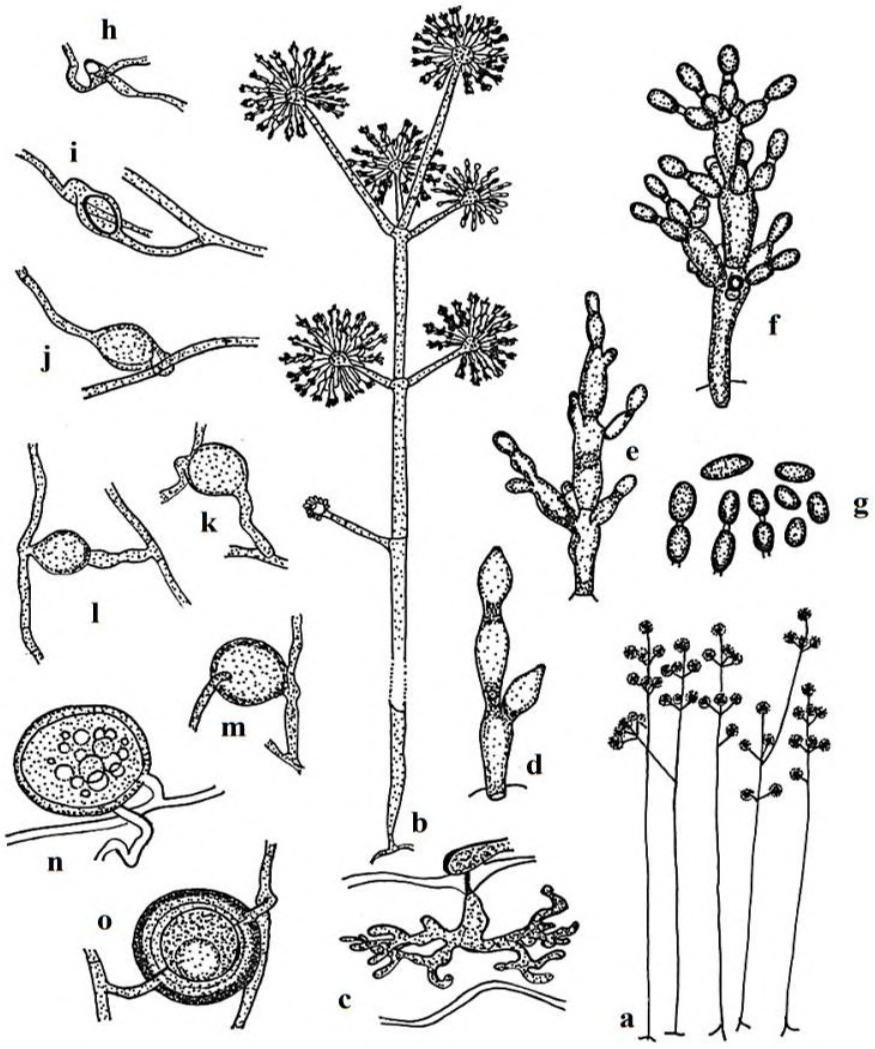


Figure 63 – *Dimargaris arida*. a Habit sketches of sporophores × 30. b Typical sporophore showing characteristic pseudovericillate branching pattern × 145. c Haustorium × 1080. d-f Three successive stages in the development of the sporiferous branchlets and merosporangia × 1360. g Three mature merosporangia prior to disappearance of the sporangia wall and five sporangiospores

× 1360. h-o Successive stages in the development of the zygospore × 600 (redrawn from Benjamin 1965).

Harpellomycetes Tedersoo, Sanchez-Ramirez, Kõljalg, Bahram, M. Döring, Schigel, T.W. May, M. Ryberg & Abarenkov
Harpellales Lichtw. & Manier
Harpellaceae L. Léger & Duboscq ex P.M. Kirk & P.F. Cannon, Fungal Families of the World: 152 (2007)
Index Fungorum Identifier 80838

Thalli are unbranched, attached to the host's peritrophic membrane or, less frequently, to the lining of the host's hindgut (Frost & Manier 1971, Lichtwardt et al. 1986).

Family type – *Harpella* L. Léger & Duboscq, C. r. hebd. Séanc. Acad. Sci., Paris 188: 951 (1929)

Ecology & life modes – Reported as endo-commensal or parasites of arthropods from different environments (Lichtwardt et al. 1986, Kirk et al. 2008).

Notes – Léger & Duboscq (1929) introduced *Harpellaceae* L. Léger & Duboscq 1929 but invalid (Art. 32.1(c)) thus, Cannon & Kirk (2007) validated it. White et al. (2006) and Tretter et al. (2014) provided phylogenetic analyses for the order including *Harpellaceae*.

Other genera included
Carouxella Manier, Rioux & Whisler, Naturalia Monspel., Sér. bot. 16: 87 (1965) [1964-65]
= *Carouxella* Manier, Rioux & Whisler, Naturalia Monspel., Sér. bot. 13: 30 (1961)
Index Fungorum Identifier 20102; Index Fungorum (2025) and Species Fungorum (2025) accepted two species.

Type species – *Carouxella scalaris* Manier, Rioux & Whisler, Naturalia Monspel., Sér. bot. 16: 87 (1965) [1964-65]

Harpellomyces Lichtw. & S.T. Moss, Mycotaxon 20(2): 512 (1984)
Index Fungorum Identifier 25808; Index Fungorum (2025) and Species Fungorum (2025) accepted four species.

Type species – *Harpellomyces eccentricus* Lichtw. & S.T. Moss, Mycotaxon 20(2): 514 (1984)

Klastostachys Lichtw., M.C. Williams & M.M. White, Mycologia 103(4): 915 (2011)
Index Fungorum Identifier 519277; Index Fungorum (2025) and Species Fungorum (2025) accepted four species

Type species – *Klastostachys reflexa* (Lichtw. & M.C. Williams) Lichtw., M.C. Williams & M.M. White, Mycologia 103(4): 915 (2011)
Basionym: *Stachylina reflexa* Lichtw. & M.C. Williams, Mycologia 80(3): 401 (1988)

Stachylina L. Léger & M. Gauthier, C. r. hebd. Séanc. Acad. Sci., Paris 194(no. 26): 2262 (1932)
Index Fungorum Identifier 20550; Index Fungorum (2025) accepts 46 epithets and Species Fungorum (2025) accepted 43 species.

Type species – *Stachylina macrospora* L. Léger & M. Gauthier, C. r. hebd. Séanc. Acad. Sci., Paris 194(no. 26): 2263 (1932)

Stachylinoides Lichtw. & López-Lastra, Mycologia 91(6): 1069 (1999)
Index Fungorum Identifier 28353; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Stachylinoides arctata* Ferrington, Lichtw. & López-Lastra, in Lichtwardt, Ferrington & López-Lastra, Mycologia 91(6): 1069 (1999)

Legeriomycetaceae Pouzar, Folia geobot. phytotax. 7: 319 (1972)
Index Fungorum Identifier 80938

Thalli, eucarpic, branched with simple or bulbous base. Vegetative hyphae simple or branched, septate. Each septum with a lenticular cavity containing a biconvex plug. Asexual reproduction by the formation, in basipetal succession, of unispored trichospores with one or more long, thin appendages or appendages lacking. Sexual reproduction by variously attached biconical or fusiform zygospores, lanceolate zygospores attached basally, or spores that are elongate-cylindrical or somewhat coiled at one end. Symbionts typically attached with an acellular holdfast to the hindguts of the nymphs of the insect order Diptera, Ephemeroptera and Plecoptera (modified from Pouzar 1972, Benny et al. 2016b).

Family type – *Legeriomyces* Pouzar 1972

Ecology & life modes – Cosmopolitan, commonly found in mid- or hindgut of immature aquatic insects usually collected from fast-flowing streams, rarely in ponds and other still waters (Vojvodic & McCreadie 2008, Tretter et al. 2013, Valle 2013, Valle & Stoianova 2020).

Notes – Pouzar (1972) introduced *Legeriomycetaceae* with eight genera, *Glotzia*, *Graminella*, *Legeriomyces*, *Orphella*, *Pennella*, *Pteromaktron*, *Smittium* and *Spartiella* to replace the illegitimate name *Genistellaceae* L. Léger & M. Gauthier. Tretter et al. (2014) and Wang et al. (2014) resolved the phylogeny of *Legeriomyces* and other genera such as *Capniomyces*, *Zancudomyces*, *Pteromaktron*, *Lancisporomyces*, *Genistelloides* and accepted them in *Legeriomycetaceae* based on LSU and SSU gene sequences.

Legeriomyces Pouzar, Folia geobot. phytotax. 7: 319 (1972); Fig. 64
= *Genistella* L. Léger & M. Gauthier, *C*. r. hebd. Séanc. Acad. Sci., Paris 194 (no. 26): 2264 (1932).
Index Fungorum Identifier 20303

Highly branching thallus, Obpyriform trichospores without a collar with two filaments. Zygospores are biconical with an oblique peduncle. Commonly isolated from the larvae of Ephemerides, Nemurids, Simulids, Chironomids and Tipulids (adapted from Pouzar 1972).

Notes – Léger & Gauthier (1932) introduced *Genistella* L. Léger & M. Gauthier, but it is illegitimate since being a latter homonym of *Genistella* Ortega 1773 (Papilionaceae) (Art. 53.1). Thus, Pouzar (1972) proposed a new name, *Legeriomyces*, to accommodate *Genistella*.

Type species – *Legeriomyces ramosus* (L. Léger & M. Gauthier) Pouzar 1972

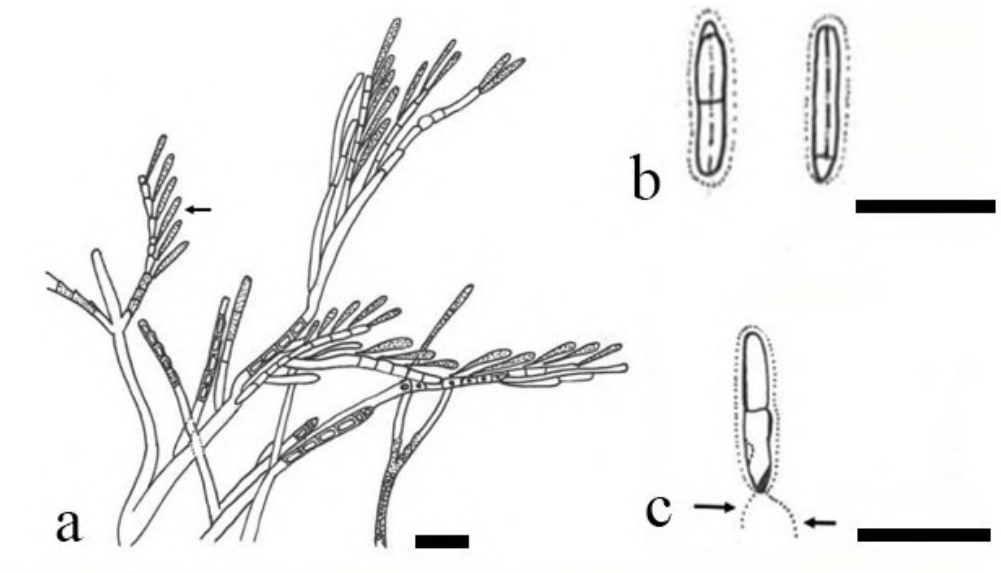


Figure 64 – *Legeriomyces limnephilidarum*. a Thallus with fertile branches producing trichospores (arrow). b Released obpyriform trichospores. c Released trichospore showing two appendages (arrows). Scale bars a–c = 20 µm.

Other genera in *Legeriomycetaceae*

Austrosmittium Lichtw. & M.C. Williams, in Williams & Lichtwardt, Canadian Journal of Botany 68(5): 1047 (1990).

Index Fungorum Identifier 25432; Index Fungorum (2025) accepted six species, and no species accept in Species Fungorum (2025).

Type species – *Austrosmittium kiwiorum* M.C. Williams & Lichtw. 1990.

Notes – This genus is regarded as an invalid genus (Index Fungorum 2024).

Bactromyces William & Strongman, Botany 9(2): 102 (2012).

Index Fungorum Identifier 561721; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Bactromyces fluminalis* William & Strongman 2012.

Baetimyces L.G. Valle & Santam., Mycologia 94(2): 321 (2002).

Index Fungorum Identifier 28592; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Baetimyces ancorae* L.G. Valle & Santam. 2002.

Bojamyces Longcore, Mycologia 81(3): 482 (1989).

Index Fungorum Identifier 25284; Index Fungorum (2025) and Species Fungorum (2025) accepted three species.

Type species – *Bojamyces repens* Longcore 1989.

Capniomyces S.W. Peterson & Lichtw., Mycologia 75(2): 242 (1983).

Index Fungorum Identifier 25790; Index Fungorum (2025) and Species Fungorum (2025) accepted three species.

Type species – *Capniomyces stellatus* S.W. Peterson & Lichtw. 1983.

Caudomyces Lichtw., Kobayasi & Indoh, Trans. Mycol. Soc. Japan 28(4): 376 (1988) [1987].

Index Fungorum Identifier 25162; Index Fungorum (2025) and Species Fungorum (2025) accepted three species.

Type species – *Caudomyces japonicus* Lichtw., Kobayasi & Indoh 1988.

Coleopteromyces Ferrington, Lichtw. & López-Lastra, Mycologia 91(6): 1064 (1999).

Index Fungorum Identifier 28351; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Coleopteromyces amnicus* Ferrington, Lichtw. & López-Lastra 1999.

Dacryodiomyces Lichtw., Mycologia 103(4): 912 (2011).

Index Fungorum Identifier 519323; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Dacryodiomyces oklahomensis* Lichtw. 2011.

Ejectosporus S.W. Peterson, Lichtw. & M.C. Williams, Mycologia 83(4): 389 (1991).

Index Fungorum Identifier 13996; Index Fungorum (2025) and Species Fungorum (2025) accepted three species.

Type species – *Ejectosporus magnus* S.W. Peterson, Lichtw. & M.C. Williams 1991.

Ephemerellomyces M.M. White & Lichtw., Mycologia 96(4): 893 (2004).

Index Fungorum Identifier 13996; Index Fungorum (2025) and Species Fungorum (2025) accepted two species.

Type species – *Ephemerellomyces aquilonius* M.M. White & Lichtw. 2004.

Furculomyces Lichtw. & M.C. Williams, Canadian Journal of Botany 70(6): 1196 (1992).
Index Fungorum Identifier 26463; Index Fungorum (2025) and Species Fungorum (2025) accepted three species.

Type species – *Furculomyces boomerangus* (M.C. Williams & Lichtw.) M.C. Williams & Lichtw. 1992.

Gauthieromyces Lichtw., Mycotaxon 17: 213 (1983).
Index Fungorum Identifier 25804; Index Fungorum (2025) and Species Fungorum (2025) accepted four species.

Type species – *Gauthieromyces microsporus* Lichtw. 1983.

Genistelloides S.W. Peterson, Lichtw. & B.W. Horn, Mycologia 73(3): 477 (1981).
Index Fungorum Identifier 20235; Index Fungorum (2025) and Species Fungorum (2025) accepted five species.

Type species – *Genistelloides hibernus* S.W. Peterson, Lichtw. & B.W. Horn 1981.

Genistellospora Lichtw., Mycologia 64(1): 168 (1972).
Index Fungorum Identifier 20236; Index Fungorum (2025) and Species Fungorum (2025) accepted six species.

Type species – *Genistellospora homothallica* Lichtw. 1972.

Glotzia Glotzia M. Gauthier ex Manier & Lichtw., Annls Sci. Nat., Bot. Biol. Vég., sér. 12 9: 528 (1970) [1969].
Index Fungorum Identifier 20245; Index Fungorum (2025) and Species Fungorum (2025) accepted 10 species.

Type species – *Glotzia centroptili* M. Gauthier ex Manier & Lichtw. 1970.

Graminella L. Léger & M. Gauthier ex Manier, Bull. Soc. Hist. nat. Toulouse 97: 251 (1962).
Index Fungorum Identifier 20249; Index Fungorum (2025) and Species Fungorum (2025) accepted three species.

Type species – *Graminella bulbosa* L. Léger & M. Gauthier ex Manier 1962.

Laculus William & Strongman, Botany 9(2): 103 (2012).
Index Fungorum Identifier 561718; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Laculus insecticola* William & Strongman 2012.

Lancisporomyces Santam., Mycologia 89(4): 639 (1997).
Index Fungorum Identifier 27694; Index Fungorum (2025) and Species Fungorum (2025) accepted six species.

Type species – *Lancisporomyces vernalis* Santam. 1997.

Legerioides M.M. White, Mycologia 91(6): 1022 (1999).
Index Fungorum Identifier 28354; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Legerioides tumidus* M.M. White 1999.

Legeriosimilis M.C. Williams, Lichtw., M.M. White & J.K. Misra, in Williams & Lichtwardt, Mycologia 91(2): 400 (1999).
Index Fungorum Identifier 28339; Index Fungorum (2025) and Species Fungorum (2025) accepted eight species.

Type species – *Legeriosimilis tricaudata* M.C. Williams, Lichtw., M.M. White & J.K. Misra 1999.

Pennella Manier, Annls Sci. Nat., Bot. Biol. Vég., sér. 12 9: 106 (1968).
Index Fungorum Identifier 28339; Index Fungorum (2025) and Species Fungorum (2025) accepted eight species.

Type species – *Pennella hovassei* Manier 1968.

Plecopteromyces Lichtw., Ferrington & López-Lastra, Mycologia 91(6): 1066 (1999).
Index Fungorum Identifier 28352; Index Fungorum (2025) and Species Fungorum (2025) accepted three species.

Type species – *Plecopteromyces patagoniensis* Lichtw., Ferrington & López-Lastra 1999.

Pseudoharpella Ferrington, M.M. White & Lichtw., Aquatic Insects 25(2): 86 (2003).
Index Fungorum Identifier 28897; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Pseudoharpella arcolamylica* Ferrington, M.M. White & Lichtw. 2003.

Pteromaktron Whisler, Canadian Journal of Botany 41: 897 (1963).
Index Fungorum Identifier 20455; Index Fungorum (2025) and Species Fungorum (2025) accepted two species.

Type species – *Pteromaktron protrudens* Whisler 1963.

Simuliomyces Lichtw., Mycologia 64(1): 179 (1972).
Index Fungorum Identifier 20521; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Simuliomyces microsporus* Lichtw. 1972.

Sinotrichium Juan Wang, S.Q. Xu & Strongman, Mycologia 102(1): 135 (2010).
Index Fungorum Identifier 513199; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Sinotrichium chironomidarum* Juan Wang, S.Q. Xu & Strongman 2010.

Smittium R.A. Poiss., Bull. Soc. sci. Bretagne 14(no. 85): 30 (1937) [1936].
Index Fungorum Identifier 20528; Index Fungorum (2025) accepts 98 species, and species Fungorum accepts 92 species (2024).

Type species – *Smittium arvernense* R.A. Poiss. 1937.

Spartiella Tuzet & Manier ex Manier, Annls Sci. Nat., Bot. Biol. Vég., sér. 12 9: 104 (1968).
Index Fungorum Identifier 20532; Index Fungorum (2025) and Species Fungorum (2025) accepted three species.

Type species – *Spartiella barbata* Tuzet & Manier ex Manier 1968.

Stipella L. Léger & M. Gauthier, C. r. hebd. Séanc. Acad. Sci., Paris 194(no. 26): 2263 (1932).
Index Fungorum Identifier 20553; Index Fungorum (2025) and Species Fungorum (2025) accept two species.

Type species – *Stipella vigilans* L. Léger & M. Gauthier 1932.

Stypomyces Doweld, Index Fungorum 112: 1 (2014).
Index Fungorum Identifier 550288; Index Fungorum (2025) and Species Fungorum (2025) accepted two species.

Type species – not indicated.

Tectimyces L.G. Valle & Santam., Mycol. Res. 106(7): 842 (2002).
Index Fungorum Identifier 28648; Index Fungorum (2025) and Species Fungorum (2025) accepted three species.

Type species – *Tectimyces leptophlebiidarum* L.G. Valle & Santam. 2002.

Trichozygospora Lichtw., Mycologia 64(1): 173 (1972).
Index Fungorum Identifier 20584; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Trichozygospora chironomidarum* Lichtw. 1972.

Trifoliellum Strongman & M.M. White, Mycologia 103(1): 220 (2011).
Index Fungorum Identifier 517875; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Trifoliellum bioblitzii* Strongman & M.M. White 2011.

Zancudomyces Yan Wang, Tretter, Lichtw. & M.M. White, Mycologia 105(1): 96 (2013).
Index Fungorum Identifier 563343; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Zancudomyces culisetae* Lichtw. ex Yan Wang, Tretter, Lichtw. & M.M. White 2013.

Zygopolaris S.T. Moss, Lichtw. & Manier, Mycologia 67(1): 122 (1975).
Index Fungorum Identifier 20608; Index Fungorum (2025) and Species Fungorum (2025) accepted two species.

Type species – *Zygopolaris ephemeridarum* S.T. Moss, Lichtw. & Manier 1975.

Zygopolaropsis Hiroki Sato & Degawa, in Sato & Degawa, Mycologia 110(1): 262 (2018).
Index Fungorum Identifier 822143; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Zygopolaropsis sphaerica* Hirok. Sato & Degawa 2018.

Kickxellomycetes Tedersoo, Sanchez-Ramirez, Kõljalg, Bahram, M. Döring, Schigel, T.W. May, M. Ryberg & Abarenkov
Kickxellales Kreisel ex R.K. Benj.
Kickxellaceae Linder, Farlowia 1(1): 56 (1943) [1943-1944]
Index Fungorum Identifier 80916

Vegetative hyphae are septate, branched, and hyaline. Sporangiophores erect or ascending, septate, simple or branched, white or light-coloured, forming sessile or stalked spore-bearing banchlets (sporocladia) with deciduous single-spored sporangiola produced by hyaline, ovoid, elongate-ellipsoid, flask-shaped or subcylindrical, non-deciduous cells (pseudophialides); sporangiospores one-celled, hyaline or yellowish, acicular, cylindrical, ellipsoid, fusoid or ovoid, with or without a long apical spinous protuberance, enveloped in fluid at maturity or remaining dry; septa of vegetative hyphae and sporangiophores typically with a median disk-shaped cavity containing a hyaline biconvex plug, with or without protuberances on each pole, persistent in 2–3% KOH and acidic stains. Zygospores, when present, formed from the fusion of similar hyphae, thick-walled, hyaline or yellowish, smooth (Linder 1943, Benjamin 1958, 1959, 1961, Kurihara et al. 2001, Kurihara & Degawa 2006, Ri et al. 2022).

Family type – *Kickxella* Coem.

Ecology & life modes – Saprobes in soil and dung (Benjamin 1959, 1961), mycoparasitic (Jackson & Dearden 1948), at least one species can live as an arthropod gut symbiont and a saprobe on the faeces of its host (Ri et al. 2022).

Notes – Traditionally, *Kickxellaceae* has been considered the only family in *Kickxellales* Kreisel ex R.K. Benj. (Linder 1943, Benjamin 1979). Multi-locus phylogenetic studies have corroborated this and revealed that *Kickxellales* is closely related to the insect-associated orders *Asellariales* Manier ex Manier & Lichtw., *Barbatosporales* Doweld, *Harpellales* Lichtw. & Manier and *Orphellales* L.G. Valle et al. (Tretter et al. 2014, White et al. 2018, Reynolds et al. 2023). DNA sequence data (O'Donnell et al. 1998, Chuang et al. 2013) recently prompted the reallocation of three genera, which were traditionally placed in *Kickxellales*, into segregate orders, i.e. *Ramicandelaber* in *Ramicandelaberales*, and *Spiromyces* and *Mycoëmilia* in *Spiromycetales* (Doweld 2014a, b, Reynolds et al. 2023).

Kickxella Coem. Bull. Soc. R. Bot. Belg. 1: 156 (1862)
Index Fungorum Identifier 20287
Heterotypic synonyms: *Coemansiella* Sacc., Syll. Fung. (Abellini) 2: 815 (1883)
Coronella P. Crouan & H. Crouan, Florule Finistère (Paris): 12 (1867)

Colonies are white or light to dark yellow. Hyphae septate, with a single septal plug. Sporangiophores are more or less straight, simple, or branched. Stalked sporocladia arising from a small apical vesicle, umbellately or laterally from the sporangiophore. Sporocladial stalks unicelled, rarely 2-celled. Sporocladia arcuate or geniculate, multicelled, all cells except the terminal cell bearing several pseudophialides. Pseudophialides are more or less flask-shaped, each forming a single, unispored merosporangium. Sporangiospores are elongate, variously shaped, and either fill or do not fill the merosporangium. Spores are released into a droplet of fluid at maturity. Zygospores are more or less globose, arising from three or fewer hyphoid suspensors, formed at or below the surface of the substrate, not observed in all taxa (*fide* Reynolds et al. 2023).

Type species – *Kickxella alabastrina* Coem., 1862; Fig. 65

Notes – *Kickxella* was a monotypic genus, typified by *K. alabastrina*. This fungus shows an unusual morphology, characterized by sporangiophores with apical vesicles bearing sporocladia in whorls, which produce sporangiospores on the upper surface (Linder 1943, Benjamin 1958). This arrangement of the reproductive structures is not observed in any other member of *Kickxellales* (Benjamin 1959, 1961, 1979). However, multilocus phylogenetic analyses demonstrated that *K. alabastrina* is nested within a clade which contains *Coemansia asiatica* Kurihara & Sukarno and other unidentified *Coemansia* spp., all of which produce sporangiophores without vesicles and with lateral sporocladia (Reynolds et al. 2023). Those authors consequently transferred *C. asiatica* to *Kickxella*, as *K. asiatica* (Kurihara & Sukarno) Reynolds et al. Isolates of *K. alabastrina* are available at ATCC and CBS. Sequences of ribosomal and protein-coding loci of *K. alabastrina* and *K. asiatica* are available in GenBank.

Other Genera in *Kickxellaceae*

Coemansia Tiegh. & G. Le Monn., Annls Sci. Nat., Bot., sér. 5 17: 392 (1873).
Index Fungorum Identifier 20139; Index Fungorum (2025) accepted 28 species, and Species Fungorum (2025) accepted 27 species.

Type species – *Coemansia reversa* Tiegh. & G. Le Monn. 1873.

Notes – According to Reynolds et al. (2023), this genus will probably be split into several segregate genera, saprobes associated with soil, dung, and dead animals.

Dipsacomyces R.K. Benj., Aliso 5(1): 15 (1961).
Index Fungorum Identifier 20185; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Dipsacomyces acuminosporus* R.K. Benj. 1961.

Notes – Species were reported as saprobes in soil from Honduras. Cultures and sequences are available.

Linderina Raper & Fennell, Am. J. Bot. 39: 81 (1952)
Index Fungorum Identifier 20310; Index Fungorum (2025) and Species Fungorum (2025) accepted two species.

Type species – *Linderina pennispora* Raper & Fennell 1952.

Notes – Species were reported as saprobes in soil in India, Hong Kong (China), Liberia. Cultures and sequences are available.

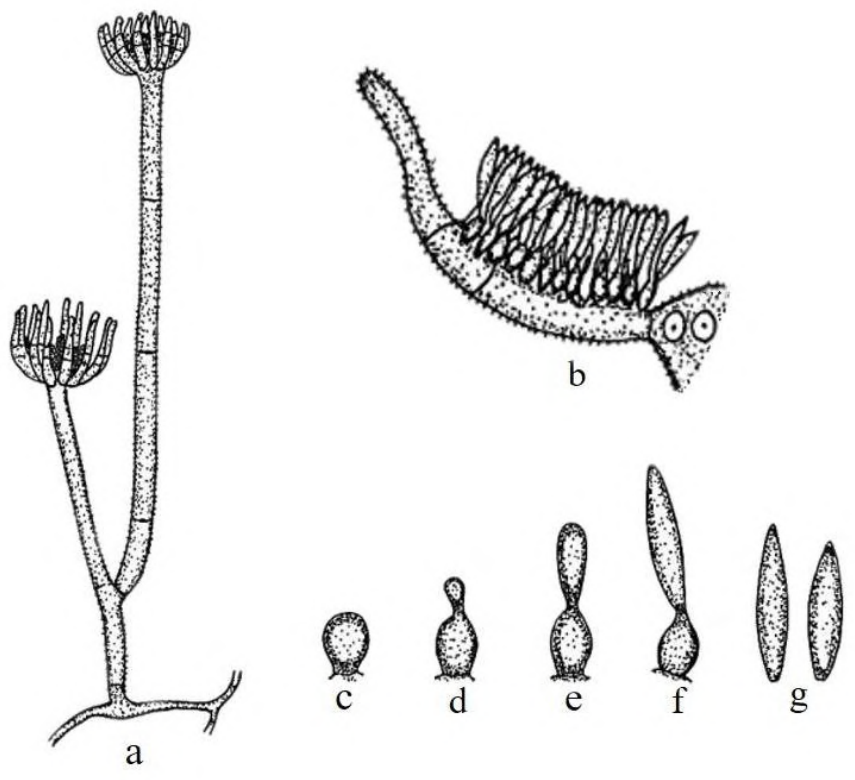


Figure 65 – *Kickxella alabastrina*. a Sporangiophore X 180. b Sporocladium with pseudophialides and merosporangia. c–f Pseudophialides showing successive stages in the aerogenous development of the unispored sporangiole X 1360. g Mature sporangiola X 1360 (Redrawn from Benjamin 1958).

Martensella Coem., Bull. Acad. R. Sci. Belg., Cl. Sci., sér. 2 15: 540 (1863).
Index Fungorum Identifier 20317; Index Fungorum (2025) accepted two species and Species Fungorum (2025) accepted one species.

Type species – *Martensella pectinata* Coem. 1863.

Martensiomyces J.A. Mey., Bull. trimest. Soc. mycol. Fr. 73: 189 (1957).
Index Fungorum Identifier 20310; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Martensiomyces pterosporus* J.A. Mey. 1957.

Notes – One species is known as a saprobe in soil from Congo. Cultures and sequences are available.

Mycoemilia Kurihara, Degawa & Tokum. [as 'Mycoëmilia'], Mycol. Res. 108(10): 1143 (2004)
Index Fungorum Identifier 39196; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Mycoemilia scoparia* Kurihara, Degawa & Tokum. 2004

Myconymphaea Kurihara, Degawa & Tokum., Mycol. Res. 105(11): 1398 (2001).
Index Fungorum Identifier 28512; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Myconymphaea yatsukahoi* Kurihara, Degawa & Tokum. 2001.

Notes – Currently, the genus comprises one species, on a dead arthropod in Japan (Kurihara et al. 2001, Reynolds et al. 2023).

Pinnaticoemansia Kurihara & Degawa, Mycoscience 47(4): 205 (2006)
Index Fungorum Identifier 29034; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Pinnaticoemansia coronantispora* Kurihara & Degawa 2006.

Unguispora T. Ri & Degawa, in Ri, Suyama, Seto & Degawa, Mycologia: 114: 937 (2022).
Index Fungorum Identifier 838785; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Unguispora rhaphidophoridarum* T. Ri & Degawa 2022.

Orphellales Doweld
Orphellaceae Doweld, Index Fungorum 65: 1 (2014)
Index Fungorum Identifier IF550368

Thallus with a main axis bearing one to several fertile branches, attached to the hindgut lining by a holdfast. Terminal branches bearing sporulating fertile heads. Basal cells produce multicelled dissemination units composed of a generative cell, a supportive generative cell, a trichospore, and a terminal cell. Trichospores are variable in shape, lacking appendages. Zygospores helicoid, homothallic or heterothallic, borne on a zygosporophore produced from an intermediate cell, with a terminal cell (White et al. 2006).

Family type – *Orphella* L. Léger & M. Gauthier 1931

Ecology & life modes – Cosmopolitan. Commonly found in the hindgut lining of members of Nemouridae, Capniidae and Leuctridae (Léger & Gauthier 1931, 1932, White & Lichtwardt 2004, Valle & Santamaria 2005, Strongman & White 2006, Valle et al. 2014, Strongman & Wang 2015).

Notes – *Orphella* was first reported from France by Léger & Gauthier (1931), who described the type species *O. coronata* L. Léger & M. Gauthier under *Legeriomycetaceae*. But later it was proved that *Orphella* differs from *Harpellales* genera by its dispersive propagule or dissemination unit, a complex of cells that includes the trichospore plus three accompanying cells (Santamaria & Girbal 1998). The sexual reproduction complex is also quite different from other members of the *Harpellales*, especially the unique shape of the zygospores, but also the subtending cells, which differ ontogenetically depending on whether they are homothallic or heterothallic (Valle & Santamaria 2005). Doweld (2014v) elevated the genus into *Orphellaceae*. Subsequently, White et al. (2018) established a new order *Orphellales*, based on molecular phylogenetic analysis of combined nuclear SSU and LSU sequence data.

White (2006) and White et al. (2006) utilised nrDNA to place the genus outside the *Harpellales*, and with a strongly supported relationship within the *Kickxellales*. James et al. (2006a) produced a six-gene phylogeny (nrDNA and protein-coding genes) that also placed *Orphellales* as a sister to *Kickxellales*. Tretter et al. (2013) investigated the *Kickxellomycotina* using two new genes (MCM7 and TSR1), and the MCM7 phylogeny suggested that *Orphella* was not a member of the *Harpellales*. Tretter et al. (2014) used eight loci (LSU, SSU, *mcm7*, *tsr1*, *rpb1*, *rpb2* and *tub*) to examine relationships between the four orders of the subphylum, and *Orphella* was strongly supported as sister to *Kickxellales*, with *Spiromyces* sister to both.

Orphella L. Léger & M. Gauthier, Trav. Lab. Hydrobiol. Piscic. Univ. Grenoble 23: 68 (1931); Fig. 66

Index Fungorum Identifier 20387

Thalli with one or more main axes, formed by a few elongated cells, with or without accessory branches. Basal holdfast cells are often surrounded by amorphous material near holdfast, usually also bearing branches around the basal holdfast cell. Sporulating branches arising in a cyme-like fertile head, where dissemination units containing trichospores and zygospores are produced. Generative cells produced on separate basal cells. Each generative cell has at the base one supporting generative cell, and apically or laterally one trichospore and a terminal cell. The supporting generative cell, the generative cell, trichospore, and the terminal cell constitute the dissemination unit. Zygospores are produced homothallically or heterothallically, usually coiled but can be elongated distally, borne from the zygosporophore, which is subtended by an intermediate cell; both cells (zp, ic) can have a terminal cell (tc2 or tc1, respectively). In some species, the terminal cell of the zygosporophore can be bifurcated (tc2′ and tc2″). Below the intermediate cell, there is another supporting cell (from White et al. 2006).

Notes – Refer to the notes of the family.

Type species – *Orphella coronata* L. Léger & M. Gauthier 1931

Ramicandelaberomycetes Tedersoo, Sanchez-Ramirez, Kõljalg, Bahram, M. Döring, Schigel, T.W. May, M. Ryberg & Abarenkov

Ramicandelaberales Doweld

Ramicandelaberaceae Doweld, Index Fungorum 69: 1 (2014)

Index Fungorum Identifier 550372

Thallus producing stolons forming rhizoids. Sporangiophores are septate, arise from rhizoids, unbranched, and form supporting hyphae producing rhizoids. Fertile branches borne verticellately, terminating in a fertile vesicular apex. Sporocladium uni-celled, producing a single pseudophialide medially and laterally. Pseudophialides globose to hemispherical. Merosporangia fusiform, one produced from each pseudophialide (from Doweld 2014x).

Family type – *Ramicandelaber* Y. Ogawa, S. Hayashi, Degawa & Yaguchi, Mycoscience 42(2): 193 (2001)

Ecology & life modes – Reported from soil under leaf litter of the evergreen oak, Japan

Notes – Tedersoo et al. (2018) established a distinct class to accommodate *Ramicandelaber* and accepted the other higher taxa, *Ramicandelaberales* and *Ramicandelaberaceae*.

Ramicandelaber Y. Ogawa, S. Hayashi, Degawa & Yaguchi, Mycoscience 42(2): 193 (2001)

Index Fungorum Identifier 28497

The description is similar to *Ramicandelaberaceae*.

Type species – *Ramicandelaber longisporus* Y. Ogawa, S. Hayashi, Degawa & Y. Yaguchi 2001

MONOBLEPHAROMYCOTA Doweld

Hyaloraphidiomycetes Doweld

Hyaloraphidiales Doweld

Hyaloraphidiaceae Doweld, Prosyllabus Tracheophyllum, Tentamen Systematics Plantarum (Tracheophyta) 77: 1 (2001)

Index Fungorum Identifier 585033

Thallus holocarpic; cell usually elongate; rhizoidal system absent. Asexual reproduction by autosporos is formed within the mother cell and released by rupture of its wall cell; flagella has never been observed. Sexual reproduction is absent (Ustinova et al. 2000, Forget et al. 2002).

Family type – *Hyaloraphidium* Korshikov, Arch. Protistenk. 74: 251 (1931)

Ecology & life modes – This family is composed of one genus, *Hyaloraphidium*. It is a rare representative of freshwater nanoplanktons (Forget et al. 2002).

Notes – *Hyaloraphidium curvatum* is a member of this genus, and the cultures resemble yeast (Amses et al. 2022). The family comprises only one genus. Molecular studies based on 18S

ribosomal RNA and mitochondrial DNA sequences analyses of *Hyaloraphidium curvatum* showed that it is a sister group of the monoblephs (Ustinova et al. 2000, Forget et al. 2002, Amses et al. 2022). Doweld (2001) proposed *Hyaloraphidiomycetes*/*Hyaloraphidiales*/*Hyaloraphidiaceae* to accommodate this genus (see notes under *Gonapodyaceae*).

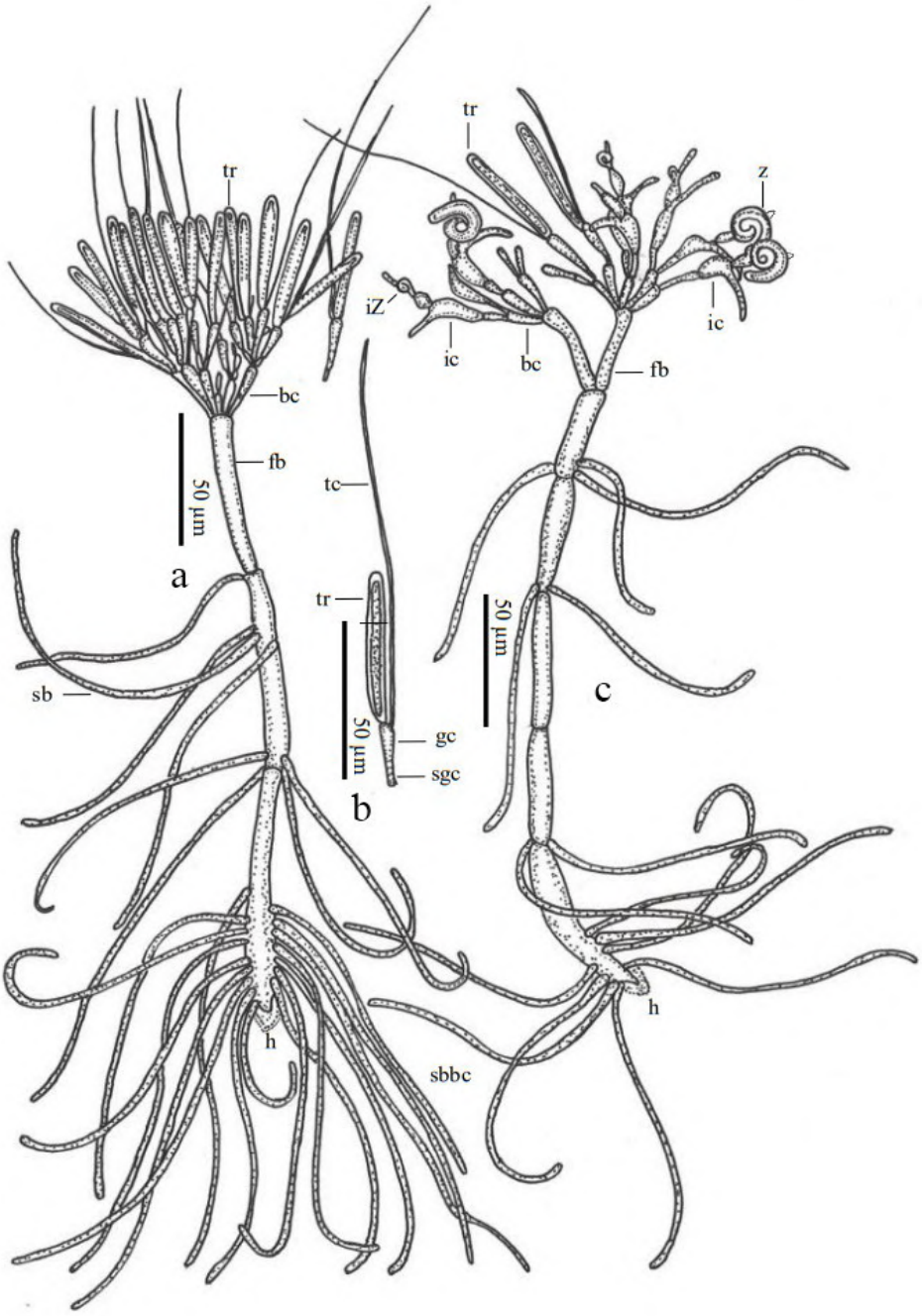


Figure 66 – *Orphella cataloochensis* from *Leuctridae*. a Thallus overview, with fertile head bearing trichospores. b Trichospore dissemination unit. c Thallus overview with fertile heads mostly bearing zygospores but with two attached trichospores, (bc) basal cell of the sporulating head: (bhc), basal holdfast cell; (fb), fertile branches; (gc), generative cell; (h), holdfast cell; (ic), intermediate cell; (iZ), immature zygospore (sb), subsidiary branches (sbbc), subsidiary branches from basal cell; (sgc), supporting generative cell; (tc), terminal cell; (tc2), terminal cell formed from zygosporophore; (tr), trichospore; Z, zygospore; a and b from slide TN-40-A1. c from slide TN-45-W10 (Redrawn from White et al. 2018).

Hyaloraphidium Korshikov, Arch. Protistenk. 74: 251 (1931)
Index Fungorum Identifier 28471

Thallus holocarpic; cell elongated and curved. Asexual reproduction by autosporos formed within the mother cell and released by rupture of its wall; usually 4–8 spores per cell; flagella never observed. Sexual reproduction is absent (Ustinova et al. 2000, Forget et al. 2002).

Type species – *Hyaloraphidium curvatum* Korshikov, Arch. Protistenk. 74: 251 (1931)

Notes – This genus was first classified within *Ankistrodesmaceae*, a family of green algae, due to their similarities in morphology and mode of reproduction (Korschikoff 1931). However, several studies based on DNA sequence analyses confirmed that this genus is accommodated in Kingdom *Fungi* (Ustinova et al. 2000, Forget et al. 2002). Doweld (2001) established *Hyaloraphidiaceae* (*Hyaloraphidiomycetes*/ *Hyaloraphidiales*) to accommodate *Hyaloraphidium*. *Hyaloraphidium curvatum* in some aspects resembles *Chytridiomycetes*, however, the flagellar apparatus has never been observed. The life-cycle reduced without flagella formation reveals this chytrid as an interesting model for evolution studies of morphological reduction (Amses et al. 2022). Cultures are available on CZEUM (Collection of Zoosporic Eufungi at the University of Michigan), and sequences are also available in GenBank.

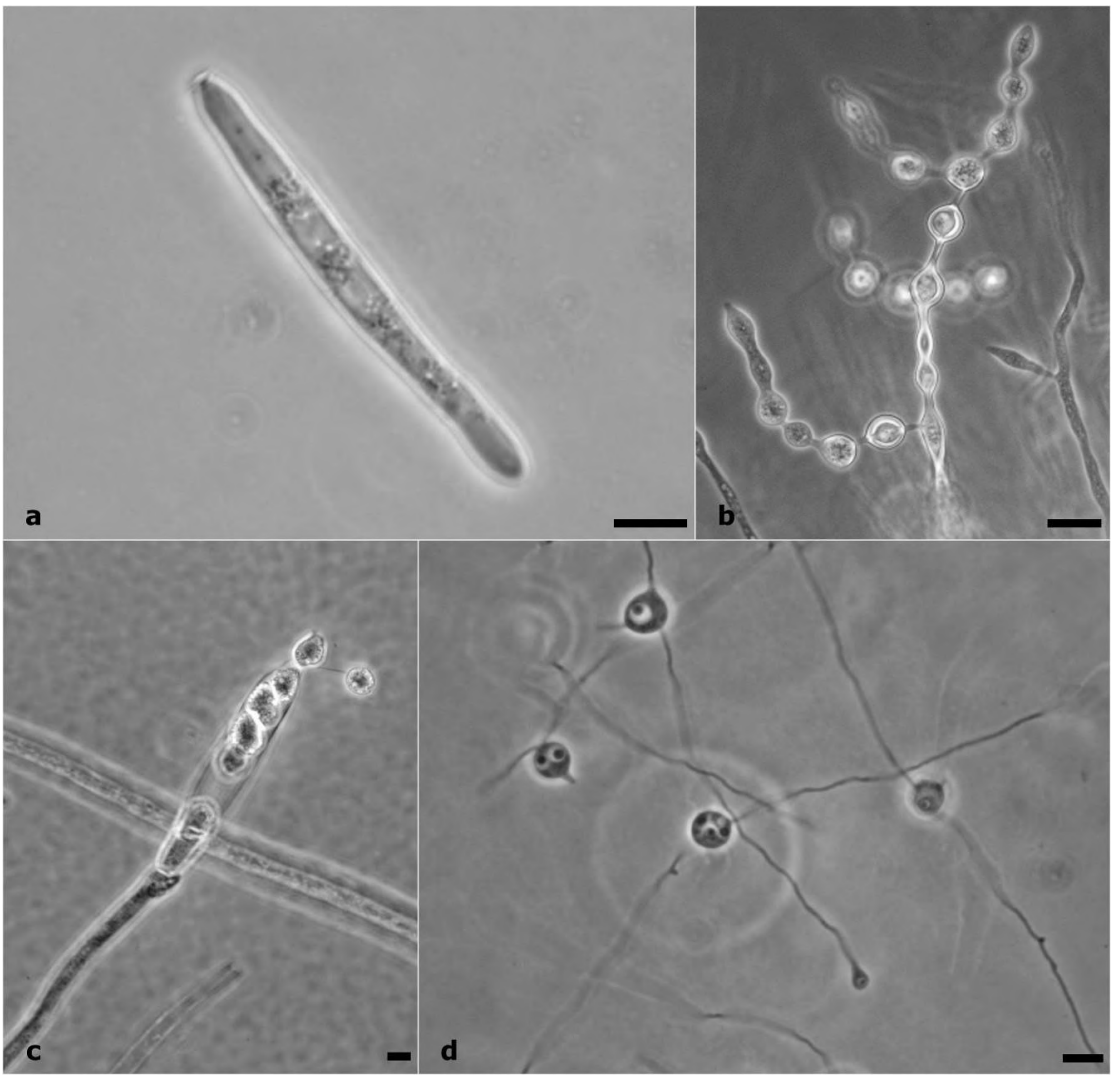


Figure 67 – a-d. *Monoblepharomycota*. a Monoaxial thallus of *Harpochytrium* sp. b Hyphae with swellings of *Monoblepharella*. c Zoospores' discharge of the zoosporangium of *Monoblepharis*. d Polycentric thallus of *Telasphaerula*. Scale bars = 10µm (Photos: a, d – photos of Dr. Joyce E. Longcore, b, c – photos of Dr. Marilyn R.N. Mollicone – courtesy of Dr. Joyce E. Longcore).

Monoblepharidomycetes J.H. Schaffn.
Monoblepharidales Sparrow
Gonapodyaceae H.E. Petersen ex P.M. Kirk, P.F. Cannon & J.C. David, Ainsworth & Bisby's Dictionary, Ed 9 (Wallingford): IX (2001)
Index Fungorum Identifier 82121

Mycelial thallus with or without constrictions, pseudosepta and catenulations; vacuolate protoplasm absent or present; zoosporangia terminal, commonly elongate or ovoid, with or without internal proliferation; zoospores completely formed into the zoosporangium, posteriorly uniflagellate. Sexual reproduction oogamous; female and male gametangia terminal, with or without internal proliferation, female gamete variable in number; the gametes (oogonium and antherozoid) fusion occurs outside of or within the oogonium, producing zygote that becomes motile outside of the oogonium (Sparrow 1960, Karling 1977, Kirk et al. 2001).

Ecology & life modes – Saprobic on submerged fruits and twigs in freshwater ecosystems and organic material in tropical and subtropical soils (Sparrow 1960, Karling 1977, Milanez et al. 2007).

Family type – *Gonapodya* A. Fisch., Rabenh. Krypt.-Fl., Ed 2 (Leipizig) 1: 382 (1892)

Notes – *Gonapodya* and *Monoblepharella* lack the tightly organized clusters of vesicles that characterize a Spitzenkörper, and their hyphae seem to have an independent evolutionary origin from hyphae of the Dikarya (Dee et al. 2015, Karpov et al. 2017c). Dee et al. (2015) presented the phylogeny of *Monoblepharidomycetes s. l.*, based on SSU and LSU rDNA regions and confirmed that the mycelial genera, such as *Gonapodya*, *Monoblepharella* and *Monoblepharis*, formed a monophyletic sister group to the monocentric *Harpochytrium* and *Oedogoniomyces.* Hence, *Hyaloraphidium is* herein classified into *Hyaloraphidiomycetes*/ *Hyaloraphidiales*/ *Hyaloraphidiaceae* as proposed by Doweld (2001) (see *Hyaloraphidiaceae*). *Telasphaerula*, the last genus, was introduced in *Monoblepharomycota* showing as sister to mycelial genera (Karpov et al. 2017c).

Gonapodya A. Fisch., Rabenh. Krypt.-Fl., Ed 2 (Leipizig) 1: 382 (1892); Fig. 68
Index Fungorum Identifier 20246

Mycelial thallus with constrictions, pseudosepta and catenulations; irregularly or dichotomously branched, attached to the substratum by rhizoids. Zoosporangia terminal, commonly elongate or ovoid, with internal proliferation; zoospores are posteriorly uniflagellate and are completely formed into the zoosporangium usually discharging by one pore. Sexual reproduction oogamous; female and male gametangia terminal, with internal proliferation, similar to the zoosporangia, and more than one gamete by female gametangium usually fertilized by male gametangium outside of the gametangia. Resting spores not observed (Sparrow 1960, Karling 1977, Fuller & Clay 1983).

Type species – *Gonapodya prolifera* (Cornu) A. Fisch., Rabenh. Krypt.-Fl., Ed 2 (Leipizig) 1: 382 (1892)

Notes – *Gonapodya* with five valid epithets (Index Fungorum 2024) is a genus with worldwide distribution (Karling 1977). Cultures are available on CZEUM (Collection of Zoosporic Eufungi at the University of Michigan) and ATCC (American Type Culture Collection), and sequences are available in GenBank.

Other genus in *Gonapodyaceae*
Monoblepharella Sparrow, Allan Hancock Found. Publ., Occass. Pap., Ser. 1 3(6): 103 (1940)
Index Fungorum Identifier 20337; Index Fungorum (2025) and Species Fungorum (2025) accepted five species; Fig. 67b

Type species – *Monoblepharella taylorii* (Sparrow) Sparrow

Harpochytriaceae Wille, Petermann's Geogr. Mitt. Ergänz. 28: 370 (1900)
Index Fungorum Identifier 82102

Thallus eucarpic, monoaxial, epibiotic, with an extracellular basal foot or holdfast. Sporangia proliferous discharging zoospores by rupture of the wall near the apex, delimiting a cap-like portion that can be detached or remain joined at one side of the zoosporangium. Zoospores posteriorly uniflagellate. Sexual reproduction unknown (Emerson & Whisler 1968, Karling 1977).

Family type – *Harpochytrium* Lagerh., Hedwigia 29: 143 (1890); Fig. 67a

Ecology & life modes – This family is represented by a single genus, *Harpochytrium*. Members of the genus are considered saprobic, and they were always found in association with algae and vegetable debris.

Notes – *Harpochytrium* was described by Lagerheim (1890) as an epibiotic in the freshwater algae *Hyalotheca dissiliens*. Their species were included among the algae by some mycologists. However, Jane's studies (Jane 1946) proved that the colourless isolates belonged to the fungi in the *Phycomycetes* (Emerson & Whisler 1968).

Harpochytrium Lagerh., Hedwigia 29: 143 (1890)
Index Fungorum Identifier 20260

Thallus eucarpic, monoaxial, epibiotic, sometimes septate, stalked, straight, coiled, falcate or curved, erect or adpressed, rarely branched, with an extracellular basal foot or holdfast. Sporangia proliferous discharging zoospores by rupture of the wall near the apex, delimiting a cap-like portion that can detached or remain joined at one side of the zoosporangium. Zoospores posteriorly uniflagellate. Sexual reproduction unknown (Emerson & Whisler 1968, Karling 1977).

Type species – *Harpochytrium hyalothecae* Lagerh., Hedwigia 29: 143 (1890)

Notes – This genus has 13 epithets (Index Fungorum 2024) (*H. hyalothecae* J. Schröt. is invalid) which were found in association with algae and vegetable debris (Emerson & Whisler 1968, Karling 1977). Isolates were collected from Europe, North and South America and Tibet (Jane 1946, Emerson & Whisler 1968). Cultures are available in CZEUM (Collection of Zoosporic Eufungi at the University of Michigan) and ATCC (American Type Culture Collection), and sequences are available in GenBank (genus level only).

Monoblepharidaceae Warm., Haandbog i den systematiske botanik ed. 2: 57 (1884)
Index Fungorum Identifier 816411

Mycelium without pseudosepta, sparingly or profusely and sympodially branched or unbranched; hypha highly vacuolate with "foamy" appearance; attached by rhizoids to the substratum; zoosporangia usually elongate. Sexual reproduction oogamous; gametangia not proliferous; oogonium with one oosphere, male gamete engulfed at fertilization, female gamete converted usually in an oospore which remains in intimate contact with the oogonium (Sparrow 1960, 1973).

Family type – *Monoblepharis* Cornu, Bull. Soc. bot. Fr. 18: 59 (1871)

Ecology & life modes – This family is represented by *Monoblepharis*, whose species were found mainly as saprobic on twigs, fruits, animal remains and *Oomycetes* from freshwater ecosystems.

Notes – This small family is characterized by oogamous sexual reproduction, with an oospore that remains in intimate contact with the oogonium after its fertilization by the male gamete (Sparrow 1960, Karling 1977). *Monoblepharis*, as a mycelial genus, lacks the tightly organized clusters of vesicles that characterize a Spitzenkörper, and its hyphae seem to have an independent evolutionary origin from hyphae of the *Dikarya* (Dee et al. 2015, Karpov et al. 2017c).

Monoblepharis Cornu, Bull. Soc. bot. Fr. 18: 59 (1871); Fig. 67c & 69
Index Fungorum Identifier 20340

Mycelium with pseudosepta, branched or unbranched, attached by rhizoids to the substratum, hypha highly vacuolate with "foamy" appearance; zoosporangia usually terminal, elongate or irregular, cut off the hyphae by cross walls, renewed by branching or internal proliferation; zoospores posteriorly uniflagellate formed into the zoosporangium and escaping of it by the

dissolution of its apex. Sexual reproduction oogamous; oogonium intercalary or terminal, and in the maturity with one oosphere; antheridia of different shapes producing small antherozoids; oosphere after the fertilization remaining in the oogonium or emerging; oospore smooth or ornamented (Sparrow 1960, Karling 1977).

Type species – *Monoblepharis sphaerica* Cornu, Bull. Soc. bot. Fr. 18: 59 (1871), Ann. Sci. Nat. Bot. 15: 82 (1872)

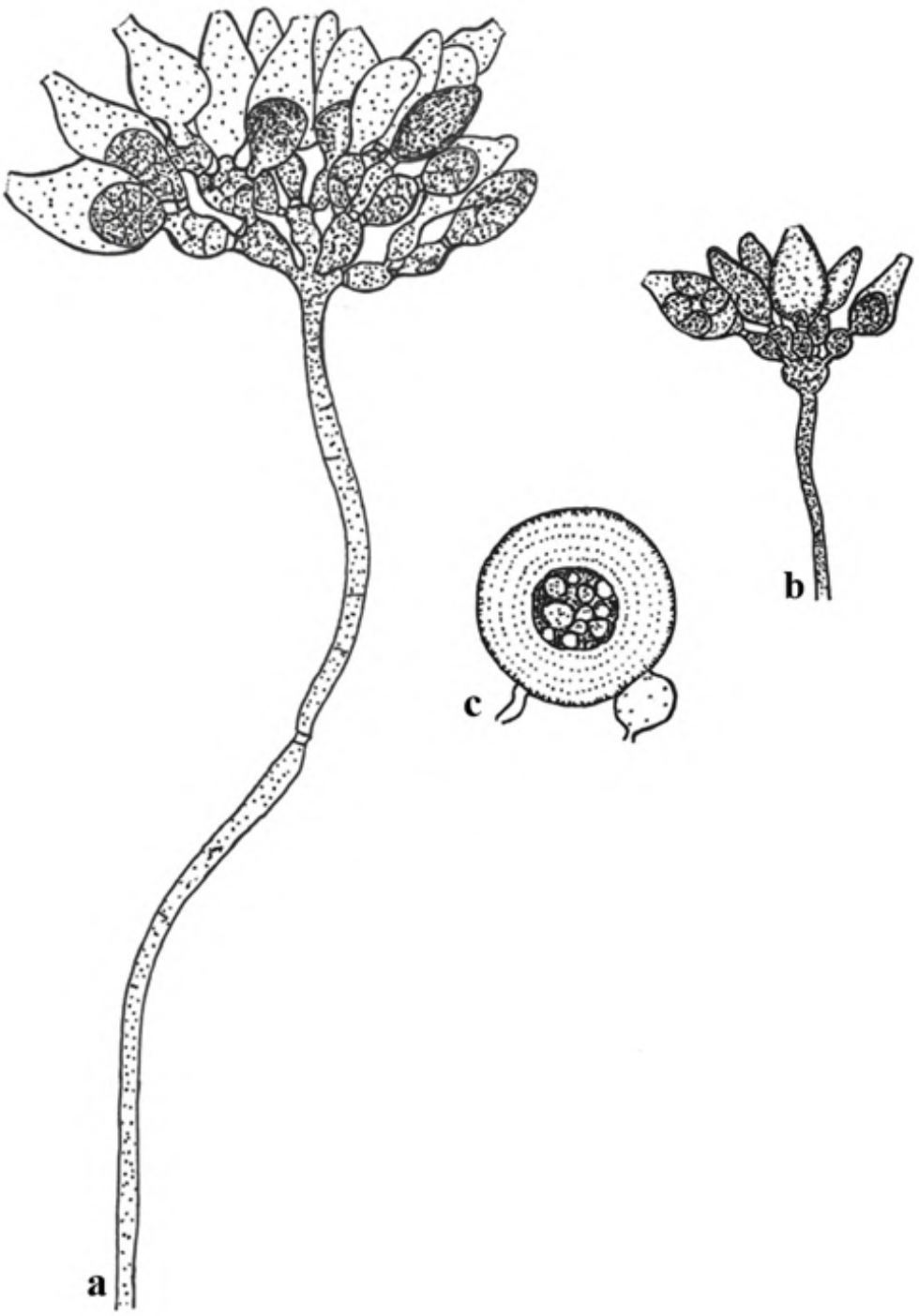


Figure 68 – *Gonapodya polymorpha* a,b Portion of two sporangia in which the segmented parts are borne sub-umbellately on slender hyphae. c Thick-walled oospore with antheridium found associated with the zoosporic form but not connected with it (Redrawn from Thaxter 1895).

Notes – Thirteen epithets are listed under this genus (Index Fungorum 2024). The species were found as saprobic on twigs, fruits, animal remains and *Oomycetes* from freshwater ecosystems in Europe, North and South America, and Oceania (Sparrow 1960, Milanez et al. 2007, Steciow et al. 2012). Cultures are available on ATCC (American Type Culture Collection) and sequences on GenBank.

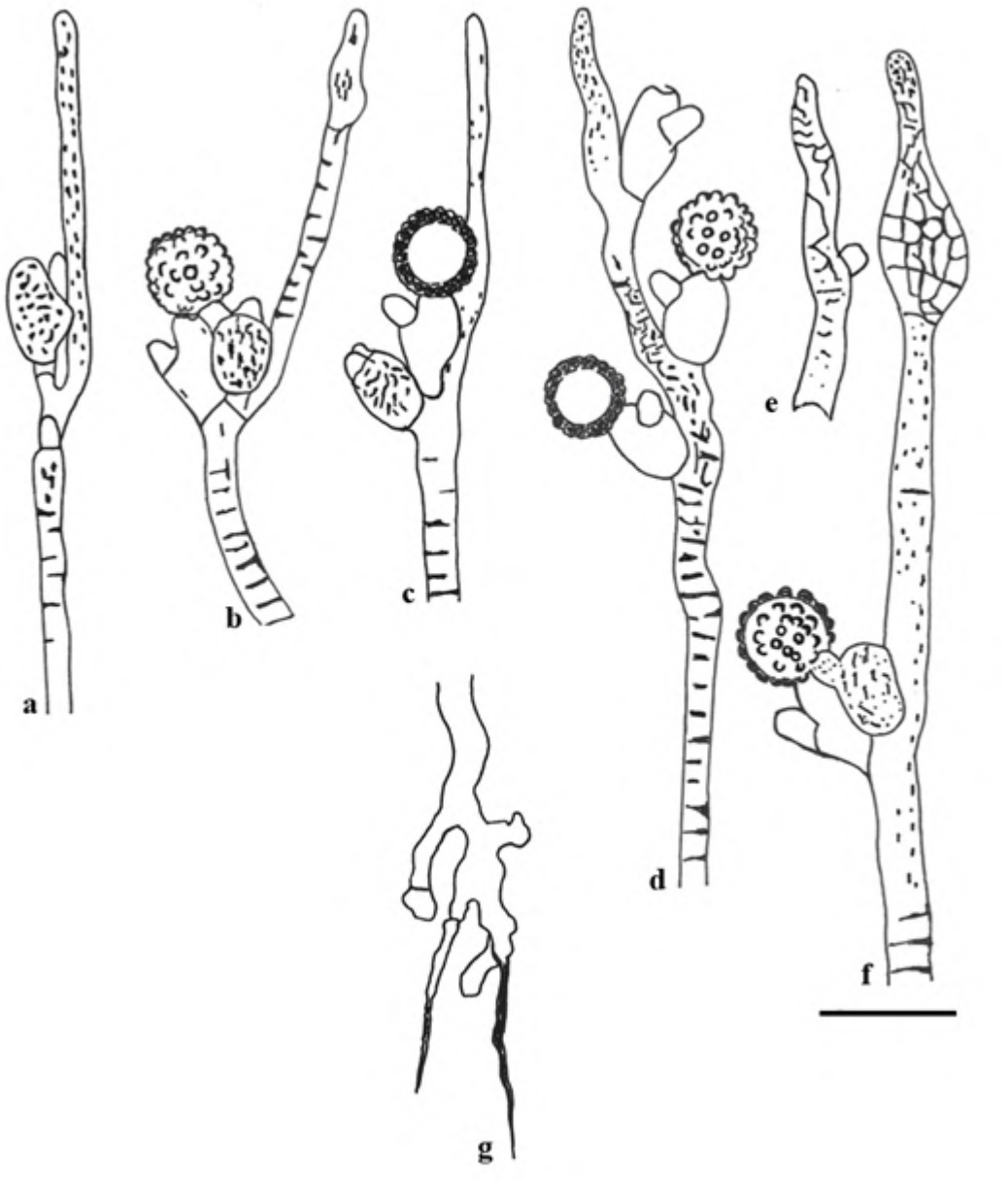


Figure 69 – *Monoblepharis micrandra*. a Tip of a hypha showing developing sex organs. b-d hyphal tips showing sex organs and exogenous, bullate oospores. e hypha bearing a short antheridium apart from oogonium. f tip bearing sex organs and hyphal swelling. g hold-fast system showing rhizoidal nature of ultimate branches (Redrawn from Sparrow 1965).

Oedogoniomycetaceae D.J.S. Barr, Handbook of Protoctista (Boston): 463 (1990)
Index Fungorum Identifier 82006

Thallus eucarpic, monocentric, epibiotic, filamentous, commonly rod-shaped, with an extracellular basal disc-like holdfast or appressorium. Sporangia delimitate and mature in basipetal succession discharging zoospores by rupture of the wall near the apex of each segment. Zoospores

posteriorly uniflagellate. Sexual reproduction unknown (Kobayashi & Ôkubo 1954, Emerson & Whisler 1968, Karling 1977, Gauriloff et al. 1980, Barr 1990).

Family type – *Oedogoniomyces* Kobayasi & M. Ôkubo, Bull. Natn. Sci. Mus. (Tokyo): 1: 62 (1954)

Ecology & life modes – This family is represented by only one genus, *Oedogoniomyces*. Their isolates were found as saprobic on the surface of shells of living snails and grass leaves from Japanese ponds (Kobayashi & Ôkubo 1954), as well as in submerged fruits and superficial soil from water bodies of Costa Rica, and angiosperm twigs from a shallow pool in USA (Emerson & Whisler 1968).

Notes – *Oedogoniomycetaceae* was introduced by Barr (1990) to accommodate the single genus *Oedogoniomyces*, considering the development of the sporangia. This genus was originally described in Japan by Kobayashi & Ôkubo (1954), who accommodated it in *Blastocladiales*. Subsequently, Emerson & Whisler (1968) studied isolates from Costa Rica and USA and placed the genus in *Harpochytriales*. However, based on zoospore ultrastructure, Gauriloff et al. (1980) placed the family in *Monoblepharidales*. Currently, the family comprises only one genus.

Oedogoniomyces Kobayashi & M. Ôkubo, Bull. Natn. Sci. Mus. (Tokyo): 1: 62 (1954)
Index Fungorum Identifier 20376

Saprobic and monocentric genus with uniaxial, filamentous, cylindrical, straight, curved, coiled or spiral, apically tapering thallus attached in the substratum by a disc-like holdfast or appressorium. Thallus septate at maturity, presenting basipetal succession with each segment considered a zoosporangium with zoospores' discharge by rupture of the wall. Zoospores are posteriorly uniflagellate. Sexual reproduction unknown (Kobayashi & Ôkubo 1954, Emerson & Whisler 1968, Karling 1977).

Type species – *Oedogoniomyces lymnaeae*, Bull. Natn. Sci. Mus. (Tokyo): 1: 62 (1954)

Notes – Only one species, *Oedogoniomyces lymnaeae* (*fide* Index Fungorum 2024) is known. It was found on the surface of shells of living snails and grass leaves from Japanese ponds (Kobayashi & Ôkubo 1954). Cultures are not available, and sequences are available on GenBank (genus level).

Telasphaerulaceae Longcore & T.Y. James, Fungal Biology 121: 734 (2017)
Index Fungorum Identifier 818658

Thallus rhizomycelial, delicate, with isodiametric filaments presenting intercalary components, commonly spherical in older material. Zoosporangia are reduced, often producing a single zoospore. Sexual reproduction is unknown (Karpov et al. 2017c).

Family type – *Telasphaerula* Longcore & T.Y. James, Fungal Biology 121: 734 (2017)

Ecology & life modes – This family contains only one genus and species, *Telasphaerula gracilis*, which was found in a mesotrophic lake in Maine, USA associated with green algae of the genus *Chara* (Karpov et al. 2017c).

Telasphaerula Longcore & T.Y. James, Fungal Biology 121: 734 (2017)
Index Fungorum Identifier 818659

Thallus with indeterminate growth and swellings connected by isodiametric tubes. Swellings are commonly spherical, some irregular, and are produced in older material. Zoospores are ovate, slightly pointed at apex, and discharged from terminal zoosporangia with delicate walls. Sexual reproduction unknown (Karpov et al. 2017c).

Type species – *Telasphaerula gracilis* Longcore & T.Y. James, Fungal Biology 121: 734 (2017)

Notes: This saprobic species was found in a mesotrophic lake in Maine, USA associated with green algae of the genus *Chara* (Karpov et al. 2017c). Only the type species is known for this genus. Cultures are available in CZEUM (Collection of Zoosporic Eufungi at the University of Michigan) and sequences are available in GenBank.

MORTIERELLOMYCOTA Tedersoo, Sanchez-Ramirez, Kõljalg, Bahram, M. Döring, Schigel, T.W. May, M. Ryberg & Abarenkov
Mortierellomycetes Doweld
Mortierellales Caval.-Sm.
Mortierellaceae Luerss., Handbuch der systematischen Botanik mit besonderer Berücksichtigung der Arzneipflanzen 1: 63 (1877)
Index Fungorum Identifier 816415

Some taxa are known to produce garlic-like odour. Hyphae are fine, branched, and mostly aseptate, and may produce chlamydospores. Sporangia one- to many-spored, with a strongly reduced columella. Zygospores are formed on opposed suspensors (Gams 1977).

Family type – *Mortierella* Coem., Bull. Acad. R. Sci. Belg., Cl. Sci., sér. 2 15: 536 (1863)

Ecology and life modes – *Mortierellaceae* representatives are commonly detected and isolated from soils, plant debris, insect guts, mosses, and living plant roots (Gams 1977), and have been found on every continent, including Antarctica (www.gbif.org).

Notes – *Mortierellaceae* was described by Luerssen (1877) within *Mucorales* and covered only representatives of the genus *Mortierella*.Early treatment of the family also included other genera, and classification was modified. The first systematic revision of the family was provided by Gams (1977) divided *Mortierella* into *Micromucor* and *Mortierella*. Within the subgenus, *Mortierella* Gams (1977) proposed nine sections: *Alpina*, *Actinomortierella*, *Haplosporangium*, *Hygrophila*, *Schmuckeri*, *Simplex*, *Spinosa*, *Stylospora*, and *Mortierella*. An additional twelve genera were subsequently proposed and accepted within *Mortierellaceae* (Vandepol et al. 2020). The first classification based on molecular phylogenetics defined twelve new clades (Petkovits et al. 2011). Next large revision reorganized and combined several clades into a total of seven clades: selenospora, verticillata-humilis, lignicola, dissophora, capitata, alpina, and gamsii (Wagner et al. 2013). Vandepol et al. (2020) revised the family using multi-gene phylogenetics based on low-coverage genome (LCG) sequencing and high-throughput, multiplexed targeted amplicon sequencing. Resolving the *Mortierellaceae* phylogeny resulted in the definition of 14 genera, seven of which were newly proposed (Vandepol et al. 2020).

Mortierella Coem., Bull. Acad. R. Sci. Belg., Cl. Sci., sér. 2 15: 536 (1863)
Index Fungorum Identifier 20345

White, zonate colonies are formed by coenocytic, anastomosing hyphae. Sporangia and sporangiospores may be absent in some species. When present, sporangiophores are hyaline. The sporangial wall is smooth and deliquescent. Spores may vary in shape. Chlamydospores, where present, are scarce and either smooth or spiny. When known, brownish zygospores are formed on opposed suspensors (Gams 1977, Vandepol et al. 2020).

Notes – *Mortierella* was introduced by Coemans (1863) based on specimens observed in a fir (*Abies*) forest on *Polyporus perennis* and *Daedalea* sp. in Belgium. The concept of this genus changed over time. The current species refer to the former clade 6 (Wagner et al. 2013) and *Alipina* and *Mortierella* sections (Gams 1977). Several taxa currently treated as separate genera are still known under this generic name and, as not all taxonomic revisions followed the phylogenetic study of Vandepol et al. (2020), the genus remains polyphyletic. Currently, there are more than 100 species described within the genus. Although in general the representatives are known as soil saprobes, several *Mortierella* species are mycoparasites, common especially in colder regions (Vandepol et al. 2020).

Type species – *Mortierella polycephala* Coem., Bull. Acad. R. Sci. Belg., Cl. Sci., sér. 2 16: 536 (1863)

Other genera in *Mortierellaceae*

Actinomortierella Chalab., Nov. sist. Niz. Rast., 1968 5: 129 (1968)
Index Fungorum Identifier 20012; Index Fungorum (2025) lists nine epithets, and Species Fungorum (2025) accepted five species.

Type species – *Actinomortierella capitata* (Marchal) Vandepol & Bonito, Fungal Diversity: 10.1007/s13225-020-00455-5, (2020)

= *Actinomortierella vesiculosa* (B.S. Mehrotra, Baijal & B.R. Mehrotra) Chalab., Nov. sist. Niz. Rast., 1968 5: 129 (1968)

Notes – The representatives of this genus are mostly soil saprobes known from Asia, America and Europe. Some taxa are thermotolerant and pathogenic to mammals (Vandepol et al. 2020).

Aquamortierella Embree & Indoh, Bull. Torrey bot. Club 94: 464 (1967)
Index Fungorum Identifier 20047; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Aquamortierella elegans* Embree & Indoh, Bull. Torrey bot. Club 94: 464 (1967)

Notes – *Aquamortierella* is a monotypic genus similar to the species of *Mortierella* in morphology, but its phylogenetic placement is not known. Found on submerged insect larvae in New Zealand and in Japan (Vandepol et al. 2020). No living material of this taxon exists.

Benniella Vandepol & Bonito, Fungal Diversity 104: 281 (2020)
Index Fungorum Identifier 833778; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Benniella erionia* Liber & Bonito, Fungal Diversity104: 281 (2020)

Notes – The genus comprises one species known from America, Australia, and Africa (Vandepol et al. 2020).

Dissophora Thaxt., Bot. Gaz. 58: 361 (1914)
Index Fungorum Identifier 20187; Index Fungorum (2025) and Species Fungorum (2025) accepted four species.

Type species – *Dissophora decumbens* Thaxt., Bot. Gaz. 58: 361 (1914)

Entomortierella Vandepol & Bonito, Fungal Diversity 104: 281 (2020)
Index Fungorum Identifier 833613; Index Fungorum (2025) and Species Fungorum (2025) accepted ten species.

Type species – *Entomortierella lignicola* (G.W. Martin) Vandepol & Bonito, Fungal Diversity 104:282 (2020)

Notes – *Entomortierella* species appear to be arthropod-associated. However, they are also frequently isolated from soil, roots, and rotting plant matter. Ten species have been described within the genus (Vandepol et al. 2020).

Gamsiella (R.K. Benj.) Benny & M. Blackw., Mycologia 96(1): 147 (2004)
Index Fungorum Identifier 28820; Index Fungorum (2025) and Species Fungorum (2025) accepted two species.

Type species – *Gamsiella multidivaricata* (R.K. Benj.) Benny & M. Blackw., Mycologia 96(1): 147 (2004)

Gryganskiella Vandepol & Bonito, Fungal Diversity 104: 282 (2020)
Index Fungorum Identifier 833857; Index Fungorum (2025) and Species Fungorum (2025) accepted two species.

Type species – *Gryganskiella cystojenkinii* (W. Gams & Veenb.-Rijks) Vandepol & Bonito, Fungal Diversity 104: 282 (2020)

Linnemannia Vandepol & Bonito, Fungal Diversity 104: 282 (2020)
Index Fungorum Identifier 833612; Index Fungorum (2025) lists 25 epithets, but Species Fungorum (2025) accepted 24 species.

Type species – *Linnemannia hyalina* (Harz) Vandepol & Bonito, Fungal Diversity 104: 283 (2020)

Notes – *Linnemannia* was proposed by Vandepol et al. (2020) to accommodate *Mortierella* species previously assigned to clade seven (Wagner et al. 2013). This genus contains some of the most widely distributed *Mortierellaceae* species. Most *Linnemannia* species are isolated from soils and are usually associated with plant rhizospheres or decaying plant matter (Vandepol et al. 2020). The species commonly harbour endohyphal bacteria (Okrasińska et al. 2021).

Lobosporangium M. Blackw. & Benny, Mycologia 96(1): 144 (2004)
Index Fungorum Identifier 28819; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Lobosporangium transversale* (Malloch) M. Blackw. & Benny, in Benny & Blackwell, Mycologia 96(1): 144 (2004)

Lunasporangiospora Vandepol & Bonito, Fungal Diversity 104: 283 (2020)
Index Fungorum Identifier 833611; Index Fungorum (2025) and Species Fungorum (2025) accepted two species.

Type species – *Lunasporangiospora chienii* (P.M. Kirk) Vandepol & Bonito, Fungal Diversity 104: 283

Modicella Kanouse, Mycologia 28(1): 60 (1936)
Index Fungorum Identifier 20336; Index Fungorum (2025) and Species Fungorum (2025) accepted four species.

Type species – *Modicella malleola* (Harkn.) Gerd. & Trappe, Mycol. Mem. 5: 67 (1974)

Notes: *Modicella* species are found growing as saprobes on soils and decaying plant matter and have been recorded in Asia, America, Europe and New Zealand (Vandepol et al. 2020).

Necromortierella Vandepol & Bonito, Fungal Diversity 104: 284 (2020)
Index Fungorum Identifier 833725; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Necromortierella dichotoma* (Linnem. ex W. Gams) Vandepol & Bonito, Fungal Diversity104: 284 (2020)

Notes – The genus was proposed by Vandepol et al. (2020) and consists of only one necrotrophic mycophilic species, which has only been reported from mouse dung in Germany.

Podila Stajich, Vandepol & Bonito, Fungal Diversity 104: 284 (2020)
Index Fungorum Identifier 833766; Index Fungorum (2025) and Species Fungorum (2025) accepted nine species.

Type species – *Podila minutissima* (Tiegh.) Vandepol & Bonito, Fungal Diversity 104: 284 (2020)

Notes – *Podila* was proposed by Vandepol et al. (2020) to accommodate seven *Mortierella* species. Currently, the genus comprises nine species. They are frequently isolated from forest and agricultural soils, compost, dung, and municipal waste. They have been reported from Europe, New Zealand, and North America (Vandepol et al. 2020).

MUCOROMYCOTA Doweld
Mucoromycotina Benny
Endogonomycetes Doweld
Bifiguratales Tedersoo
***Bifiguratace*ae** Tedersoo
Index Fungorum Identifier 853689

Cultured mycelium composed of coenocytic hyphae with intercalary and terminal, globose to subglobose chlamydospores, often producing yeast-like budding cells (Torres-Cruz et al. 2017, Tedersoo et al. 2024).

Family type – *Bifiguratus* T.J. Torres-Cruz & A. Porras-Alfaro

Ecology and life modes – Endophytic in the moss *Leucobryum* sp., also isolated from roots of the orchid *Cymbidium kanran* and *Castanea sativa* (sweet chestnut), and soil (Peintner et al. 2007, Torres-Cruz et al. 2017).

Notes – *Bifiguratales* comprises only *Bifiguratus*, which is monotypic. The generic type, *B. adelaidae* Torres-Cruz & Porras-Alfaro was originally detected during Illumina amplicon sequencing of soil in a temperate pine forest in the southeastern USA (Hesse et al. 2016). It was a common, nitrogen-responsive fungal genotype representing 9% of the fungal community.

Bifiguratus T.J. Torres-Cruz & A. Porras-Alfaro, in Torres-Cruz, Tobias, Almatruk, Hesse, Kuske, Desirò, Benucci, Bonito, Stajich, Dunlap, Arnold & Porras-Alfaro, Mycologia 109(3): 371 (2017).
Index Fungorum Identifier 818093; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Cultured mycelium composed of coenocytic hyphae with intercalary and terminal, globose to subglobose chlamydospores, often producing yeast-like budding cells

Type species – *B. adelaidae* Torres-Cruz & Porras-Alfaro

Notes – The type and only species of *Bifiguratus*, *B. adelaidae*, was originally recognized from environmental DNA sequences and provisionally named "OTU69" (Hesse et al. 2016). In view of its high prevalence in pine forest soils in USA, enigmatic phylogenetic affinities, and unknown ecological role, it was included in the dynamic list of "Top 50 Most Wanted Fungi" (Nilsson et al. 2016). Subsequently, the fungus was formally proposed as a new genus and species based on an isolate previously obtained from moss by U'ren et al. (2010) and two isolates newly obtained from soil using serial dilution and particle filtration-pasteurisation methods by Torres-Cruz et al. (2017).

Densosporales Tedersoo, ex Madrid, P.M. Kirk & Wijayaw.
Densosporaceae Desirò, M.E. Sm., Bidart., Trappe & Bonito ex Madrid, P.M. Kirk & Wijayaw.
Index Fungorum Identifier 900630

Sporophores epigeous or hypogeous, usually subglobose, white, cream-coloured or yellow, sometimes pubescent due to the presence of superficial tapered hyphal clusters, with or without a peridium, containing hyaline, globose hyphae and one-celled, and subglobose to ellipsoidal chlamydospores.

Family type – *Densospora* McGee

Ecology and life modes – Ectomycorrhizal fungi (Warcup 1985, McGee 1996), putative saprobes on dead leaves, twigs and wood (Thaxter 1922, Gerdemann & Trappe 1974), symbionts of vascular and non-vascular plants (Desirò et al. 2017).

Notes – *Densosporaceae* was introduced to accommodate all descendants of "node D" of the 18S-based phylogenetic tree in the study by Desirò et al. (2017). The *Densosporaceae* clade included 57 sequences, which consisted of four sequences of *Sphaerocreas pubescens*, two of *Densospora solicarpa*, one of *D. nuda* and 50 of unidentified environmental *Mucoromycotina* associated with bryophytes and other plants. Multilocus phylogenetic studies by Yamamoto et al. (2020) and Tedersoo et al. (2024) confirmed *Densosporaceae* as a family distinct from *Endogonaceae*.

Since a description of the family *Densosporaceae* was not given by Desirò et al. (2017) or Tedersoo et al. (2024), it has been considered a *nomen invalidum* according to Art. 38.1(a) of the ICN. In this paper, we validate the family by providing a morphological description based on the identified *Densospora* and *Sphaerocreas* species that were included in the family by those authors. However, most sequences in the *Densosporaceae* clade (Desirò et al. 2017) belong to unidentified environmental *Mucoromycotina* whose morphological features are unknown. Further studies will

probably prompt refinements in the circumscription of this fungal family. *Densosporaceae* clade (Desirò et al. 2017) showed a remarkable phylogenetic diversity based mostly on sequences from unidentified fungi. Therefore, future studies are expected to reveal additional genera as members of *Densosporaceae*.

Densospora McGee Aust. Syst. Bot. 9(3): 330 (1996)
Index Fungorum Identifier 27693; Index Fungorum (2025) and Species Fungorum (2025) accepted four species.

Sporophores epigeous or hypogeous, containing numerous chlamydospores. Chlamydospores are terminal or intercalary, mostly globose, subglobose, or ovoid, developed on thin hyphae, with the lumen of the hyphal appendages completely occluded. In some mature chlamydospores, the wall is irregularly thickened and the lumen deformed with contents becoming viscid (*fide* McGee 1996).

Type species – *D. tubiformis* (P.A. Tandy) McGee

Notes – *Densospora* includes four species, *D. nanospora* McGee, *D. nuda* McGee, *D. solicarpa* McGee and *D. tubiformis*, reported as ectomycorrhizal or putative ectomycorrhizal fungi in Australia and Spain (McGee 1996). DNA sequences are available only for *D. nuda* and *D. solicarpa* (Desirò et al. 2017). Cultures of *Densospora* spp. are not available in major fungal collections such as ATCC, CBS or MUCL.

Endogonomycetes Doweld
Endogonales Jacz. & P.A. Jacz.
Jimgerdemanniaceae Tedersoo ex Madrid, P.M. Kirk & Wijayaw.
Index Fungorum Identifier: IF903314
= *Jimgerdemanniaceae* Tedersoo, in Tedersoo, Magurno, Alkahtani & Mikryukov, MycoKeys 107: 311 (2024) **Nom. inval.,** Art. 38.1(a) (Shenzhen); Index Fungorum Identifier: 853692

Sporophores hypogeous or rarely subhypogeous, peridium absent or thin and often disappearing at maturity. Gleba commonly exudes a sticky latex. Zygosporangia are borne from gametangia of unequal size and often covered by a well-developed hyphal mantle composed of thick-walled hyphae (Trappe & Gerdemann 1972, Desirò et al. 2017, Yamamoto et al. 2020).

Family type – *Jimgerdemannia* Trappe, Desirò, M.E. Sm., Bonito & Bidartondo

Ecology and life modes – Ectomycorrhizal fungi (Trappe & Gerdemann 1972, Desirò et al. 2017)

Notes – *Jimgerdemanniaceae* was recently erected for a clade comprising the genus *Jimgerdemannia* and numerous undescribed fungi considered to represent six separate potentially mycorrhizal genera (Tedersoo et al. 2024). Since this family was originally proposed only based on phylogenetic analyses, it was considered invalid according to the Art. 38.1(a), Shenzen code. A morphological description was given here to validate *Jimgerdemanniaceae*.

Jimgerdemannia Trappe, Desirò, M.E. Sm., Bonito & Bidart., in Desirò, Rimington, Jacob, Vande Pol, Smith, Trappe, Bidartondo & Bonito, IMA Fungus 8(2): 249 (2017)
Index Fungorum Identifier 821846; Index Fungorum (2025) and Species Fungorum (2025) accepted three species.

Sporophores hypogeous or rarely subhypogeous, usually globose, subglobose, ellipsoid, reniform or lobed and convoluted, peridium absent or thin and often disappearing partially or completely at maturity. Gleba commonly exuding a sticky latex in young or mature specimens. Gametangia of unequal size, the tip of a small gametangium fusing to the side of a large one. Zygosporangia borne from the tip of the large gametangium and, at maturity, often covered by a hyphal mantle composed of thick-walled, intertwining and anastomosing or spirally arranged hyphae (Trappe & Gerdemann 1972, Desirò et al. 2017, Yamamoto et al. 2020).

Type species – *Jimgerdemannia flammicorona* (Trappe & Gerd.) Trappe, Desirò, M.E. Sm., Bonito & Bidart.

Notes – *Jimgerdemannia* was segregated from *Endogone* by Desirò et al. (2017) to accommodate two atypical species (*E. flammicorona* (= *J. flammicorona*) and *E. lactiflua* (= *J. lactiflua*)) from Europe and North America, which formed a distinct clade and produced zygosporangia from gametangia of unequal size. A third species, *J. ambigua*, was subsequently described from Japan by Yamamoto et al. (2020).

Endogonaceae Paol., Syll. fung. (Abellini) 8: 905 (1889)
Index Fungorum Identifier 81877

Sporocarps epigeous or hypogeous, globose, irregularly-shaped or sometimes resupinate, containing zygosporangia, sometimes accompanied by azygosporangia. Peridium white, yellow, or absent. Zygosporangia homogametic or heterogametic (borne from gametangia of equal or unequal size, respectively), with walls composed of two main zones, an outer sporangiothecium (zygosporangial wall), with single or 2–4 openings, and an inner eusporium (zygospore wall) without openings (*fide* Gerdemann & Trappe 1974, Morton & Benny 1990, Desirò et al. 2017, Yamamoto et al. 2020).

Family type – *Endogone* Link

Ecology & life modes – Ectomycorrhizal fungi of woody plants (Warcup 1990, Yamamoto 2017), biotrophic symbionts of ferns, lycophytes, hornworts and liverworts (Bidartondo et al. 2011, Desirò et al. 2013, Field et al. 2015, Rimington et al. 2015), and putative saprophytes associated with soil, leaf litter, wood, and decaying basidiomes of polypores (Thaxter 1922, Gerdemann & Trappe 1974, Tandy 1975, Yao et al. 1995).

Notes – *Endogonaceae* was previously considered the only family in *Endogonales* (Morton 1988). However, a recent phylogenetic study based on four loci, 18S, 28S, *tef1-α* and *rpb2*, revealed that this order contains two main clades, which were recognized as distinct families, *Endogonaceae* and *Densosporaceae* (Desirò et al. 2017). Tedersoo et al. (2024) placed *Densosporaceae* in the newly erected order *Densosporales* Tedersoo. This order, however, is invalid according to Art. 38.1(a) of the ICN. Chang et al. (2019) analyzed whole-genome data of four collections of *Endogonaceae* and confirmed the placement of this family within *Mucoromycotina*. In addition, the genomes studied by those authors showed signatures of an ectomycorrhizal lifestyle, including a large genome size with high repeat content, and a low diversity of plant-cell-wall-degrading enzymes.

Family type – *Endogone* Link 1809, Mag. Gesell. naturf. Freunde, Berlin 3(1–2): 33 (1809)

Notes – *Endogonaceae* is considered one of the most ancient groups of fungi with the ability to establish mutualistic symbioses with plants and probably contributed to the colonization of terrestrial environments by them (Bidartondo et al. 2011, Desirò et al. 2015). This family includes five genera: *Endogone*, *Jimgerdemannia* Trappe et al., *Jimwhitea* M. Krings & T.N. Taylor, *Peridiospora* C.G. Wu & Suh J. Lin, and *Sclerogone* Warcup (Desirò et al. 2017, Yamamoto et al. 2020, Zhao et al. 2023). The phylogenetic affinities of *Jimwhitea*, *Peridiospora*, and *Sclerogone*, however, have not been evaluated using molecular methods, and Desirò et al. (2017) suggested that *Peridiospora* is probably related to *Glomeromycotina*.

Endogone Link, Mag. Gesell. Naturf. Freunde, Berlin 3(1–2): 33 (1809)
Heterotypic synonym: ***Youngiomyces*** Y.J. Yao in Yao, Pegler & Young, Kew Bull. 50(2): 350 (1995)
Index Fungorum Identifier 20210; Index Fungorum (2025) lists 66 epithets, but Species Fungorum (2025) accepted 30 species.

Sporocarps epigeous or hypogeous, usually sequestrate, containing structural and reproductive hyphae and one-celled, thick-walled zygospores produced within homogametic zygosporangia. Sporangiothecium with single or 2–4 openings, gametangia fusing near the tips and zygospores mostly budding from the junction of the two. Saprobic or participating in mutualistic symbioses with plants (Yao et al. 1995, Desirò et al. 2017, Yamamoto et al. 2015, 2017, 2020).

Type species – *E. pisiformis* Link

Notes – The taxonomic circumscription of *Endogone* has undergone important changes since its original proposal by Link (1809). It comprises 65 names of which at least 34 have been transferred to other genera, such as *Funneliformis*, *Glomus*, *Jimgerdemannia*, *Modicella*, *Redeckera*, *Rhizoglomus*, and *Rhizophagus* (Gerdemann & Trappe 1974, Oehl et al. 2011f, Sieverding et al. 2014, Desirò et al. 2017, Index Fungorum 2024). The type species, *E. pisiformis*, is geographically widespread, but several *Endogone* species have been scarcely mentioned in the literature (Thaxter 1922, Gerdemann & Trappe 1974, Yamamoto et al. 2020). Most *Endogone* species are unable to grow in axenic culture, but successful isolation and sporulation in vitro have been reported in *E. pisiformis* (Berch & Castellano 1986, Jabaji-Hare & Charest 1987). The ability of other species, such as *E. aggregata* and *E. tuberculosa* (Warcup 1990) to grow in culture needs to be verified using molecular tools (Desirò et al. 2017). Few strains are available, but DNA sequences of ribosomal and protein-coding loci of several species have been deposited in GenBank (Yamamoto et al. 2020). The production of zygosporangia from gametangia of similar size distinguishes the genus *Endogone* from *Jimgerdemannia* (Desirò et al. 2017).

Illustration – Refer to Wijayawardene et al. (2024)

Other genera in *Endogonaceae*

Bifiguratus Torres-Cruz & Porras-Alfaro, Mycologia 109(3): 371 (2017)

Index Fungorum Identifier 818093; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Bifiguratus adelaidae* Torres-Cruz & Porras-Alfaro

Notes – The type of *Bifiguratus* is dimorphic (Torres-Cruz et al. 2017). It is mainly distributed in deeper horizons and rarely found on the forest floor (Hesse et al. 2016).

Jimwhitea M. Krings &T.N. Taylor, Mycologia 104(4): 836 (2012)

Index Fungorum Identifier 563662; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Jimwhitea circumtecta* M. Krings & T.N. Taylor 2012

Notes – This genus is the most persuasive fossil representative of *Endogonaceae*. It was discovered from the Middle Triassic epoch (roughly 247–237 Mya, Krings et al. 2011, Taylor et al. 2014, Zhao et al. 2023).

Peridiospora C.G. Wu & Suh J. Lin, Mycotaxon 64: 180 (1997)

Index Fungorum Identifier 27770; Index Fungorum (2025) and Species Fungorum (2025) accepted two species.

Type species – *Peridiospora tatachia* C.G. Wu & Suh J. Lin 1997

Sclerogone Warcup, Mycol. Res. 94(2): 176 (1990)

Index Fungorum Identifier 25385; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Sclerogone eucalypti* Warcup 1990.

Notes – Cultures and sequences are unavailable.

Vinositunicaceae Tedersoo, in Tedersoo, Magurno, Alkahtani & Mikryukov, MycoKeys 107: 311 (2024)

Index Fungorum Identifier 853693

Sporophores epigeous or semi-hypogeous, often with a short stipe-like sterile base. Peridium single layer, sometimes indistinguishable from the glebal tissue, composed of coenocytic hyphae. Gleba is composed of radially or randomly distributed chlamydospores and coenocytic, thin to thick-walled hyphae. Chlamydospores are broadly ellipsoid, terminal (Yamamoto et al. 2020, Tedersoo et al. 2024).

Family type – *Vinosotunica* Koh. Yamam., Degawa & A. Yamada

Ecology and life modes – Probably saprobic fungi in humus (Yamamoto et al. 2020)

Notes – *Vinositunicaceae* is a monotypic family recently proposed to accommodate *Vinositunica* (Tedersoo et al. 2024), a probable saprobe collected from soil in Japan.

Vinositunica Koh. Yamam., Degawa & A. Yamada, Mycologia 112(2): 319 (2020)
Index Fungorum Identifier 829985; Index Fungorum (2025) and Species Fungorum (2025) accepted two species.

Sporophores epigeous or semi-hypogeous, reniform or irregularly shaped, often with a short stipe-like sterile base. Peridium white, partly purple, single layer, sometimes indistinguishable from glebal tissue, composed of coenocytic hyphae. Gleba is pale yellow to purplish-grey, composed of radially or randomly distributed chlamydospores and coenocytic, thin to thick-walled hyphae. Chlamydospores are broadly ellipsoid, terminal, with a wall composed of a purplish to vinaceous outer layer and a colourless inner layer (Yamamoto et al. 2020, Tedersoo et al. 2024).

Type species – *Vinositunica radiata* Koh. Yamam., Degawa & A. Yamada

Notes – *Vinositunica* was introduced with two species, *V. ingens* and *V. radiata*. The genus name refers to the presence of a peculiar wine-coloured pigmentation on the peridium and outer wall of the chlamydospores. Heretofore, no sexual morph has been described in this genus and, despite representing a sister clade to *Endogone*, which includes numerous mycorrhizal species, no symbiotic relationship with plants has been reported in *Vinositunica* (Yamamoto et al. 2020).

Mucoromycetes Doweld, Prosyllabus Tracheophytorum, Tentamen Systematis Plantarum Vascularium (Tracheophyta) (Moscow): LXXVII (2001)
Mucorales Dumort., [as 'Mucorarieae'], Analyse des familles des plantes: avec l'indication des principaux genres qui s'y rattachent: 73 (1829)
Backusellaceae K. Voigt & P.M. Kirk, Index Fungorum 11: 1 (2012)
Index Fungorum Identifier 550011

Sporophores arising directly from the substrate mycelium or from aerial hyphae, simple or sympodially branched, transitorily recurved. Sporangia terminal, multispored, deliquescent-walled. Sporangiola, if present, are few-spored and/or unispored, persistent-walled. Zygospores with opposed suspensors (adapted from Voigt & Kirk in 2012).

Family type – *Backusella* Hesselt. & J.J. Ellis, Mycologia 61: 863 (1969)

Ecology & life modes – Members of the family are cosmopolitan and saprobic. The species are reported in various substrates such as soil, dung, and invertebrates (de Souza et al. 2014, Lima et al. 2016, Urquhart et al. 2021, Hurdeal et al. 2022). It has been isolated in varied temperatures and climates ranging from the Americas, southeast and east Asia and Australia (Nguyen & Lee 2018, Nguyen et al. 2021, Urquhart et al. 2021, Hurdeal et al. 2022, Lima et al. 2022, Cordeiro et al. 2023). There are no reports on human infection by *Backusella*.

Notes – *Backusellaceae* is a monotypic family, erected by Kirk & Voigt (2012) to accommodate *Backusella*. The genus was previously classified in *Mucoraceae*, and later in *Thamnidiaceae*. In molecular phylogenetic analyses, the family is sister to *Pilobolaceae* (Hoffmann et al. 2013). The placement of taxa in this family relies heavily on phylogenetic inference. Species are usually cosmopolitan and saprobic. They are isolated from varied climatic zones all over the globe (de Souza et al. 2014, Lima et al. 2016, Nguyen et al. 2021, Urquhart et al. 2021, Cordeiro et al. 2023). Since this is a monotypic family, its morphology is reflected by *Backusella*, which produces sporangia, multi- or unispored sporangiola on sporophores (Kirk & Voigt 2012). When the sexual morph is observed, zygospores are produced on opposed suspensors (Lima et al. 2016, Nguyen et al. 2021, Urquhart et al. 2021).

Backusella Hesselt. & J.J. Ellis, Mycologia 61: 863 (1969); Fig. 70
Index Fungorum Identifier 20067; Index Fungorum (2025) lists 39 epithets, but Species Fungorum (2025) accepted 37 species.

Sporophores arising directly from the substrate mycelium or from aerial hyphae, transitorily recurved when young and erect when mature, simple or sympodially branched. Tall sporophores terminate in a sporangium, some with pedicellate unispored and/or multispored sporangiola formed laterally. Short sporophores bearing only unispored and/or multispored may be formed near the substrate. Sporangia deliquescent-walled. Sporangiola, if present, are few-spored and/or unispored, persistent-walled. Zygospores with opposed suspensors (adapted from Ellis & Hesseltine 1969, Benny 2005, Voigt & Kirk 2012).

Type species – *Backusella circina* J.J. Ellis & Hesselt. Mycologia 61: 865 (1969)

Notes – This genus was erected by Hesselt & Ellis (1969) with *B. circina* as the type species. *Backusella* has similar morphological traits to *Mucor* (Ellis & Hesseltine 1969). Primarily, *Backusella* species are differentiated from *Mucor* by the production of transitorily recurved sporophores (Hoffmann et al. 2013, Walther et al. 2019, Hurdeal et al. 2022). The formation of sporangia cannot be used for distinguishing the genera as *Mucor* species produce them intermittently. *Backusella* can be resolved from *Mucor* using phylogenetic inference of combined ITS and LSU (Wagner et al. 2019).

ITS and LSU loci have been more commonly used for species delimitation (Hurdeal et al. 2022, Lima et al. 2022). However, Cordeiro et al. (2023) have established the gene encoding the largest subunit of RNA polymerase II (*rpb1*) as a phylogenetic marker in *Backusella*, and Urquhart et al. (2021) have shown that *argA* is also a reliable marker for this genus.

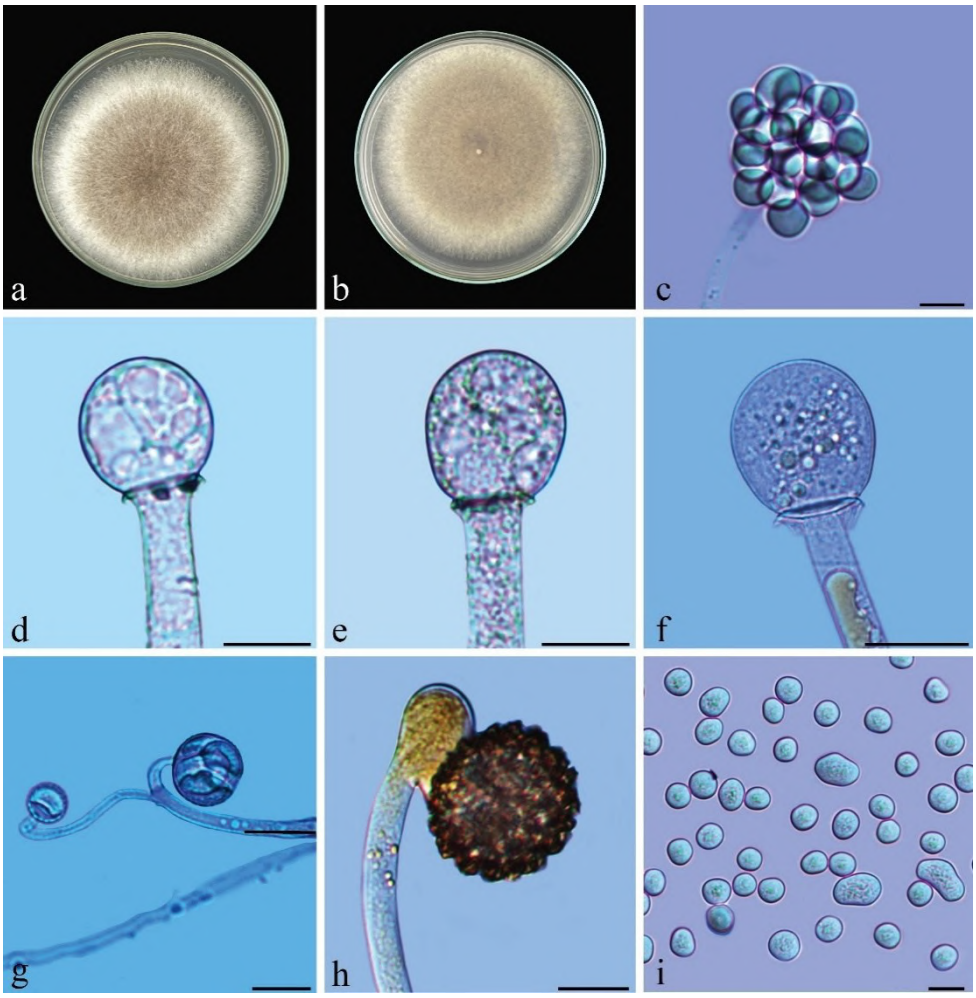


Figure 70 – *Backusella azygospora*. a Colony surface on PDA at 25°C. b Colony reverse on PDA at 25°C. c Sporophore with sporangium. d–f Sporophore with columella. g Short sporophore with sporangiola. h Azygosporangium. i Sporangiospores. Scale bars: c, i = 10 µm; d–h = 25 µm.

Circinellaceae H. Zhao, Y.C. Dai, B.K. Cui, F. Wu, Yuan Yuan & X.Y. Liu, Fungal Diversity 123(1): 55 (2023)
Index Fungorum Identifier 570878

Rhizoids formed or not. Sporangiophores arising from substrate and aerial hyphae, simple or branched, with a straight main stem and circinate, curved, or twisted lateral branches. Terminal sporangia subglobose to globose, multi-spored. Lateral sporangia subglobose to globose, uni- to multispored. Sporophores may form lateral or terminal vesicles bearing uni- or multispored sporangiola. Apophyses present or not. Chlamydospores are sometimes present in substrate hyphae. Zygospores are ornamented, pigmented, with opposed suspensors (Benny 2005, Zhao et al. 2023).

Family type – *Circinella* Tiegh. & G. Le Monn., Annls Sci. Nat., Bot., sér. 5 17: 298 (1873)

Ecology & life modes – Species of the family have been found in soil, dung, rotten materials, and poplin fabric (Benny & Benjamin 1975, Zheng et al. 2017).

Notes – Zhao et al. (2023) introduced *Circinellaceae*, which is phylogenetically close to *Lichtheimiaceae* and *Thermomucoraceae*.

Circinella Tiegh. & G. Le Monn.
Index Fungorum Identifier 20129; Index Fungorum (2025) lists 33 epithets, but Species Fungorum (2025) accepted eleven species.

Sporangiophores circinate, single or in whorls, and borne alternately on both sides of the main sporangiophores, simple or branched. Branches are sometimes with a sterile spine. Sporangia borne at the tip of the circinate branches, multispored. Columellae well developed, variously shaped, always with a well-defined collar. Sporangiospores numerous, hyaline, globose to ovoid, always single-celled. Zygosporangia are smooth-walled with opposed suspensors (Hesseltine & Fennel 1955, Zheng et al. 2017).

Type species – *Circinella umbellata* Tiegh. & G. Le Monn., Annls Sci. Nat., Bot., sér. 5 17: 300 (1873)

Notes – *Circinella* was established by van Tieghem & le Monnier (1873) to accommodate mucor-like species that form sporangiophores with circinate branches bearing sporangia with persistent-walled (Hesseltine & Fennell 1955).

Other genera in *Circinellaceae*

Fennellomyces Benny & R.K. Benj., Aliso 8(3): 328 (1975)
Index Fungorum Identifier 20230; Index Fungorum (2025) and Species Fungorum (2025) accepted four species.

Type species – *Fennellomyces linderi* (Hesselt. & Fennell) Benny & R.K. Benj., Aliso 8(3): 328 (1975)

Notes – In the phylogenetic analyses, *Fennellomyces* is closely accommodated to *Thamnostylum* (Walther et al. 2013), but *Fennellomyces* can easily be distinguished by the distinct enlargement of the sporophore just beneath the terminal sporangium.

Phascolomyces Boedijn ex Benny & R.K. Benj., Aliso 8(4): 417 (1976)
Index Fungorum Identifier 30618; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Phascolomyces articulosus* Boedijn ex Benny & R.K. Benj., Aliso 8(4): 417 (1976)

Notes – *Phascolomyces* was described by Boedijn (1959). However, a holotype was not designated, rendering the new genus invalid. Benny & Benjamin (1976) provided a neotype, thereby amending the introduction of the new taxa. The genus has one species which was initially isolated from Indonesia.

Thamnostylum Arx & H.P. Upadhyay, Gen. Fungi Sporul. Cult. (Lehr): 247 (1970); Fig. 71
Index Fungorum Identifier 20571; Index Fungorum (2025) and Species Fungorum (2025) accepted four species

Type species – *Thamnostylum piriforme* (Bainier) Arx & H.P. Upadhyay, in Arx, Gen. Fungi Sporul. Cult. (Lehr): 247 (1970)

Notes – *Thamnostylum* was erected by von Arx (1970) to accommodate *H. pyriforme* and *H. lucknowense* as both species differed from the type species of *Helicostylum*. Morphologically, the genus is characterized by its apophysate terminal sporangia and pedicellate sporangiola borne in terminal fascicles or on vesicular enlargements arising laterally from the sporophoral axes. Zygospores are globose to subglobose with opposed suspensors (Benny & Benjamin 1975).

Zychaea Benny & R.K. Benj., Aliso 8(3): 334 (1975)
Index Fungorum Identifier 20602; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Zychaea mexicana* Benny & R.K. Benj., Aliso 8(3): 335 (1975)

Notes – The genus is closely related to *Thamnostylum* (Walther et al. 2013). The sporangiola of these two genera resemble each other but the pedicles of *Zychaea* are only slightly, though abruptly, bent distally but never strongly reflexed as in *Thamnostylum* (Benny & Benjamin 1975). According to Benny & Benjamin (1993), *Z. mexicana* never produced mucor-like sporangia as do? species of *Helicostylum* and *Thamnostylum*.

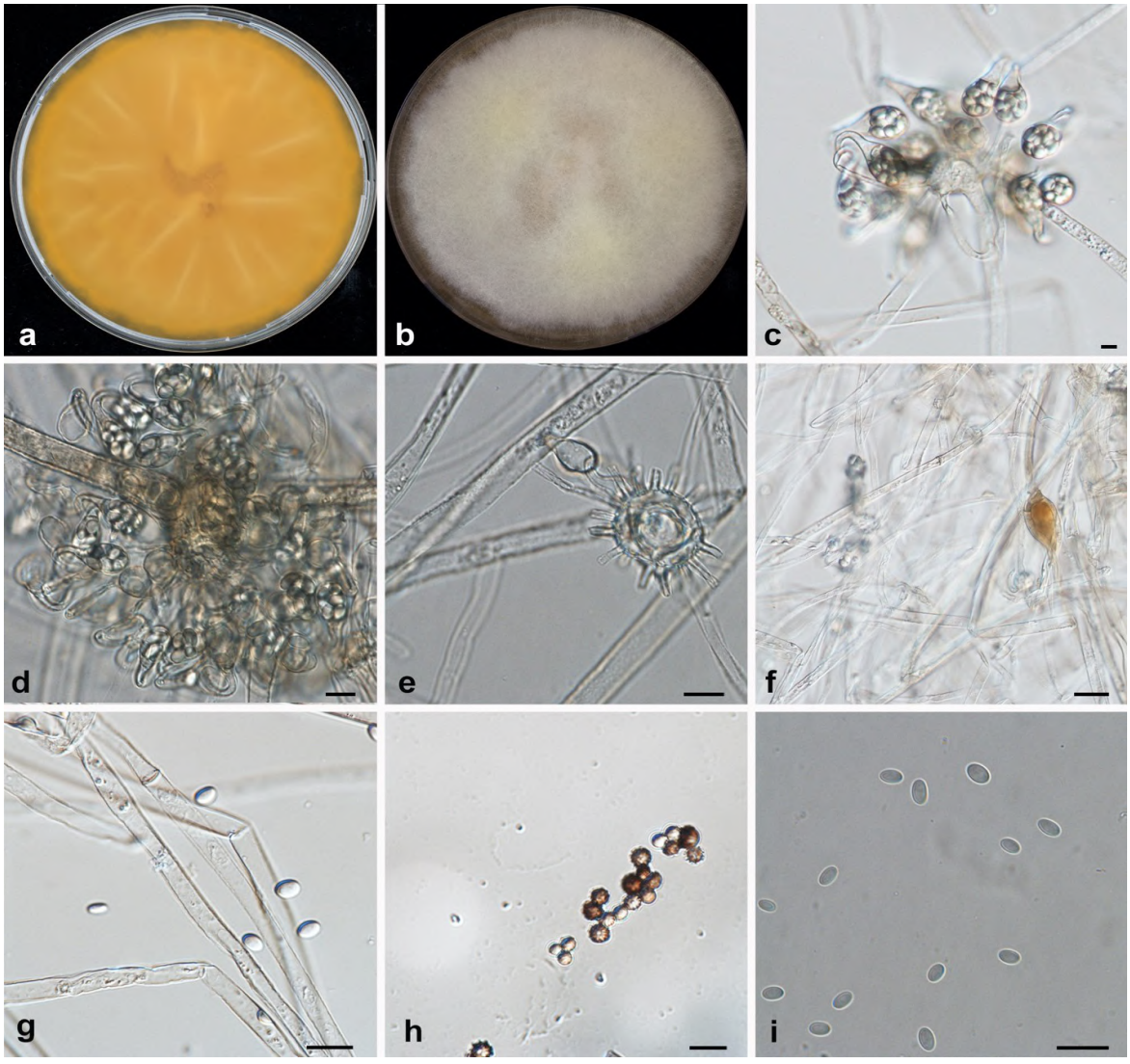


Figure 71 – *Thamnostylum lucknowense* (CBS 576.69). a, b Colony on MEA after 5d. c, d Sporangiophore with sporangiola. e Ornamented sporangiola. f Chlamydospore. g Aseptate Hyphae. h Sporangiospores. i Spores. Scale bars = 10 µm.

Cunninghamellaceae Naumov ex R.K. Benj, 4 (2): 415 (1959)
Index Fungorum Identifier 80668

Mycelium aseptate, often irregularly septate with age, branched, hyaline or pigmented. Sporangiophores or sporophores simple or branched with terminal columellate sporangium or terminal vesicle with sporangiola. Sporangiola may be formed on vesicles originating from multivesiculate sporophores. Sporangiola unispored, acolumellate, smooth or echinulate. Zygospores globose, with rough, pigmented wall, lack appendages, suspensors opposed.

Family type – *Cunninghamella* Matr, Annls mycol. 1(1): 46 (1903)

Ecology & Life modes – Most species are saprobes that are isolated from substrates such as soil.

Notes – Naumov (1935) proposed *Cunninghamellaceae*, however, the description lacked a Latin diagnosis. Benjamin (1959) provided the Latin diagnosis and effectively introduced the family. Initially, the family comprised three genera, *Cunninghamella*, *Sigmoideomyces*, and *Thamnocephalis*. Subsequently, *Benjaminia*, *Chaetocladium*, *Mycotypha*, and *Phascolomyces* were erroneously placed within *Cunninghamellaceae*. Currently, the family comprises only six genera (Wijayawardene et al. 2022, Zhao et al. 2023).

Cunninghamella Matr, Annls mycol. 1(1): 46 (1903); Fig. 72
Index Fungorum Identifier 20150; Index Fungorum (2025) 143 epithets but Species Fungorum (2025) accepted 123 species

Mycelium smooth, coenocytic, often irregularly septate with age. Rhizoids scant to abundant. Stolons present or absent. Sporophores simple or branched, verticillate or pseudo verticillate to cymosely, monopodially, sympodially or iregularly branched, bearing a terminal varied-shaped vesicle or sometimes without a terminal vesicle and branched into several branches. Sporangiola pedicellate, unispored, spinulose on terminal vesicles. Sporangiospores similar to sporangiola in size and shape. Zygosporangia unispored with wart-like projections. Zygospores sub-smooth to slightly ridged, rarely tuberculate. Suspensors opposed more or less equal in size (Zheng & Chen 2001, Benny 2005, Alcorn & Yeager 2018).

Type species – *Cunninghamella echinulata* (Thaxt.) Thaxt. ex Blakeslee, Bot. Gaz. 40: 161 (1905)

Notes – The genus was established by Matruchot (1903) and is typified by *C. africana*. *Cunninghamella* species have single or branched sporophores, with unispored, spinulose sporangiola on terminal vesicles. The taxonomy of this genus was revised using morphological traits, maximum growth temperature, mating compatibility and phylogenetic inference whereby several species and varieties were accepted (Yu et al. 2014, Zheng & Chen 2001, Zhao et al. 2023). Currently, the ITS and LSU rDNA sequences are effective in species delimitation. Zheng & Chen (2001) monographed the genus and accepted twelve species and four varieties. The genus has 26 species (Species Fungorum 2025), which are common saprobes from the soil, mammalian excrement, fruits, and decaying organic matter (Zheng & Chen 2001, Yu et al. 2014, Nguyen et al. 2017), but also includes pathogens or endophytes (Guo et al. 2015, Bellanger et al. 2018).

Other genera in *Cunninghamellaceae*

Absidia Tiegh., Annls Sci. Nat., Bot., sér. 6 4(4): 350 (1878) [1876]
Index Fungorum Identifier 20001; Index Fungorum (2025) lists 115 epithets, but Species Fungorum (2025) accepted 70 species.

Type species – *Absidia reflexa* Tiegh., Annls Sci. Nat., Bot., sér. 64(4): 363 (1878)

Notes – *Absidia* was introduced by van Tieghem (1876) and consists of fungal species that are ubiquitous soil inhabitants (Hoffmann et al. 2007, Zhang et al. 2018b, Cordeiro et al. 2020, Lima et al. 2020, Hurdeal et al. 2021). They are also commonly associated with decaying plant matter and herbivorous dung (van Tieghem 1876). Previously, *Absidia* species encompassed mesophilic and thermotolerant species as well as mycoparasites. Hoffmann et al. (2007, 2009)

refined the taxonomy of the genus, and now *Absidia* consists of mesophilic species that have an ideal growth between 25°C and 34°C. Mycoparasite species of other mucoralean fungi were transferred to *Lentamyces*, while thermotolerant species were moved to *Lichtheimia* (Hoffmann et al. 2007, Hoffmann & Voigt 2009). The asexual morphs of *Absidia* species consist of sporangiophores with apophysate, pyriform sporangia with deliquescent walls.

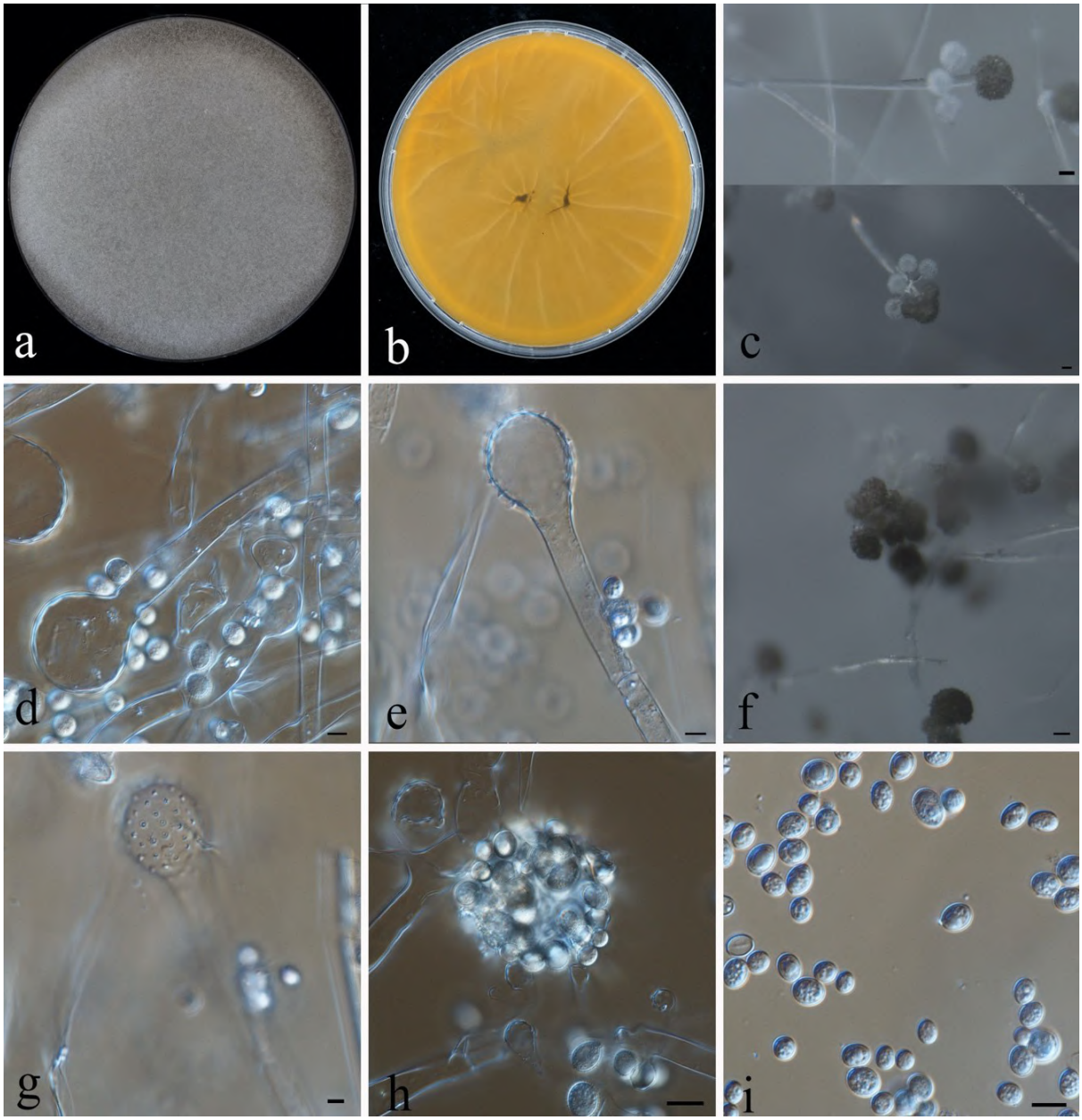


Figure 72 – *Cunninghamella bertholletiae* (CBS 190.84). a, b colony on MEA after 5d. c, f, h sporophores with sporangiola. d, e, g sporophore with vesicle. i sporangiola. Scale bars = 10 µm.

Chlamydoabsidia Hesselt. & J.J. Ellis, Mycologia 58(5): 761 (1966)
Index Fungorum Identifier 20114; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Chlamydoabsidia padenii* Hesselt. & J.J. Ellis [as 'padeni'], Mycologia 58(5): 763 (1966)

Notes – This genus comprises only *C. padenni*, which differs from *Absidia* species by forming pigmented chlamydospores, typically elliptical and sometimes with a papilla at the distal end, nearly fusiform, in the aerial mycelium. Zygospores are unknown (Hesseltine & Ellis 1966).

Gongronella Ribaldi, in Riv. Biol. 44: 164 (1952)
Index Fungorum Identifier 20247; Index Fungorum (2025) lists 27 epithets, but Species Fungorum (2025) accepted 26 species.

Type species – *Gongronella urceolifera* Ribaldi, Riv. Biol. 44: 157 (1952)

Notes – *Gongronella* species have relatively slow growth and are typically isolated from soil (Zhang et al. 2019). They differ from other mucoralean fungi by forming sporangiophores with strongly apophysate sporangia. Sporangiospores are bean-shaped, elliptical, and lacrymoid (Freitas et al. 2020). Delimitation of species within the genus is usually based on morphological characters and phylogenetic inferences using ITS and LSU rDNA sequence data.

Halteromyces Shipton & Schipper, in Antonie van Leeuwenhoek 41: 337 (1975)
Index Fungorum Identifier 20251; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Halteromyces radiatus* Shipton & Schipper, Antonie van Leeuwenhoek 41(3): 337 (1975)

Notes – There is only one species, *Halteromyces radiatus*, in the genus. It differs from *Absidia* species mostly by forming sporangiophores with a dumbbell-shaped sporangium, occasionally pyriform to globose. Zygospores are unknown. To our knowledge, this species has only been reported in Australia, where the initial specimen was isolated from mud from a mangrove forest contaminated with effluent (Shipton & Schipper 1975).

Hesseltinella H.P. Upadhyay, Persoonia 6(1): 111 (1970)
Index Fungorum Identifier 20266; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Hesseltinella vesiculosa* H.P. Upadhyay, Persoonia 6 (1): 111 (1970)

Notes – *Hesseltinella* is characterized by forming pedicellate, spiny and multi-spored sporangiola, which are on vesicles originating from multivesiculate sporophores (Upadhyay 1970, Benny 2005).

Lentamycetaceae K. Voigt & P.M. Kirk, Index Fungorum 11: 1 (2012) (Wilk)
Index Fungorum Identifier 550009
Stolons and rhizoids are produced. Produce sucker-like substrate mycelium and galls in the presence of other fungi (potential hosts). Sporangiophores single, unbranched or rarely branched, curved to circinate, subsporangial septum often present. Sporangia apophysate, spherical or subpyriform, and with spherical or hemispherical columella. Sporangiospores hyaline, ovoid to subcylindrical, smooth-walled; predominantly homothallic, ornamented and melanized zygospores with opposing suspensors and without appendages (Hoffmann & Voigt 2009, Voigt & Kirk 2012).

Family type – *Lentamyces* Kerst. Hoffm. & K. Voigt, Pl. Biol. [11] ([4]): 14 [of prepr.; 550] (2008) [2009]

Ecology & life modes – Members of the family were mainly reported as soil saprobes, facultative mycoparasites, and hyperparasites on other mucoralean fungi.

Notes – The family was erected by Voigt & Kirk (2012) and is typified by *Lentamyces* (Hoffmann & Voigt 2009), with two formally described species, *L. parricida* (basionym: *Absidia parricida* Renner & Muskat ex Hesselt. & J.J. Ellis, neotype CBS 174.67), and *L. zychae* (basionym: *Absidia zychae* Hesselt. & J. J. Ellis, type CBS 104.35). To study their relationships with the most likely conspecific genus *Siepmannia* (Kwaśna & Nirenberg 2008a, b) requires resampling and further formal investigation using multilocus studies, since no living cultures are available.

Lentamyces Kerst. Hoffm. & K. Voigt, Pl. Biol. 11(4): 550 (2009)

Index Fungorum Register Identifier 511979; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

The generic description is similar to the family description above.

Type species – *Lentamyces parricidus* (Renner & Muskat ex Hesselt. & J.J. Ellis) Kerst. Hoffm. & K. Voigt 2008.

Notes – *Lentamyces* is typified by *L. parricidus* (Renner & Muskat ex Hesselt. & J.J. Ellis) Kerst. Hoffm. & K. Voigt (basionym *Absidia* parricida Renner & Muskat; Hoffmann & Voigt 2009). The genus is characterized by a slow-growth colony and a maximum growth temperature of <30°C (Hoffmann & Voigt 2009). It contains four species (Species Fungorum 2025).

Lichtheimiaceae Kerst. Hoffm., G. Walther & K. Voigt, Mycol. Res. 113(3): 277 (2009)
Index Fungorum Identifier 508680

Fast-growing colonies with optimum temperatures ranging from 37°C to 42°C, with a maximum temperature for growth at 53°C. Hyphae are aseptate or irregularly septate with age. Subsporangial septum are often observed. Sporangiophores are simple or branched with collumellate sporangia usually spherical or subpyriform, apophysate or sporophores forming fertile heads consisting of a dichotomous branch system, some branches become a sterile spine and the other still branch sucessively and terminate in a fertile vesicle that bears unispored, pedicellate, and minutely columelate sporangiola. Columellae with or without one or more projections on its surface. Giant cells, abundant if produced, irregularly shaped with finger-like projections. Zygospores globose to oval, thick-walled, non-appendaged, with suspensors equal in size, and surrounded by equatorial rings (Benny & Benjamin 1975, Hoffmann et al. 2007)

Family type – *Lichtheimia* Vuill., Bull. Soc. mycol. Fr. 19: 126 (1903)

Ecology & life modes – Saprobic on soil and from dung, associated with humans (e.g. *Lichtheimia corymbifera* from the cornea of *Homo sapiens*, Italy).

Notes – The family was established by Hoffmann et al. (2007) to segregate thermotolerant species, formerly classified within *Absidia*. Phylogenetic inference based on ITS and LSU provided evidence that mesophilic *Absidia* species formed a well-separated clade from thermotolerant ones. This was backed up by the study of O'Donnell et al. (2001), which used SSU, LSU and the exons of *tef-1*α, together with morphological criteria, to reveal the polyphyly of what was considered *Absidia* at the time. Hoffmann et al. (2007) also provided phylogenetic evidence showing that thermotolerant and mesophilic *Absidia* species were not sister taxa. Morphologically, some species of *Lichtheimiaceae* often produce irregularly shaped giant cells with lateral finger-like projections, which are rarely observed in *Absidia* and never in *Lentamyces*. This family includes all thermotolerant *Absidia* species, which lack appendages on their zygospore suspensors. Physiological data provided further evidence of the separation. Growth at temperatures of 37°C or above distinguishes between the mesophilic and thermotolerant species in the group (Hoffmann et al. 2007, 2009, Hoffmann & Voigt 2009).

Lichtheimia Vuill., Bull. Soc. mycol. Fr. 19: 126 (1903); Fig. 73
Index Fungorum Identifier 20308; Index Fungorum (2025) lists 24 epithets, but Species Fungorum (2025) accepted eleven species.

Sporangiophore is simple or rarely branched, erect, bent or circinate, arising from aerial hyphae or stolons, with an occasional subsporangial septum. Sporangia spherical or subpyriform, with bell-shaped apophyses. Columellae spherical, hemispherical and occasionally conical, with or without collars and one or more projections on their surface. Sporangiospores are spherical or ellipsoidal. Giant cells, when produced, are abundant, globose, and irregularly shaped with finger-like projections. Zygospores arise from opposed gametangia, globose to oval, smooth, thick-walled, occasionally developing equatorial rings surrounding the spores. Suspensors non-appendaged.

Type species – *Lichtheimia corymbifera* (Cohn) Vuill., Bull. Soc. mycol. Fr. 19: 126 (1903)

Notes – *Lichtheimia* is phylogenetically distinct from *Absidia*, with morphophysiological differences. The two are classified within different families (Hoffmann et al. 2007, 2009, 2013, Hoffmann & Voigt 2009, Hoffmann 2010, Wijayawardene et al. 2020). The pivotal diagnostic features of *Lichtheimia* comprise the production of zygospores that lack appendaged suspensors and also their optimal and maximum growth temperatures above 37°C (Hoffmann et al. 2007).

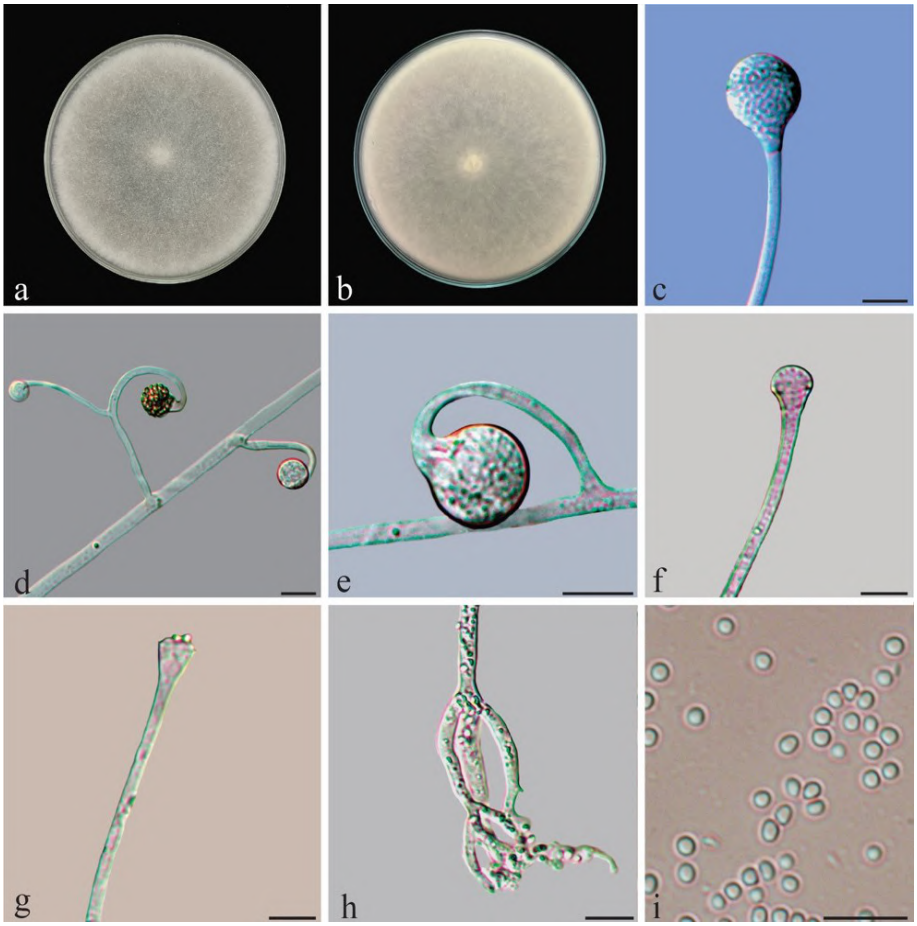


Figure 73 – *Lichtheimia brasiliensis*. a Colony surface on PDA at 25°C. b Colony reverse on PDA at 25°C. c Sporangiophore with sporangium. d Sporangiophores arising from stolon. e Curved sporangiophore with sporangium. f, g Sporangiophore with columella. h Rhizoid. i Sporangiospores. Scale bars: a–i = 20 µm.

Other genera included in *Lichtheimiaceae*

Dichotomocladium Benny & R.K. Benj., Aliso 8(3): 338 (1975)

Index Fungorum Identifier 20173; Index Fungorum (2025) and Species Fungorum (2025) accepted five species.

Type species – *Dichotomocladium elegans* Benny & R.K. Benj., Aliso 8(3): 339 (1975)

Notes – Macroscopically, the genus resembles *Chaetoclaclium*, which also produces unispored sporangiola. However, the two are fundamentally different and can be distinguished by the development of the spore-bearing structures (Benny & Benjamin 1975, 1993). In phylogenetic inference, the genus is close to *Lichtheimia* but is morphologically different in that it produces dichotomous branched fertile hyphae, sterile spines, and sporangiola (Hoffmann et al. 2007, 2009).

Mucoraceae Fr. [as 'Mucoreae'], Syst. Mycol. (Lundae) 1: 69 (1821)

Index Fungorum Identifier 81030

Hyphae are hyaline or pigmented. Sporangiophore aseptate or irregularly septate, simple or branched. Sporangia apophysate or non-apophysate, columellate. Sporangiola pedicellate or non-

pedicellate may be formed. Sporangia and sporangiola may dehisce or not along preformed sutures. Sporangiospores with or without appendages. Zygosporangia with warty to smooth zygosporangial wall, opposed suspensors, non-appendaged.

Family type – *Mucor* Fresen., Beitr. Mykol. 1: 7 (1850)

Ecology & life modes – Most species are saprobes, while some genera, such as *Dicranophora*, and *Parasitella* are facultative mycoparasites (Lima et al. 2018, de Souza et al. 2020, Hurdeal et al. 2021). Some species are also opportunistic pathogens causing mucormycosis (Wang et al. 2019, Dannaoui & Lackner 2019, Reid et al. 2020).

Notes – *Mucoraceae* is the largest family and presumably the most derived in the *Mucorales*. Previously, species lacking diagnostic features to be classified within any other family were assigned to this family. Hurdeal et al. (2021) provided more insight and circumscribed a monophyletic family that has highly diverse phenotypic features for the delimitation of species and genera.

Mucor Fresen., Beitr. Mykol. 1: 7 (1850); Fig. 74
Index Fungorum Identifier 25484

Sporangiophore is simple or branched. Sporangia non-apophysate, globose, subglobose, and deliquescent-walled. Zygospores with opposed, equally shaped suspensors. Rhizoids and sporangiola are rarely observed.

Type species – *Mucor mucedo* Fresen., Beitr. Mykol. 1: 7 (1850)

Notes – *Mucor* was erected by Fresenius (1850) and has over 300 species cited in previous literature (Kirk 1986, Jacobs & Botha 2008, Nguyen et al. 2024, Lima et al. 2020, Zhao et al. 2023). Wijayawardene et al. (2022) accepted 98 species as valid. The genus comprises mostly saprobic species, but also endophytes, and plant and human pathogens (Hurdeal et al. 2021). *Mucor* species are mesophilic, with some growing at higher temperatures, but none seem to grow above 42°C (Walther et al. 2019).

Other genera in *Mucoraceae*

Actinomucor Schostak., Ber. dt. bot. Ges. 16: 155 (1898)
Index Fungorum Identifier 20013; Index Fungorum (2025) lists eleven epithets, however, Species Fungorum (2025) accepted one species.

Type species – *Actinomucor elegans* (Eidam) C.R. Benj. & Hesselt., Mycologia 49(2): 241 (1957)

Notes – *Actinomucor* is a monotypic genus. It was originally described by Schostakowitsch (1898) from Siberia. The protologue indicates that the genus bears a close morphological resemblance to *Mucor*, however differs in the formation of stolons, and in the branching pattern of the sporangiophores.

Ambomucor R.Y. Zheng & X.Y. Liu, Mycotaxon 126: 99 (2014) [2013]
Index Fungorum Identifier 518101; Index Fungorum (2025) lists six epithets, however, Species Fungorum (2025) accepted three species.

Type species – *Ambomucor seriatoinflatus* X.Y. Liu & R.Y. Zheng, Mycotaxon 126: 99 (2014) [2013]

Notes – *Ambomucor* was established by Zheng & Liu (2014) and is typified by *A. seriatoinflatus*. The genus comprises three species from China. The species differ from *Mucor* by forming sporangiophores with both fertile sporangia with columella and sporangiospores and aborted sporangia (in chains) that lack columella and sporangiospores (Liu & Zheng 2015). *Ambomucor seriatoinflatus* can synthesize sialidases, which are widely applied in food and pharma industries (Abrashev et al. 2021).

Benjaminiella Arx, Gen. Fungi Sporul. Cult., Edn 3 (Vaduz): 60 (1981)

Index Fungorum Identifier 20072; Index Fungorum (2025) and Species Fungorum (2025) accepted three species.

Type species – *Benjaminiella poitrasii* (R.K. Benj.) Arx, Gen. Fungi Sporul. Cult., Edn 3 (Vaduz): 60 (1981).

Notes – This genus was introduced as *Benjaminia* Pidopl. & Milko (Pidoplichko & Mil'ko 1971), but it was illegitimate (Art. 64.1 of the ICBN). von Arx (1981) proposed *Benjaminiella* with a single species, *B. poitrasii* (R.K. Benjamin) von Arx, which was originally described as *Cokeromyces poitrasii* R.K. Benj., and later transferred to *Mycotypha*, as *M. poitrasii* (R.K. Benj.) Benny & R. K. Benj. This genus comprises three homothallic species that form sporophores with a vesicle that bears sporangiola on long, curved to twisted and contorted pedicels. Zygosporangia have pigmented and ornamented walls (Kirk 1989, Benny 2005). The species are found in soil and rat dung, and sometimes as pathogens of humans (von Arx 1970, Gade et al. 2017). In the phylogeny of Walther et al. (2013), *Benjaminiella* was close to *Cokeromyces*.

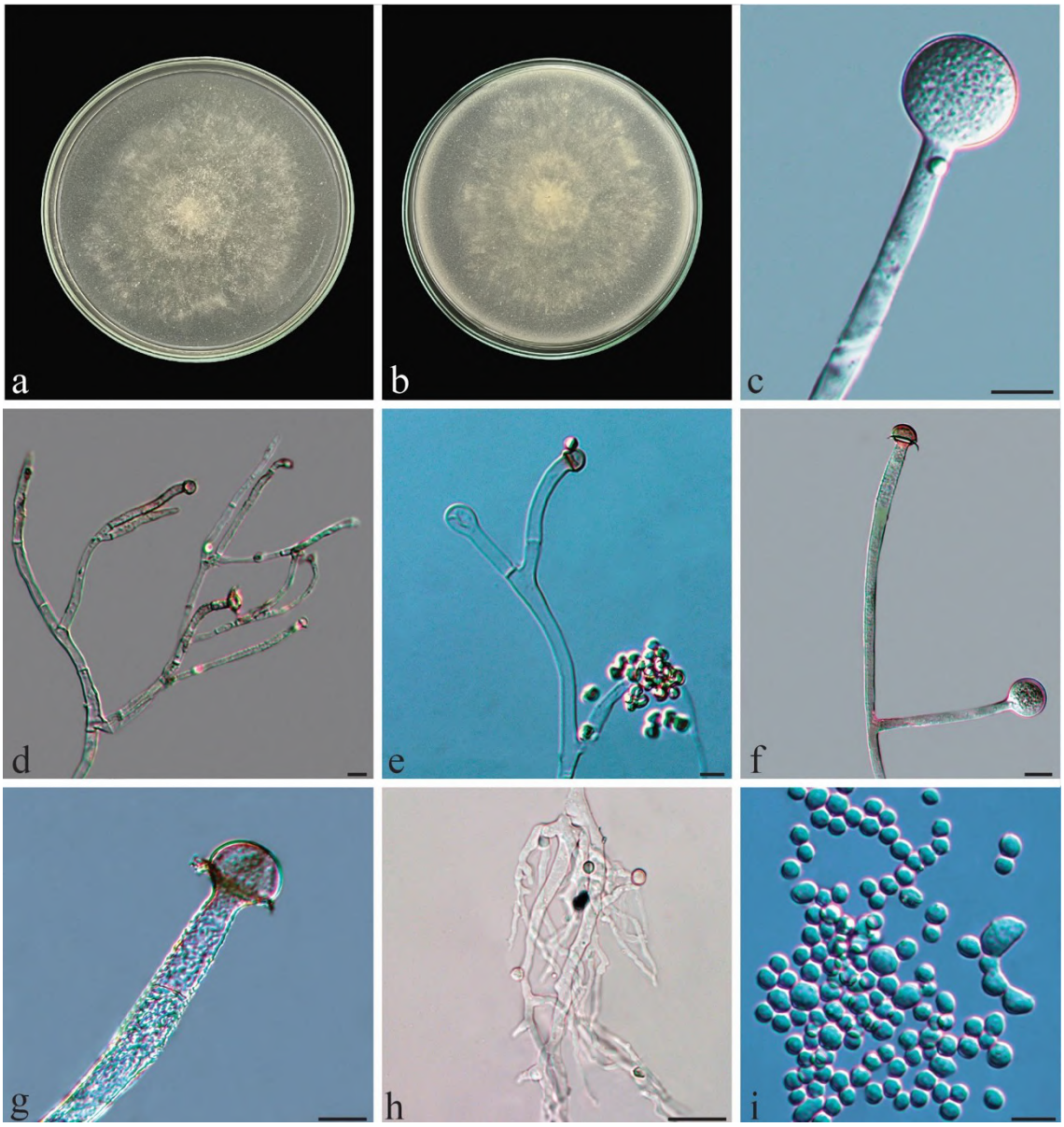


Figure 74 – *Mucor septatiphorus*. a Colony surface on PDA at 25°C. b Colony reverse on PDA at 25°C. c Sporangiophore with sporangium. d, e Branched sporangiophore with columellae. f Branched sporangiophore with terminal sporangium and lateral columella. g Sporangiophore with columella. h Rhizoid. i Sporangiospores. Scale bars: a–i = 20 µm.

Blakeslea Thaxt., Bot. Gaz. 58: 353 (1914)
Index Fungorum Identifier 20076; Index Fungorum (2025) and Species Fungorum (2025) accepted two species.

Type species – *Blakeslea trispora* Thaxt., Bot. Gaz. 58: 353 (1914)

Notes – This genus comprises two species, *B. trispora* and *B. monospora* B.S. Mehrotra & Baijal, which can be differentiated by the number of spores within sporangiola, being 3(–4) in *B. trispora* and 1(–2) in *B. monospora* (Ho & Chang 2003). *Blakeslea* species are facultative parasites of flowers, but they can also be isolated from soil (Mehrotra 1964, Benny 2010). Nguyen & Lee (2016) isolated *B. trispora* from the guts of grasshoppers and soldier fly larvae. *Blakeslea* has been reported in Australia, Brunei Darussalam, China, Chinese Taipei, Fiji, French Southern Territories, India, Indonesia, Kiribati, Malaysia, Madagascar, Malta, Nigeria, Oman, Panama, Papua New Guinea, Sierra Leone, Sri Lanka, Sweden, Vietnam, Thailand, USA, and Trinidad and Tobago.

Chaetocladium Fresen., Beitr. Mykol. 3: 97 (1863)
Index Fungorum Identifier 20111; Index Fungorum (2025) lists eleven epithets, however, Species Fungorum (2025) accepted four species.

Type species – *Chaetocladium jonesiae* (Berk. & Broome) Fresen. [as 'jonesii'], Beitr. Mykol. 3: 98 (1863)

Notes – *Chaetocladium* is currently classified within *Mucoraceae*. It differs from *Dichotomocladium* mostly by forming sporophores that are verticillately branched, whereas species of the latter form sporophores dichotomously branched. In addition, species of *Chaetocladium* are psychrophiles, while *Dichotomocladium* spp. can grow well at temperatures from 18 to 31°C (Benny & Benjamin 1975).

Choanephora Curr., J. Linn. Soc., Bot. 13: 578 (1873)
Index Fungorum Identifier 20117

Type species – *Choanephora infundibulifera* (Curr.) D.D. Cunn., Syll. fung. (Abellini) 9: 339 (1891)

Notes – *Cunninghamia* was introduced by Currey (1873) to accommodate *C. infundibulifera*, but this genus was illegitimate for being a homonym of *Cunninghamia* R. Br., a genus of conifers. Currey (1873) renamed the species as *Choanephora cunninghamiana* Curr. Some years later, Saccardo (1891) named it *C. infundibulifera*.

Both sporangia and zygospores of *Choanephora* are identical to those of *Blakselea* (Benny 2010). However, sporangiola of the latter dehisce along preformed sutures into 1–3 segments (see description below), and its spores have polar appendages. Two species are known for this genus, *C. infundibulifera* and *C. cucurbitatum* (Berk. & Ravenel) Thaxt. While the former forms ellipsoid to broadly ellipsoid sporangiola, and commonly distinctly striate spores, sporangiola of the latter are subglobose to obovoid, and spores are smooth or rarely faintly striate (Kirk 1984).

Choanephora species cause fruit rots, flower rots and leaf blights on a variety of plants (Chandrakala et al. 2018), such as aubergine (eggplant), bean, cucumber, Chinese cabbage, green beans, millet, okra, papaya, pea, pumpkin, pepper, rice, sorghum, and summer squash, in tropical and subtropical regions (Agrios 2005, Kwon & Jee 2005, Pornsuriya et al. 2017, Das et al. 2017a, b, c, Sangeeta et al. 2018). The genus shows worldwide distribution.

Cokeromyces Shanor, in Shanor, Poitras & Benjamin, Mycologia 42(2): 272 (1950)
Index Fungorum Identifier 23001; Index Fungorum (2025) lists two epithets, however, Species Fungorum (2025) accepted one species.

Type species – *Cokeromyces recurvatus* Poitras, Mycologia 42(2): 272 (1950); Fig. 75

Notes – The genus was erected by Shanor et al. (1950) to accommodate *Cokeromyces recurvatus.* Initially, *Cokeromyces* was classified within *Choanephoraceae*, due to its pedicellate, multispored sporangiola borne on enlarged tips (vesicles) of erect sporophores. Currently, it is classified within *Mucoraceae*. The species are saprobes on dung and soil (rare) (Benny 2005),

however, there are some cases of mucormycosis caused by this fungus (Gomes et al. 2011). In the phylogeny of Walther et al. (2013) *Cokeromyces* was close to *Benjaminiella*.

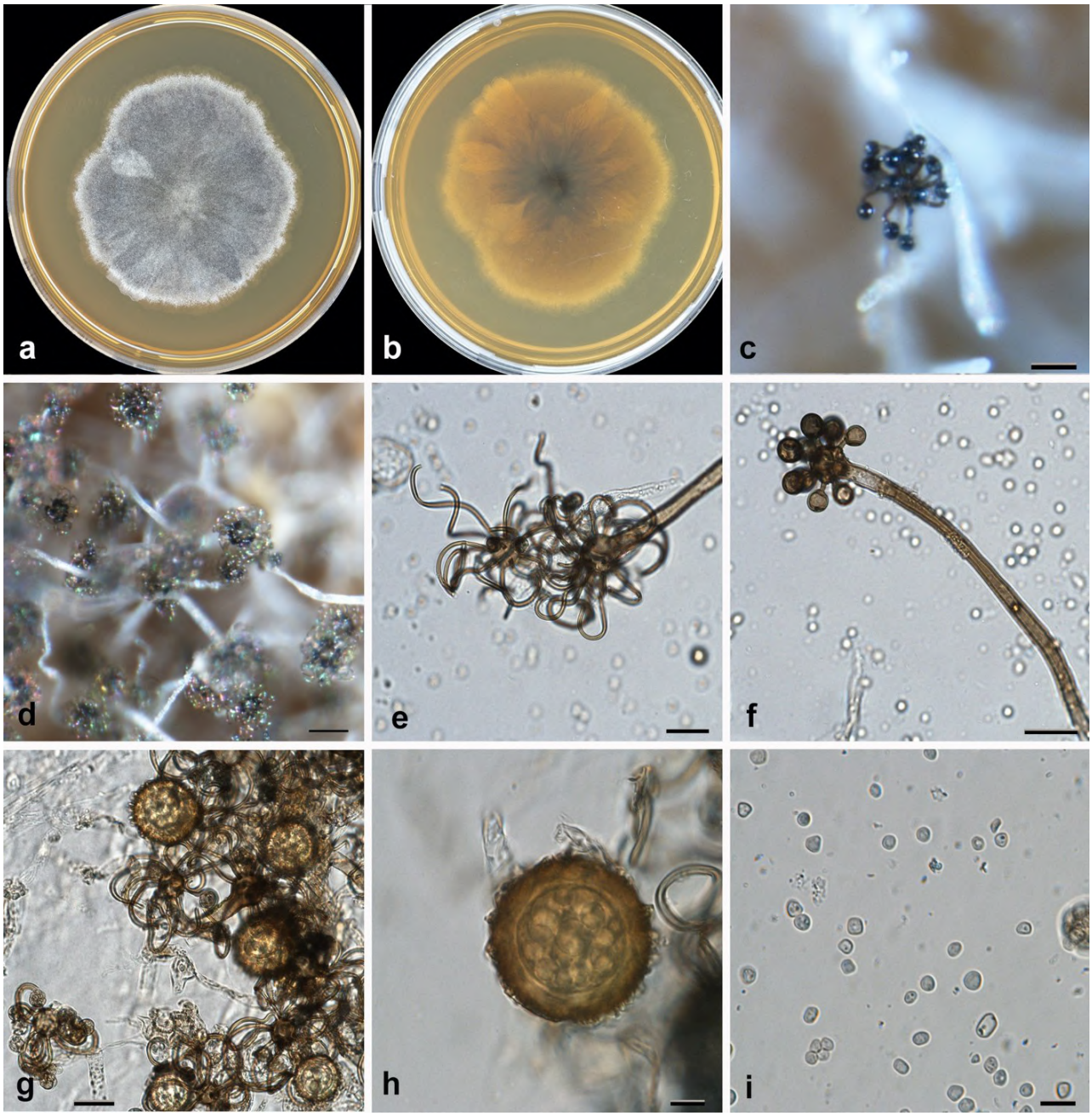


Figure 75 – *Cokeromyces recurvatus* (CBS 158.50). a, b Colony on MEA after 5d. c–f Sporangiophore with pedicellate sporangiola. g, h zygosporangia. i spores. Scale bars: a–i = 10 µm.

Dicranophora J. Schröt., Jber. schles. Ges. vaterl. Kultur 64: 184 (1886)
Index Fungorum Identifier 20175; Index Fungorum (2025) lists two epithets, however, Species Fungorum (2025) accepted one species.

Type species – *Dicranophora fulva* J. Schröt., Jber. schles. Ges. vaterl. Kultur 64: 184 (1886)

Notes – *Dicranophora* is characterized by forming simple or branched sporangiophores terminating in a sporangium as well as repeatedly dichotomously branched sporophores with unispored sporangiola (Benny 2005). *Dicranophora fulva* is homothallic and characterized by pronouced aniosigamy. It is a parasite of boletaceous fungi (Voglmayr & Krisai-Greilhuber 1996). In molecular phylogenetic analyses, the genus nested with *Mucor* (Hoffmann et al. 2013).

Ellisomyces Benny & R.K. Benj., Aliso 8(3): 330 (1975)
Index Fungorum Identifier 20200; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Ellisomyces anomalus* (Hesselt. & P. Anderson) Benny & R.K. Benj., Aliso 8(3): 330 (1975)

Notes – The genus differs from *Mucor* by the production of multispored sporangiola and the branching pattern of the sporangiophore (Hoffmann et al. 2013), which has bifurcate or trifurcate apical branches with globose, columellate, multi-spored, and persistent-walled sporangiola (Benny & Benjamin 1975). Most cultures of *Ellisomyces anomalus* have been isolated from dung (Benny 2005).

Gilbertella Hesselt., Bull. Torrey bot. Club 87: 24 (1960)
Index Fungorum Identifier 20240; Index Fungorum (2025) lists four epithets, but Species Fungorum (2025) accepted one species.

Type species – *Gilbertella persicaria* (E.D. Eddy) Hesselt., Bull. Torrey Bot. Club. 87: 24 (1960)

Notes – Hesseltine (1960) was the first to include *Gilbertella* in *Mucoraceae*. This genus was monographed by Benny (1991), who proposed the family *Gilbertellaceae*. However, a multi-gene genealogy (*act*, *tef1*-α, SSU and LSU rDNA) and scanning electron microscopic analyses (Voigt & Olsson 2008) were enough to reduce *Gilbertellaceae* to *Choanephoraceae*.

Gilbertella has been described as a storage-rot fungi on apples, bananas, black plums (*Syzygium cumini*), Barbados cherry (*Malpighia glabra*), dragon fruit, eggplant, papaya, peach, pear, tomato, and strawberry (Benny 1991, Guo et al. 2012, Pinho et al. 2014, Cruz-Lachica 2016, Vieira et al. 2018, Takushi et al. 2020, Zhang et al. 2020). Mehrotra & Mehrotra (1963) isolated this species (as *G. persicaria* var. *indica*) from the soil. *Gilbertella persiaria* was found infecting black tiger shrimp (*Penaeus monodon*), causing respiratory dysfunctions, degeneration of the basement membrane, and degeneration of epithelial cells in the muscles (Karthikeyan & Gopalakrishnan 2014).

Helicostylum Corda, Icon. fung. (Prague) 5: 18, 55 (1842)
Index Fungorum Identifier 20263; Index Fungorum (2025) 17 epithets, but Species Fungorum (2025) accepted two species.

Type species – *Helicostylum elegans* Corda, Icon. fung. (Prague) 5: 55 (1842)

Notes – *Helicostylum* is classified within *Mucoraceae*. In molecular phylogenetic analyses, the genus was nested with *Mucor*. The genus differs from *Mucor* by forming sporangiophores bearing a terminal deliquescent-walled sporangium and lateral pedicellate, persistent-walled sporangiola that arise from the sporangiophore directly or from lateral, subterminal fertile branches (Benny 1995b). *Helicostylum* is phylogenetically close to *Thamnidium* (Hoffmann et al. 2013, Zhao et al. 2023). It differs from the latter in forming sporangiola born on circinate branchlets that are not dichotomously branched (Upadhyay 1973).

Hyphomucor Schipper & Lunn, in Schipper, Mycotaxon 27: 83 (1986)
Index Fungorum Identifier 23075; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Hyphomucor assamensis* (B.S. Mehrotra & B.R. Mehrotra) Schipper & Lunn, in Schipper, Mycotaxon 27: 84 (1986)

Notes – *Hyphomucor assamensis* forms branched sporangiophores with non-apophysate, columellate sporangia. Zygospores are unknown (Schipper 1986). It is known from specimens isolated from soil in India and Nepal (Mehrotra & Mehrotra 1969, Mikawa1988).

Isomucor J.I. Souza, Pires-Zottar. & Harakava, in Souza, Pires-Zottarelli, Santos, Costa & Harakava, Mycologia 104(1): 233 (2012)

Index Fungorum Identifier 561246; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Isomucor trufemiae* J.I. Souza, Pires-Zottar. & Harakava, Mycologia 104(1): 236 (2012)

Notes – This monotypic genus was isolated from soil samples in Brazil and China (de Souza et al. 2012, de Lima et al. 2020, Zhao et al. 2023), and it has not been found elsewhere. *Isomucor trufemiae* forms uniformly septate mycelium with sympodially and monopodially branched sporangiophores terminating in a non-apophysate sporangium plus lateral sporangiophores bearing multispored sporangiola (de Souza et al. 2012).

Kirkiana L.S. Loh, Kuthub. & Nawawi, Mucoraceous Fungi from Malaysia (Kuala Lumpur): 76 (2001)

Index Fungorum Identifier 568937; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Kirkiana ramosa* L.S. Loh, Kuthub. & Nawawi, Mucoraceous Fungi from Malaysia (Kuala Lumpur): 78 (2001)

Notes – No cultures and sequences are available for this genus.

Kirkomyces Benny, Mycologia 87(6): 922 (1996) [1995]

Index Fungorum Identifier 27518; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Kirkomyces cordensis* (B.S. Mehrotra & B.R. Mehrotra) Benny [as 'cordense'], Mycologia 87(6): 922 (1996) [1995]

Notes – *Kirkomyces* (Benny 1995a) was originally proposed as *Kirkia* Benny (Benny 1995b), which was illegitimate (Art. 53.1 of the ICBN) as it was a homonym of *Kirkia* Oliver, a genus of Angiosperms. The lack of sterile spines and the higher optimal temperature growth separate *K. cordensis* from species of *Helicostylum* (Benny 1995b). *Kirkomyces* is only known from a single isolate from soil in India (Mehrotra & Mehrotra 1963, Benny 2005).

Mycotypha Fenner, Mycologia 24(2): 196 (1932); Fig. 76

Index Fungorum Identifier 20355; Index Fungorum (2025) lists six epithets, but Species Fungorum (2025) accepted four species.

Type species – *Mycotypha microspora* Fenner, Mycologia 24(2): 196 (1932)

Notes – *Mycotypha* was first assigned to *Mucoraceae* in tribe *Cephalideae*, according to the Gäumann system (Gäumann & Dodge 1928). Later, *Mycotypha* was placed in *Choanephoraceae* by Bessey (1950) and in *Cunninghamellaceae* by Hesseltine (1955). Young (1969) transferred *Mycotypha* to *Thamnidiaceae*, arguing that the sporangiolar wall of *Mycotypha africana* was separable from the sporangiospore. The genus currently comprises three species: *Mycotypha africana* R.O. Novak & Backus, *M. indica* P.M. Kirk & Benny, and the type species *M. microspora* Fenner. *Mycotypha guadalcanalensis* Matsush. It is often listed as a *Mycotypha* species (see Index Fungorum 2025).

Mycotypha microspora was described from an orange (*Citrus aurantium*) by Fenner (1932). Since then, it has been shown not only to be plant pathogenic but also pathogenic to humans. *Mycotypha microspora* was isolated from the pus of a wound and the stools of a child with myelogenous acute leukaemia (Lacroix et al. 2007). There is also a case of dual infection with both *Aspergillus fumigatus* Fresen. and *M. microspora* (Trachuk et al. 2018) and a gastric infection (Guddati et al. 2019). A feature that contributes to the pathogenicity of *M. microspora* is mesophilic, its optimal growth temperature is 35°C (Borkar 2021). *Mycotypha microspora* has been isolated not only from soil and outdoor environments but also from hospitals and houses (Lacroix et al. 2007). Two other *Mycotypha* species were originally isolated from the soil.

Potentially, *Mycotypha* could be used for endo-pectinase production from coffee pulp and biomethanation of organic waste such as coffee husk, by lowering the acidity of the husk and

increasing methane production (Venugopal et al. 2007, Jayachandra et al. 2011). Takamatsu et al. (2002) isolated three inhibitors of cell adhesion from the cultured broth of a *Mycotypha* strain. *Mycotypha microspora* affects the aggregation of firebrats (*Thermobia domestica*) (Woodbury & Gries 2013).

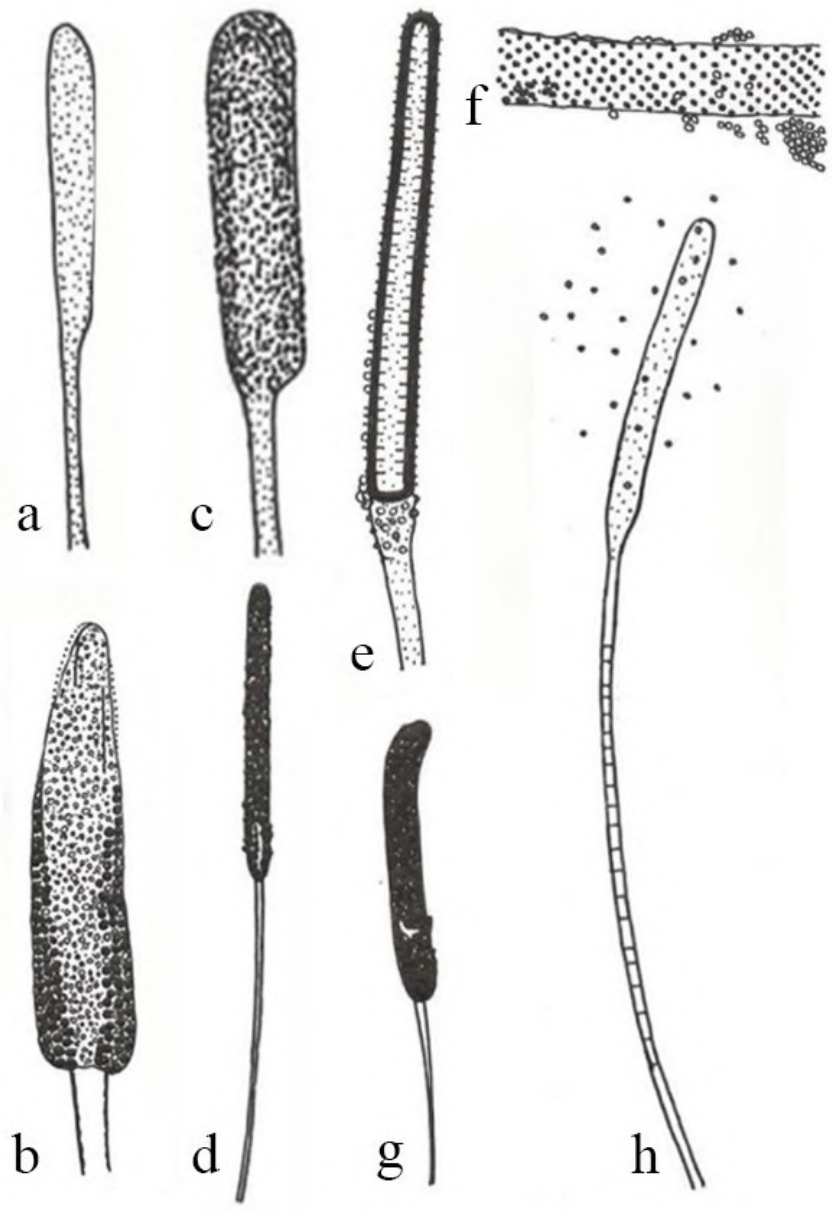


Figure 76 – *Mycotypha microspora*. a An early stage in the formation of a fruiting body, showing the dilated extremity of the filament and the dense granular protoplasm. b A head in the process of development, partially covered with conidia. Some sterigmata are noticeable. A group of spherical bodies is also present. X 500. c A more advanced stage in the development of the capitellum. X 130. d A mature cat-tail-like head, some of the conidia detached. e A portion of a naked capitellum showing the sterigmata from which the spores have fallen. f Portion of a naked collapsed capitellum showing the sterigmata from which the conidia have fallen, showing the spiral arrangement of the sterigmata as diagonal rows. A few conidia with sterigmata adhering are also shown. g A capitellum showing secondary heads which frequently develop when the organism is grown on a very rich medium. h Septation of the conidiophore, which occurs after maturity is reached. A capitellum with spores detached is also shown X 230 (Redrawn from Fenner 1932).

Nawawiella L.S. Loh & Kuthub., Mucoraceous Fungi from Malaysia (Kuala Lumpur): 73 (2001)

Index Fungorum Identifier 568935; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Nawawiella apophysa* L.S. Loh & Kuthub., Mucoraceous Fungi from Malaysia (Kuala Lumpur): 74 (2001)

Parasitella Bainier, Bull. Soc. mycol. Fr. 19(2): 153 (1903)
Index Fungorum Identifier 20392; Index Fungorum (2025) and Species Fungorum (2025) accepted two species.

Type species – *Parasitella parasitica* (Bainier) Syd., Annls mycol. 1(4): 371 (1903)

Notes – *Parasitella* was erected to accommodate *Mucor parasiticus*, which differed from other *Mucor* species due to its gall-forming parasitism and appendaged suspensors. In molecular phylogenetic analyses, the genus nested with *Mucor* (Walther et al. 2013).

Pilaira Tiegh., Annls Sci. Nat., Bot., sér. 6 1: 51 (1875)

Index Fungorum Identifier 20419; Index Fungorum (2025) lists 15 epithets, but Species Fungorum (2025) accepted ten species.

Type species – *Pilaira anomala* (Ces.) J. Schröt., in Cohn 1886

Notes – *Pilaira* comprises species usually isolated from dung. It is distinguished from *Mucor*, its phylogenetically sister taxa (Hoffmann et al. 2013), by the production of sporangia with cutinized wall. The entire sporangial wall detaches along a basal suture when the structure comes in contact with a solid object (Benny 2005).

Pirella Bainier, Étud. Mucor., (Thèse, Paris) (Paris): 83 (1882)
Index Fungorum Identifier 20423; Index Fungorum (2025) accept four epithets, but Species Fungorum (2025) accepts two species.

Type species – *Pirella circinans* Bainier, Étud. Mucor., (Thèse, Paris) (Paris): 83 (1882)

Notes – *Pirella* species form deliquescent-walled sporangia on the apex of the main sporophore or its branches, and persistent-walled sporangiola on twisted and contorted lateral branches that arise from the main sporophore or its branches (Benny & Schipper 1992). They have commonly been isolated from animal dung, especially rodents. In molecular phylogenetic analyses, the genus is phylogenetically close to *Thamnidium* (Hoffmann et al. 2013).

Poitrasia P.M. Kirk, Mycol. Pap. 152: 51 (1984)

Index Fungorum Identifier 25009; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Poitrasia circinans* (H. Nagan. & N. Kawak.) P.M. Kirk, Mycol. Pap. 152: 52 (1984)

Notes – *Poitrasia circinans* and *Gilbertella persicaria* are quite similar, never forming sporangiola but producing multi-spored and pyriform, columellate sporangia with a single longitudinal suture, causing both sporangial halves to separate at maturity (Voigt & Olsson 2008). However, *G. persicaria* forms sporangia with a single suture, as well as zygosporangia formed between opposed suspensors, whereas *P. circinans* forms up to three sutures at maturity of the persistent sporangia, and its zygosporangia are formed between apposed suspensors. *Poitrasia circinans* has been cited as causing infections in the Brazilian guaraná fruit (*Paullinia cupana*), Chinese cabbage (*Brassica chinensis*), *Gossypium* sp., peanut, *Sorghum* sp. and soybean. It has also been isolated from soil, water, leaf litter, and marine environments (Kirk 1984, Schoenlein-Crusius et al. 2006, Huang et al. 2018).

Rhizopodopsis Boedijn, Sydowia 12(1–6): 220 (1959) [1958]
Index Fungorum Identifier 20486; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Rhizopodopsis javensis* Boedijn, Sydowia 12(1–6): 332 (1959) [1958]

Notes – This homothallic fungus forms sporangiophores that terminate in an umbel of apophysate sporangia. *Rhizopodopsis* has only been reported from the initial isolate in Indonesia (Boedijn 1958). *Rhizopodopsis javanicus* is not known to be in culture; thus, there is no phylogenetic information regarding this fungus (Benny 2005).

Thamnidium Link, Mag. Gesell. naturf. Freunde, Berlin 3(1–2): 31 (1809)
Index Fungorum Identifier 20569; Index Fungorum (2025) lists 23 epithets, but Species Fungorum (2025) accepted one species.

Type species – *Thamnidium elegans* Link, Mag. Gesell. naturf. Freunde, Berlin 3(1–2): 31 (1809)

Notes – *Thamnidium* is monotypic. It forms branched sporophores terminating in deliquescent-walled sporangium along with persistent-walled sporangiola on lateral, subterminal and dichotomous fertile branchlets (Benny 1992). In phylogenetic analyses, the genus is close to *Mucor* and *Helicostylum* (Hoffmann et al. 2013, Walther et al. 2013).

Tortumyces L.S. Loh, Mucoraceous Fungi from Malaysia (Kuala Lumpur): 80 (2001)
Index Fungorum Identifier 568939; Index Fungorum (2025) and Species Fungorum (2025) accepted two species.

Type species – *Tortumyces fimicola* L.S. Loh 2001

Mycocladaceae Kerst. Hoffm., Discher & K. Voigt [as *'Mycocladiaceae'*], Mycol. Res. 111(10): 1177 (2007)
Index Fungorum Identifier 530033

Hyphae coenocytic may have stolons and rhizoids. Simple or branched sporangiophores often have a subsporangial septum. Apophysate sporangium with hemispherical or spherical columellae. Sporangiospores are spherical or subpyriform. Giant cells with finger-like projections. Zygospores are oval, dark brown, covered with scales, and developed from opposing gametangia. Suspensors are equal in size, lacking appendages (Hoffmann et al. 2007).

Family type – *Mycocladus* Beauverie; Annls Univ. Lyon, Ser. 2 3: 162 (1900).

Ecology & life modes – Saprobes (on wet wall, France fide Index Fungorum 2024)

Notes – *Mycocladaceae* was established by Hoffmann et al. (2007) to accommodate thermotolerant *Absidia* that also showed distinct phylogenetic origin from core *Absidiaceae*. It was typified by *Mycocladus verticillatus* (Beauverie 1900). After further revision, Hoffmann et. al. (2009) retracted *Mycocladaceae* as a functional taxon because of suspicion that *M. verticillatus* described in 1900 was a coculture of *Absidia* sp. and *Lentamyces parricida*. The morphology of asexual structures closely resembles that of *A. coerulea*, and scale-covered zygospores are probably tubercular exospores from mycotrophic *L. parricida*. Beauverie himself observed parasitic interactions between other molds and "*M. verticillatus*", which further supports Hoffmann et al. (2007). Because of that, *M. corymbifer*, *M. ramosus*, *M. blakesleeana*, and *M. hyalosporus* were transferred to *Lichtheimia*, leaving *M. verticillatus* as the sole representative of *Mycocladus*.

Mycocladus Beauverie; Annls Univ. Lyon, Ser. 2 3: 162 (1900)
Index Fungorum Identifier 20354; Index Fungorum (2025) lists eight epithets, but Species Fungorum (2025) accepted one species.

Optimal temperature for growth is ca. 30℃. Thermotolerant until 40℃. Colonies are white in the early stages of growth and later turn brown (Beauverie 1900).

Type species – *Mycocladus verticillatus* Beauverie; Annls Univ. Lyon, Ser. 2 3: 162 (1900); Fig. 77

Notes – *Mycocladus verticillatus* was described by Beauverie (1900), and, at that time, was the sole representative of the genus *Mycocladus*. Lendner (1908) transferred *M. verticillatus* to *Absidia*. After many changes to taxonomy during the 20th century, *Mycocladus*, *Tieghemella*, *Proabsidia*, *Pseudoabsidia*, *Protoabsidia* and *Lichtcheima* were treated as synonyms of *Absidia*

(Kirk et al. 2001). In the revision of *Absidia* Hoffmann et al. (2007), they introduced the new family *Mycocladaceae* composed of a single genus *Mycocladus* that included *M. verticillatus*, *M. corymbifer*, *M. blakesleeana*, and *M. hyalosporus*. Two years later, it was concluded that *M. verticillatus* described by Beauverie (1900) was most probably a coculture of *Absidia* and mycotrophic *Lentamyces* (Hoffmann et al. 2009). In light of new evidence *M. corymbifer*, *M. ramosus*, *M. blakesleeana* and *M. hyalosporus* were transferred to the next most suitable genus - *Lichtcheima*. *Mycocladus verticillatus* is now the sole representative of *Mycocladus* and also of *Mycocladaceae*.

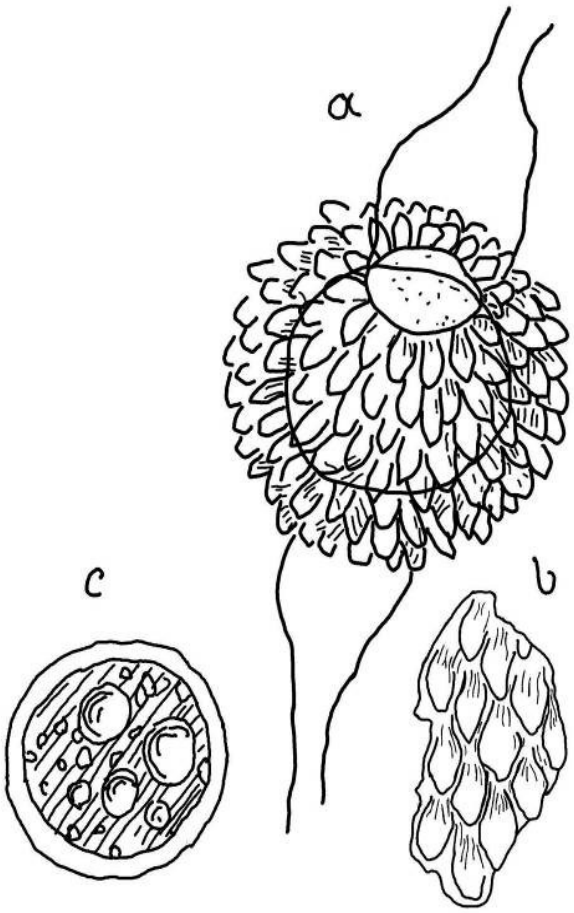


Figure 77 – a Zygosporangium of *Mycocladus verticillatus*. b Scales covering zygosporangium. c Zygospore cross-section with oil vesicles visible (Redrawn from Beauverie 1900).

Phycomycetaceae Arx, Sydowia 35: 22 (1982)
Index Fungorum Identifier 81974

Mycelium ranges from colourless, yellowish, olivaceous to brownish. Hyphae form erect, often unbranched sporangiophores, which are large and brownish or black with a metallic sheen in colour. These structures exhibit strong phototropic tendencies, especially in *Phycomyces* sp. (Fischer 1892, Sumstine 1910, Ellis & Hesseltine 1962, Moss & Baker 2002). Sporangia are columellate, globose, sometimes flattened and most often multispored with a smooth, deliquescent wall. They appear to be dark due to the greenish-brown to brown or blueish-black colour of mature spores, which can be ellipsoidal, oval, almond-shaped or narrow and spindle-shaped, occasionally flattened or curved on one side. Spores are settled in mucus, which is secreted when the sporangium wall is touched. Then the substance is passively distributed by insects, water or wind

after spores dry out (Currey 1859, Fischer 1892, Benjamin & Hesseltine 1959, Webster & Weber 2007). The family includes both homothallic and heterothallic species. Globose or barrel-shaped zygospores, which range from brown to black in colour, form either only among the aerial mycelium or within and on the surface of the substrate, depending on the genus (Fischer 1892, Ramsbottom 1914, Benjamin & Hesseltine 1959, O'Donnell et al. 1976). Tong-like suspensors are ornamented with irregularly dichotomously branched appendages or suspensors more or less equal and non-appendaged (von Arx 1982).

Family type – *Phycomyces* Kunze, Mykologische Hefte 2: 113 (1823)

Ecology & life modes – Members of *Phycomycetaceae* are often found in colder, humid environments and have been reported to be psychrophilic or psychrotolerant (Benjamin & Hesseltine 1959, Watson 1962, Benny et. al. 2016b). *Phycomycetaceae* occurrences are reported mostly from Europe and North America. However, some records from Australia, South America or Asia are also reported in GBIF (gbif.org).

Notes – *Phycomycetaceae* was delimited from *Mucoraceae* by von Arx (1982) based on the distinctive characteristics of zygospores and the presence of a large columellate sporangium. Further molecular phylogenetic studies confirmed the legitimacy of the separation of this group from *Mucoraceae* (e.g. Hoffmann et al. 2013).

Phycomyces Kunze, Mykologische Hefte (Leipzig) 2: 113 (1823)
Index Fungorum Identifier 20411; Index Fungorum (2025) lists nine epithets, but Species Fungorum (2025) accepted three species.

Mycelium coarse, branched, and usually yellowish or olivaceous. Erecting from substrate hyphae, gigantic, non-septate, usually unbranched. Sporangiophores black with a greenish metallic sheen, which can reach even more than 10 cm in length and exhibit strong phototropic tendencies. Sporangia are large, columellate, globose or flattened with a smooth and deliquescent wall and filled with ellipsoidal or oval, multinucleate, thick-walled, dark spores. Zygospores are black and globose, formed within or close to the substrate surface and between tong-like suspensors (Benjamin & Hesseltine 1959, O'Donnell et al. 1976).

Type species – *Phycomyces nitens* (C. Agardh) Kunze, Mykologische Hefte 2: 113 (1823)

Notes – *Phycomyces* was established by Kunze (1823) with the introduction of *P. nitens*. The species was split into *P. nitens* and *P. blakesleeanus* by Burgeff (1925), which was later confirmed in the review done by Benjamin & Hesseltine (1959). Representatives of this genus are saprobic and can be found in soils, on litter, decaying wood, faeces and in anthropogenic habitats like walls or floors of unkept buildings (Bergman et al. 1969). They can be distinguished from members of *Spinellus* based on visibly larger and differently coloured sporangiphores, shape and size of spores and zygospores forming near the substrate surface in opposition to aerial hyphae. The genus comprises three species: *P. nitens*, *P. microsporus* Tiegh., and *P. blakesleeanus* Burgeff.

Phycomyces species are heterothallic, but mixed germination has been reported in *P. nitens*, however, changes in mating types might be linked to prevailing conditions. Those species had been used in various research about the sexual relations of *Mucorales*, which led to the discovery of fungal sexual hormones. The discovery of *Phycomyces* sp. dependent on thiamine led to the usage of *Phycomyces* sp. growth as a quantitative measurement of thiamine concentrations in media and organic materials (Watson 1965, Cerda-Olmedo 1974, 2001). *P. blakesleeanus* is still widely used, especially in research on phototropism (Webster & Weber 2007).

Other genera of *Phycomycetaceae*

Spinellus Tiegh., Annls Sci. Nat., Bot., sér. 6 1: 66 (1875)
Index Fungorum Identifier 20539; Index Fungorum (2025) lists 11 epithets, but Species Fungorum (2025) accepted five species.

Type species – *Spinellus fusiger* (Link) Tiegh., Annales des Sciences Naturelles Botanique sér. 6, 1: 66 (1875)

Pilobolaceae Corda [as Pilobolideae], in Anleit. Stud. Mycol., Prag: 17 (1842) Adrash
Index Fungorum Identifier 81175

Sporangiophores unbranched, positively phototropic, borne on a trophocyst. Sporangia multispored, blackish-brown to black, cutinized, columellate, non-apophysate, persistent-walled. Subsporangial vesicles are globose or broadly ellipsoid, forcibly discharged or passively detached. Zygospores are smooth-walled, borne on tong-like or apposed suspensors. Zygosporangia are thin, hyaline, and rough or wavy (Benny 2010, Voigt 2012).

Family type – *Pilobolus* Tode., Schr. Ges. naturf. Freunde, Berlin 5: 46 (1784); Fig. 80

Ecology & life modes – Pilobolaceous fungi are primarily saprobes on dung (Foos et al. 2011, Voigt 2012), although there are a few reports of isolation of *Utharomyces epallocaulus* Boedijn ex P.M. Kirk & Benny from soil (deposited in the CBS 329.73) and humus (Wallace & Dickinson 1978). Species of this family are widely distributed in the tropics and subtropics.

Notes – *Pilobolaceae* initially contained *Pilobolus* and *Pilaira*, with *Utharomyces* being later described by Boedijn (1958). However, O'Donnell et al. (2001) and Voigt & Wöstemeyer (2001) suggested that *Pilaira* does not belong in *Pilobolaceae*. It was supported by a phylogenetic study carried out by Foos et al. (2011), who suggested the transference of this genus to *Mucoraceae.* Subsequent studies by Hoffmann et al. (2013) and Benny et al. (2014) agreed with it. Representatives of *Pilobolaceae* release their sporangiospores either actively (*Pilobolus*) or passively (*Utharomyces*) (Boedijn 1958). Morphologically, species of this family form sporangiophores that emerge from a trophocyst with an inflated subsporangial vesicle below a black resistant-walled sporangium (Kirk & Benny 1980, Voigt 2012).

Pilobolus Tode., Schr. Ges. naturf. Freunde, Berlin 5: 46 (1784); Fig. 78
Index Fungorum Identifier 20420; Index Fungorum (2025) lists 59 epithets, but Species Fungorum (2025) accepted eight species.

Trophocysts are ovoid to globose or elongate, with a rhizoidal extension. Sporangiophores are straight, unbranched, positively phototropic with orange carotenoid pigment, coenocytic, forming a subsporangial swelling just beneath the sporangium. Subsporangial swellings obovoid, elliptic-obovoid or subglobose, usually orange-yellow at the base. Sporangia are black, sub-hemispherical with cutinized and resistant walls, forcibly discharged at maturity. Columellae elliptical, sometimes mammiform, generally smooth-walled. Sporangiospores are hyaline or with carotenoid pigments, spherical to ellipsoid, and generally smooth-walled. Zygospores in zygosporangia, which are subsmooth to somewhat roughened, are formed between two equal and tong-shaped suspensors (Hu et al. 1989, Viriato 2008).

Type species – *Pilobolus crystallinus* (F.H. Wigg.) Tode, Schr. naturf. Fr., Berlin 5: 46 (1784)

Notes – *Pilobolus*, the speciose genus in *Pilobolaceae*, comprises obligatorily coprophilous species (Foos et al. 2011). *Pilobolus* species form trophocysts varying in shape and giving rise to a sporangiophore that exhibits positive phototropism and can be observed with the naked eye, with a length that varies from a few millimeters to one centimeter (Hu et al. 1989). Over the years, several studies have contributed to the taxonomy of *Pilobolus* (Naumov 1935, Boedijn 1958, Nand & Mehrotra 1968, 1977, Tandon 1968, Zycha et al. 1969, Foos & Rakestraw 1985, Foos & Royer 1989), and traditionally the species have been identified only on a morphological basis, including sporangiophore length, as well as size and shape of trophocysts, columellae, and sporangiospores (Santiago et al. 2008). Hu et al. (1989) monographed *Pilobolus* and accepted five species and seven varieties: *P. crystallinus* var. *crystallinus* (F.H. Wigg.) Tode, *P. crystallinus* var. *hyalosporus* (Boedijn) F.M. Hu & R.Y. Zheng, *P. crystallinus* var. *kleinii* (Tiegh.) R.Y. Zheng & G.Q. Chen, *P. lentiger* var. *lentiger* Corda, *P. lentiger* var. *minutus* (Speg.) R.Y. Zheng & G.Q. Chen, *P. longipes* Tiegh., *P. oedipus* Monti., *P. roridus* var. *roridus* (Bolton) Pers. and *P. roridus* var. *umbonatus* (Buller) F.M. Hu & R.Y. Zheng. However, Foos et al. (2011), in a study based on DNA sequences coding for three regions of rRNA, concluded that *P. kleinii* and *P. crystallinus* are different species, and the same was observed for *P. roridus* and *P. umbonatus*. In this same paper, the authors pointed

out that sporangiospore size is the most stable morphological characteristic to differentiate *Pilobolus* species.

Other genera of *Pilobolaceae*

Utharomyces Boedijn ex P.M. Kirk & Benny, Trans. Br. mycol. Soc. 75(1): 124 (1980)
= *Utharomyces* Boedijn, Sydowia 12(1–6): 340 (1959) [1958] (nom. inval.)
Index Fungorum Identifier 90931; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Utharomyces epallocaulus* Boedijn ex P.M. Kirk & Benny

Notes – The monotypic *Utharomyces* was erected by Boedijn (1958) to accommodate *U. epallocaulus.* However, the name *U. epallocaulus* was invalid (Art. 37.1 of the ICBN), due to Boedijn not indicating a holotype, but it was later validated by Kirk & Benny (1980). Based on morphological characteristics, *U. indicus* A.K. Sarbhoy et al. was later proposed, but it was synonymized with *U. epallocaulus* (Kirk & Benny 1980). Differing from *Pilobolus*, spore dispersal of *Utharomyces* occurs via extensive elongation of the sporangiophore and the attachment of the sporangium to a surface by the subsporangial cytoplasm, and sporangial release occurs when the thin wall of the mature subsporangial vesicle breaks (Benny 2012).

Protomycocladaceae H. Zhao, Y.C. Dai, B.K. Cui, F. Wu, Yuan Yuan & X.Y. Liu, Fungal Diversity 123(1): 55 (2023)
Index Fungorum Identifier FN570880

Sporangiophores arising from substrate hyphae, sympodially branched. Sporangia apophysate, pyriform and multi-spored, deliquescent and smooth-walled. Zygospores ornamented, with opposed suspensors; homothallic (Zhao et al. 2023).

Family type – *Protomycocladus* Schipper & Samson, Mycotaxon 50: 487 (1994)

Ecology & life mode – Reported from dung. According to GBIF (2024), *Protomycocladus* species occur in Antarctica, Australia, Chile, China and Pakistan.

Notes – see under *Protomycocladus*.

Protomycocladus Schipper & Samson, Mycotaxon 50: 487 (1994)
Index Fungorum Identifier 26388; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Stolons and rhizoids are absent. Sporangiophores are unbranched, weakly branched, or sympodially branched, arising from the substrate. Sporangia pyriform, apophysate with a deliquescent wall. Zygospores with an ornamented zygosporangial wall and opposed, more or less equal suspensors (Mirza et al. 1979, Schipper & Samson 1994, Benny 2005).

Type species – *Protomycocladus faisalabadensis* (J.H. Mirza, S.M. Khan, S. Begum & Shagufta) Schipper & Samson, Mycotaxon 50: 487 (1994); Fig. 79

Notes – The genus is monotypic and *P. faisalabadensis* was first isolated from rodent dung in Pakistan and described by Mirza et al (1979) as *Mucor faisalabadensis*. Schipper & Samson (1994) proposed *Protomycocladus* to accommodate the latter species.

Radiomycetaceae Hesselt. & J.J. Ellis, Mycologia 66(1): 91 (1974)
Index Fungorum Identifier 81240

Sporangiophores arising from aerial hyphae or from stolons; rhizoids present. Primary sporangiophore terminating in a vesicle from which secondary stalked vesicles arise radiately. Unisporous or multisporous sporangiola short stalked ot nearly sessile, arising from secondary vesicles. Columellate sporangia absent; zygospores smooth-walled, light brown, with appendiculate suspensors Homothallic or heterothallic (adapted from Ellis & Hesseltine 1974).

Family type – *Radiomyces* Embree, Am. J. Bot. 46: 25 (1959)

Ecology & life modes – Species of *Radiomyces* have been isolated from dung and are coprophilous. *Hesseltinella* was reported from soil. Members of the family have a cosmopolitan distribution.

Notes – *Radiomycetaceae* was erected by Ellis & Hesseltine (1974) and comprises two genera, *Hesseltinella* H.P. Upadhyay and *Radiomyces* Embree. However, based on molecular studies, *Radiomycetaceae* is treated as a monophyletic family that considers only one genus, *Radiomyces*. *Radiomycetaceae* is a sister clade of *Phycomycetaceae* Arx (Walther et al. 2013).

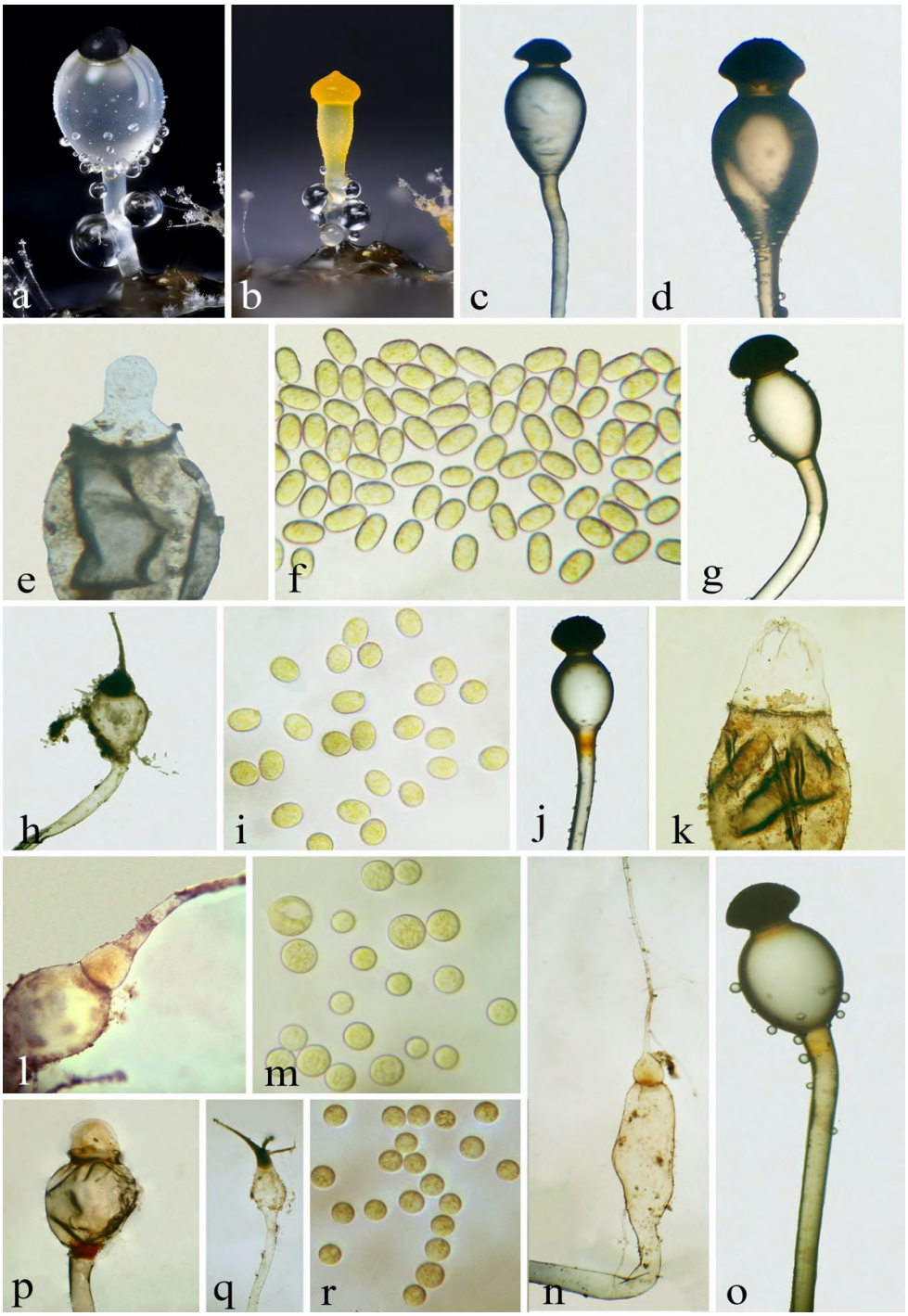


Figure 78 – Morphological characteristics of *Pilobolus* spp. a *Pilobolus roridus* Sporangiophore with subsporangial swelling and sporangium b *Pilobolus umbonatus*, young sporangiophore and sporangium c–f *Pilobolus crystallinus* c,d Sporangiophore with subsporangial swelling and sporangium e Columella f Sporangiospores g–i *P. kleinii* g Sporangiophore with subsporangial swelling and sporangium h Trophocyst i Sporangiospores j–m *P. lentiger* j Sporangiophore with subsporangial swelling and sporangium k Columella l Trophocyst m Sporangiospores n *P. longipes*, trophocyst o–q *Pilobolus* sp. o *Pilobolus* sp. with subsporangial swelling and sporangium p Columellae q Trophocyst r *P. sphareorporus*, sporangiospores. Scale bars: a–e; g–h; j–l; n–q = 100

µm; f, i, m, r = 10 µm (a, b strain numbers zqf-054 and zqf-062, respectively. The other c–o was directly from the substrate).

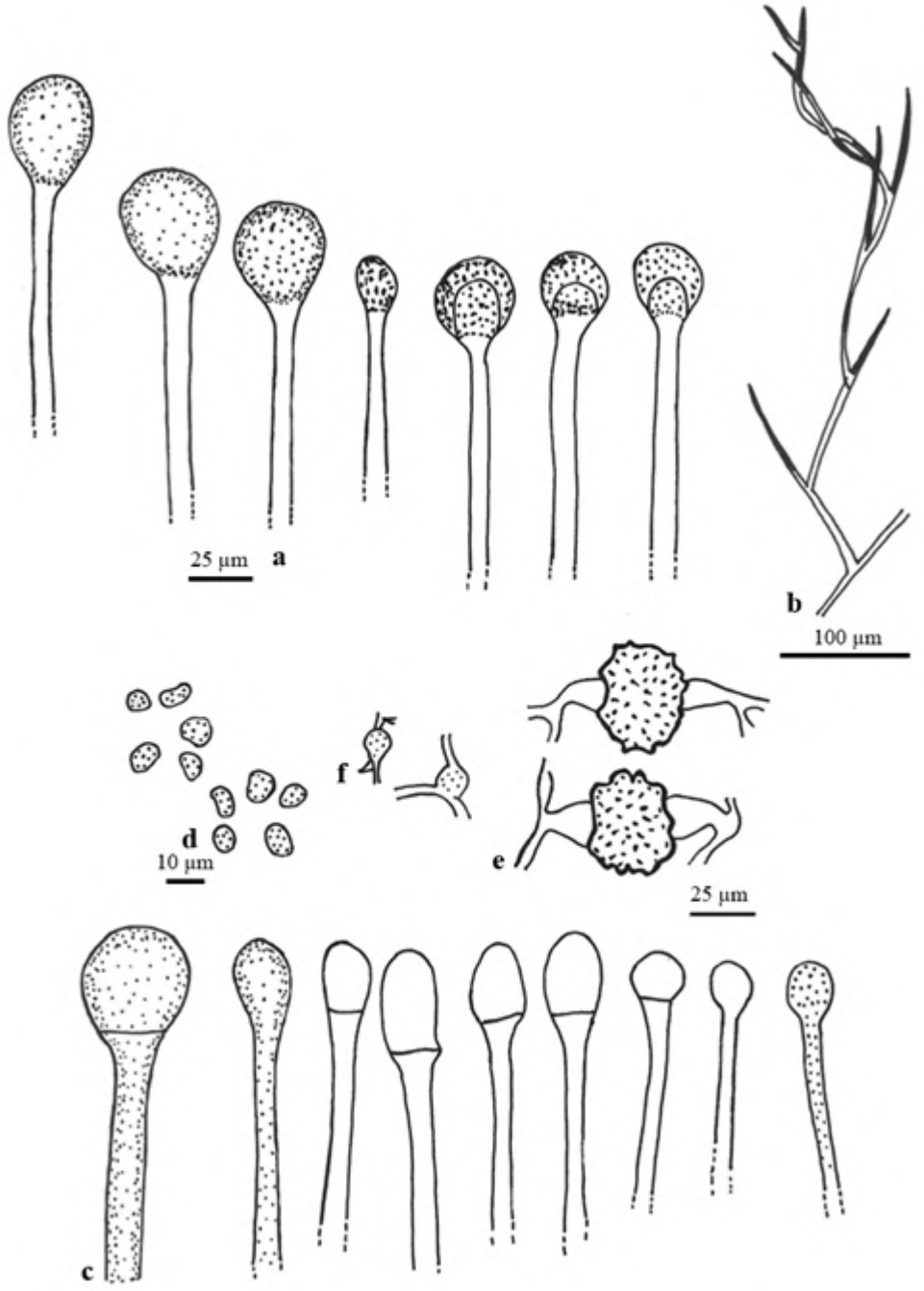


Figure 79 – *Protomycocladus faisalabadensis* (CBS 661.86). a Young sporangia. b Branching patterns of sporangiophores. c Collumellae. d Sporangiospores. e Zygospores. f Swollen substrate hyphae (Redrawn from Schipper & Samson 1994).

Radiomyces Embree, Am. J. Bot. 46: 25 (1959); Fig. 80
Index Fungorum Identifier 20466; Index Fungorum (2025) and Species Fungorum (2025) accepted three species.

Aerial hyphae form elongate, simple or branched, dark brown sporophores, wide, numerous, usually singly, near the ends of stolons terminating in rhizoids. Stolons are nearly colourless, rhizoids are dark brown and thick-walled. Sporophores are unbranched, terminating in a vesicle from which fertile vesicles arise. Fertile vesicles are usually separated from their pedicels by cross walls at maturity, thin or thick-walled. Sporangiola deciduous uni- or multispored. Homothallic.

Zygospores formed in large numbers. Suspensors becoming appendiculate, appendages 5–7 on each suspensor, branched, loosely investing the zygospores, light brown, slender, acuminate. Zygospores are smooth-walled, light brown (Benjamin 1960, Benny & Benjamin 1991).

Type species – *Radiomyces spectabilis* Embree, Am. J. Bot. 46: 25 (1959)

Notes – First discovered species of *Radiomycetaceae*, *R. spectabilis* Embree was initially assigned to *Thamnidiaceae* Fitzp., mainly because of the sinates with a fertile vesicle with many sporangiola, adorned with capitate appendages. Later, however, *Radiomyces* species were accommodated in *Choanephoraceae* J. Schröt. by Zycha et al. (1969).

Radiomyces produces smooth and thin zygosporangial walls and opposed appendaged suspensors. Sporangiophores produce apical sporophoric vesicles, which give rise to uniseptate stalks. Stolons are formed (Benny & Benjamin 1991).

All three species, *R. embreei*, *R. mexicanus*, and *R. spectabilis*, have been isolated from dung and are coprophilous. They were found in the southwestern USA and Mexico but are rarely reported (Benny & Benjamin 1991). *Radiomyces* is pathogenic to mice. *Radiomyces embreei* and *R. spectabilis* are thermotolerant and grow well at 37°C. Some of the strains are capable of growth at 45°C or above (Kitz et al. 1982). *R. spectabilis* can cause disease in mice by hyphal invasion when injected directly into the bloodstream. The examined strain of *R. embreei* was less pathogenic and did not kill the mice tested (Kitz et al. 1980).

Type species – *Radiomyces spectabilis* Embree, Am. J. Bot. 46: 25 (1959)

Rhizomucoraceae H. Zhao, Y.C. Dai, B.K. Cui, F. Wu, Yuan Yuan & X.Y. Liu, Fungal Diversity 123(1): 55 (2023)
Index Fungorum Identifier 570881

Rhizoids are always present. Sporangiophores arising from hyphae are branched. Sporangia apophysate, columellate and multi-spored. Chlamydospores are sometimes present. Zygospores are ornamented, both heterothallic and homothallic, with opposed suspensors and a pigmented zygosporangial wall. Mesophilic and thermophilic (Zhao et al. 2023).

Family type – *Rhizomucor* Lucet & Costantin

Ecology & life modes – Members of the family are cosmopolitan and commonly found in soil, decaying organic matter and also cause mucormycosis in humans (Zhao et al. 2009, Zheng et al. 2009).

Notes – *Rhizomucoraceae* is a sister to *Syncephalastraceae* clade in phylogenetic and divergence time analyses (Zhao et al. 2023).

Rhizomucor Lucet & Costantin, Rev. gén. Bot. 12: [81] (1900); Fig. 81
Index Fungorum Identifier 20481; Index Fungorum (2025) lists 15 epithets, but Species Fungorum (2025) accepted 6 species.

The generic description is similar to the family description above.

Type species – *Rhizomucor parasiticus* Lucet & Costantin, C. r. hebd. Séanc. Acad. Sci., Paris 12: 1033 (1899)

Notes – *Rhizomucor* comprises six thermophilic species. *Rhizomucor parasiticus* is an invalid name (Art. 53.1 of the ICBN) that has been synonymized with *R. pusilus* (Lindt) Schipper. The ITS sequences of *R. tauricus* and *R. pusillus* are identical, hence the two are considered to be conspecific (Walther et al. 2013).

Rhizopodaceae K. Schum., Lehrb. system. Bot. Phytopaläont. Phytogeogr. (Stuttgart): 70 (1894)
Index Fungorum Identifier 582937

Rapidly grow on sugar-rich fruits and develop fluffy, whitish to grayish cultures. Stolons and rhizoids formed on wide, sometimes slightly melanized hyphae. Sporangiophores arising directly from the substrate, commonly formed opposite the rhizoids, simple or branched and terminated by a multispored sporangium. Sporangia apophysate with large columellae. Sporangiospores gray to

brownish. Zygospores form a pigmented, rough zygosporangial wall on opposed, nonappendaged suspensors (Schipper & Stalpers 1984, Voigt 2012).

Family type – *Rhizopus* Ehrenb., Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 10(1): 198 (1821)

Ecology & life modes – *Rhizopus* consists of 13 species with a worldwide distribution (gbif.org) and they are common saprobes and facultative parasites. Some isolates may be causal agents of disease in animals, including humans. Other representatives are used as producers of enzymes in industrial biofermentation, and as fermentation agents in food production (Gryganskyi et al. 2018). Hyphae of *R. microsporus* harbor endohyphal bacteria, producing phytotoxins (Partida-Martinez et al. 2007)

Notes – *Rhizopodaceae* was described by Schumann (1894) to accommodate *Rhizopus*. However, fungi from this genus were further classified within *Mucoraceae* (O'Donnell et al. 2001, Kirk et al. 2008) and *Absidiaceae* (Zycha et al. 1969). The legitimacy of separating *Rhizopodaceae* family was re-proposed by Hoffmann et al. (2013), based on multigene phylogenetic analysis. Currently, the family consists of *Rhizopus* (Zhao et al. 2023).

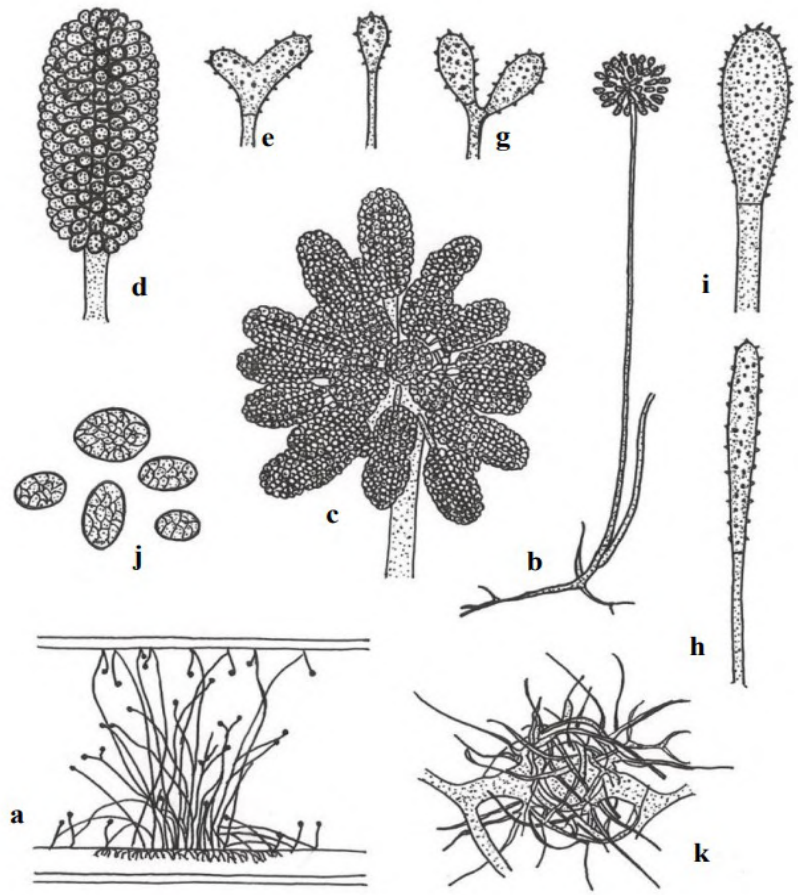


Figure 80 – *Radiomyces embreei.* a Semi diagrammatic habit sketch of colony growing on agar in Petri dish showing stoloniferous and nonstoloniferous sporangiophores X 5 (Sporangiophores). b Stoloniferous sporangiophore X 60. c Apical portion of mature sporophore showing conformation of fertile branches arising from terminal vesicle X 290. d Fertile branches before sporangiola have fallen away X 780. e–h Fertile branches after sporangiola have fallen away; these show typical variations from the usual type branch shown in the next figure X 360. i Typical fertile branch after sporangiola have fallen away; note septum separating pedicel from clavate fertile portion and the spine-like prominences on which the sporangiola were borne X 780. j Five sporangiola showing

size range X 1360. k Mature zygospore showing suspensor appendages X 240 (Redrawn from Benjamin 1960).

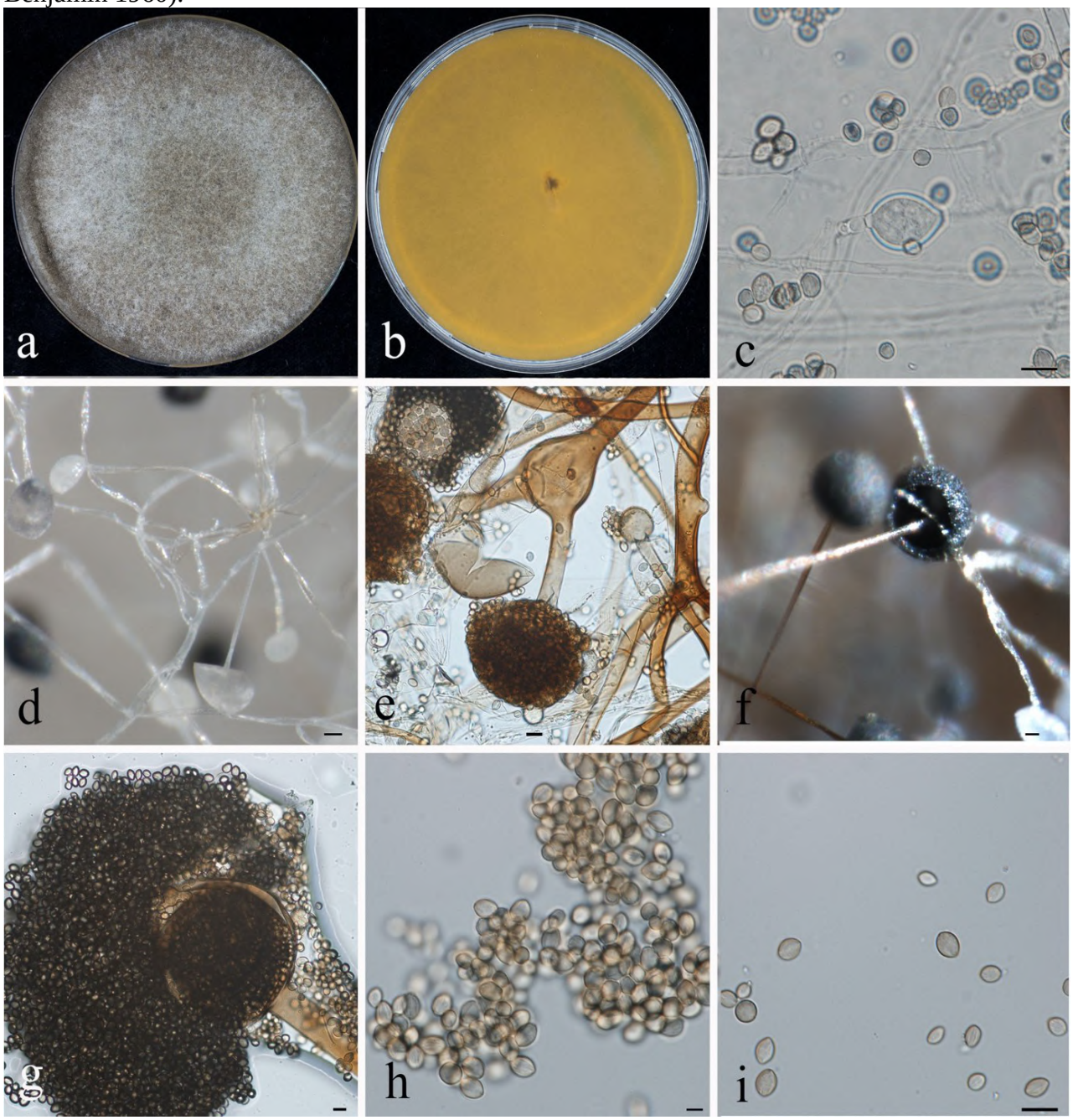


Figure 81 – *Rhizomucor miehei* (CBS 209.77a). a, b Colony on MEA after 5d. c Chlamydospore. d Columella. e Branched sporangiophore. f Sporangiophores with sporangia. g Mature sporangiospore. h, i Spores. Scale bars: a–i = 10 µm.

Rhizopus Ehrenb., Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 10(1): 198 (1821) Index Fungorum Identifier 20487; Index Fungorum (2025) 142 epithets, but Species Fungorum (2025) accepted 12 species.

Branched hyphae with stolons well or poorly developed, septate or not; rhizoids developed from stolons and opposite sporangiophores abundant to scarce, sometimes absent. Sporangiophores arising from stolon and/or form hyphae, solitary or in groups. Sporangia apophysate deliquescing or breaking in water. Columellae variously shaped, subhyaline to grayish brown, smooth to verruculose. Sporangiospores are regular or irregular in shape and size, smooth to angulate, with distinct to faint, or invisible striation. Chlamydospores and giant cells may be formed. Zygospores

are mostly hyaline, rarely palely coloured, with or without a large central oil globule. Suspensors equal in shape and size, or equal in shape but unequal in size, or unequal in shape and size. Homothallic or heterothallic (Zheng et al. 2007).

Type species – *Rhizopus stolonifer* (Ehrenb.) Vuill., Revue mycol., Toulouse 24: 54 (1902)

= *Rhizopus nigricans* Ehrenb., Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 10(1): 198 (1821)

Notes – *Rhizopus* was originally described based on the specimen isolated from the fruit and calyx of *Cornus mas* and *Morus alba* in Germany, preliminarily described as *Mucor stolonifer* Ehrenb. Therefore, the specific epithet 'stolonifer' ought to have been adapted after the new genus description. Formally, the new combination was proposed by Vuillemin (1902).

Saksenaeaceae Hesselt. & J.J. Ellis, Mycologia 66(1): 87 (1974) Wilk
Index Fungorum Identifier and MycoBank Identifier 81250

Branched and mostly aseptate mycelium; aerial mycelium floccose. Sporangia are apophysate (funnel- or bell-shaped), columellate, and multispored; piriform with a deliquescent wall (in *Apophysomyces*) or flask-shaped, with a long neck and deliquescent tip (in *Saksenaea*), formed singly or in pairs on a relatively short sporangiophore (longer in *Saksenaea*); rhizoids present, formed always opposite the sporangiophore. Sporangiospore shape varies in different species from both genera, they are mostly oblong, also broadly subspherical to ellipsoid, trapeziform, or bone-shaped. Zygospores in both genera are unknown, unsuccessful mating experiments have been reported (Ellis & Hesseltine 1974, Alvarez et al. 2010a, b, Prakash et al. 2016).

Family type – *Saksenaea* S.B. Saksena, Mycologia 45(3): 434 (1953)

Ecology & life modes – The species included in *Saksenaeaceae* were originally isolated from soil or water. Some species (mostly *Apophysomyces*) were described from clinical samples, but most are regarded as emerging human pathogens of increasing importance (Walther et al. 2019). They very often can affect immunocompromised patients (Planegger et al. 2022), and infection often follows skin damage coupled with contamination by soil or water, causing predominantly necrotizing fasciitis (Gomes et al. 2011, Samaddar et al. 2022, Skiada et al. 2022). Members of this family are more prevalent mucormycosis-causing fungi in Asia and Australia than in Europe (Prakash & Chakrabarti 2019, Skiada et al. 2022). Known also to fatally infect whales and dolphins kept in captivity (*S. vasiformis*, *A. elegans* - Robeck & Dalton 2002), cows (*S. erythrospora*, Lawhon et al. 2012; *S. vasiformis*, Hill et al. 1992), dogs (*S. vasiformis*, Reynaldi et al. 2017), mice (experimental inoculation, Salas et al. 2012). Endohyphal bacteria related to *Burkholderiaceae* were isolated from one species of *Saksenaea*; bacterial-like structures were apparently present in all fungal structures, including sporangiospores (Takashima et al. 2022). Analyses of the correlation between isolation frequency from soil and environmental factors are limited (*Apophysomyces* – Prakash et al. 2016).

Notes – *Saksenaeaceae* was erected by Ellis & Hesseltine (1974), initially to accommodate *Saksenaea* and *Echinosporangium* (currently in *Mortierellomycotina*, Benny & Blackwell 2004). This classification was later amended by Hoffmann et al. (2013), who accepted two genera, *Saksenaea*, (typified by *S. vasiformis* S.B. Saksena *fide* Saksena 1953), and *Apophysomyces* (typified by *A. elegans* P.C. Misra et al. *fide* Misra et al. 1979). Based on the combined 18S, 28S, *tef1*-α, and actin phylogeny, the family forms a strongly supported clade sister to *Phycomycetaceae* (Hoffmann et al. 2013).

The type species of both genera were regarded as species complexes by Alvarez et al. (2010a, b), and consequently, new cryptic species were separated based on multilocus phylogeny and polyphasic approach (Alvarez et al. 2010a, b). In fact, all the new species in both genera were described in the last twelve years, and there is a high possibility that earlier reports, especially from clinical samples, might in fact involve some of these new species (Walther et al. 2019). Takashima et al. (2022) described a new species, *Saksenaea boninensis* Y. Takash. & K. Narisawa, from litter in Japan, based on the combined morpho-physiological features and ITS, partial LSU, and partial *tef1*-α phylogeny.

Usually, fast growing on most standard media, but sporulation is often difficult to induce in culture (Saksena 1953). Temperature requirements vary for respective species, but generally, all species in both genera are thermotolerant, with optimum growth temperatures 25–37°C, and a maximum temperature of 45°C for *A. mexicanus* (Bonifaz et al. 2014). Availability of data on carbon and nitrogen assimilation profiles, osmotolerance, solubilization of several non-soluble metal minerals, and production of organic acids varies for different species from both genera (*Apophysomyces* – Alvarez et al. 2010b, Prakash et al. 2016, Khuna et al. 2019, Li et al. 2020, *Saksenaea* – Baijal 1967, Alvarez et al. 2010a). Data on susceptibility to various antimycotics/antibiotics are available for all clinically relevant taxa from both genera, but are sparse (*Apophysomyces* – Alvarez et al. 2010b, Prakash et al. 2016, *Saksenaea* – Alvarez et al. 2010a, Labuda et al. 2019). Preliminary analyses of the available genomes (*A. variabilis, A. elegans, A. trapeziformis, S. oblingispora, S. vasiformis*) revealed the presence of two copies of CotH-related (invasins) genes, and provided some insight into determinants of virulence and metabolic potential of these fungi (Chibucos et al. 2016, Prakash et al. 2017).

Cultures are available for all species of *Saksenaea* (at CBS, some species also at ATCC, FMR, UTHSC); for *Apophysomyces*, cultures are more dispersed (at CBS, ATCC, FMR, IMI, SDBR, UTHSC, CGMCC). Sequences, mostly ITS, 28S, 18S, and *tef1*-α, for all species in the family (including that by Takashima et al. 2022) are available in GenBank (https://ncbi.nlm.nih.gov/genbank/, accessed 18.11.2022). Genomes are available for *A. variabilis*, *A. elegans*, *A. trapeziformis*, *S. oblingispora*, *S. vasiformis*, and three unidentified strains of *Apophysomyces* (NCBI Genomes, https://ncbi.nlm.nih.gov/home/genomes/, accessed 18.11.2022).

Saksenaea S.B. Saksena, Mycologia 45(3): 434 (1953)
Index Fungorum Identifier 20503; Index Fungorum (2025) and Species Fungorum (2025) accepted eight species.

Sporangia flask-shaped with a distinct spherical venter and a long neck; formed singly or in pairs at the ends of aerial hyphae, each sporangiophore above a profusely dichotomously branched rhizoidal complex. Columella is prominent and dome-shaped. Sporangia dehiscing by the dissolution of an apical mucilaginous plug, spores are discharged through this neck (adapted from Saksena 1953).

Type species – *Saksenaea vasiformis* S.B. Saksena 1953; Fig. 82

Notes – The genus was originally introduced to accommodate *S. vasiformis* S.B. Saksena, a taxon isolated from soil. Several subsequent studies reported *S. vasiformis* as a human pathogen (Ajello et al. 1976, Kaufman et al. 1988). *Saksenaea* comprises seven epithets which were reported from soil, water, human and animals (Index Fungorum 2024, accessed on 17.11.2022), *viz.*, *S. dorisiae* R. Labuda et al. (Labuda et al. 2019), *S. erythrospora* E. Álvarez et al. (Alvarez et al. 2010a), *S. longicolla* D.J. Lee et al. (Nam et al. 2021), *S. loutrophoriformis* Deanna A. Sutton et al. (Crous et al. 2017), *S. oblongispora* E. Álvarez et al. (Alvarez et al. 2010a), *S. trapezispora* Deanna A. Sutton et al. (Crous et al. 2016), and *S. vasiformis*.

Other genera included in *Saksenaeaceae*

Apophysomyces P.C. Misra, in Misra, Srivastava & Lata, Mycotaxon 8(2): 377 (1979)
Index Fungorum Identifier 20045; Index Fungorum (2025) listed seven epithets and Species Fungorum (2025) accepted seven species.

Type species – *Apophysomyces elegans* P.C. Misra, K.J. Srivast. & Lata 1979

Syncephalastraceae Naumov ex R.K. Benj., Aliso 4(2): 327 (1959)
Index Fungorum Identifier 81447

Vegetative hyphae are hyaline, branched, and septate with age. Rhizoids present. Merosporangiophores erect, ascending, or recumbent, and stolon-like. The main stalks of the merosporangiophores and their branches form terminal vesicles bearing uni- or multispored merosporangia. Merosporangiospores globose, ovoid, rod-shaped, some narrower at the middle

portion, formed simultaneously by simple cleavage, usually uniseriate. Zygospores are nonappendaged, borne on nearly equal, opposed suspensors (Benjamin 1959, Benny 2010).

Family type – *Syncephalastrum* J. Schröt., in Cohn, Krypt.-Fl. Schlesien (Breslau) 3.1 (9–16): 217 (1886) [1889]

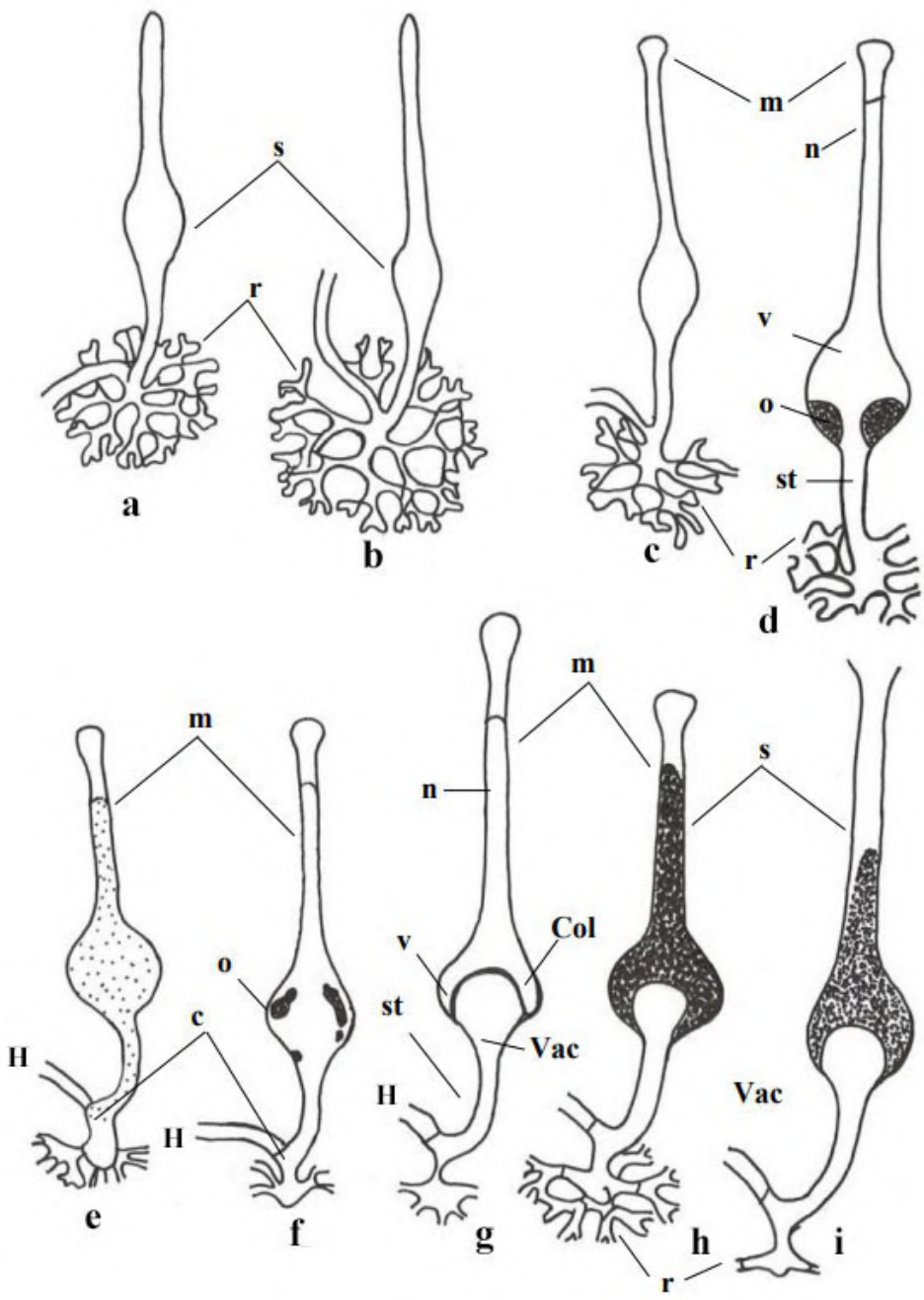


Figure 82 – *Saksenaea vasiformis.* a–f Further development of the sporangium (S) with clear differentiation of the rhizoidal complex (R), stalk (St) of the sporangium venter (V) and the neck (N) x 860. a, f Show oil globules (O). e, f Stages showing the cutting off of the sporangium from the parenthypha (H) by a septum (c). g A fully formed sporangium with a columella (Col.) rhizoidal complex (R) venter (V) and the neck (N). h, i Formation and liberation of spores from the ripe sporangium x1370. (S = spores; vac = vacuoles) (Redrawn from Saksena 1953).

Ecology & life modes – Members of this family are typically saprobic, commonly being isolated from dung and soil and have a widespread distribution.

Notes – *Syncephalastraceae* was proposed by Naumov (1935), but this name was invalidly published as it was not accompanied by a diagnosis (Article 34 of the ICBN). Hence, *Syncephalastraceae* was later validated by Benjamin (1959). According to Zhao et al. (2023), this monotypic family contains only *Syncephalastrum*, although Voigt (2012) considered seven genera in this family: *Circinella*, *Fennellomyces*, *Phascolomyces*, *Protomycocladus*, *Syncephalastrum*, *Thamnostylum*, and *Zychaea*. Voigt (2012) pointed out that *Protomycocladus* might represent a separate family, because its phylogeny appeared inconsistent, varying according to the phylogenetic markers used. Benny (2010) recognized only *Syncephalastrum* in the *Syncephalastraceae*, however according to Hoffmann et al. (2013), in a study using four molecular markers (large and small subunit of the ribosomal DNA, partial actin gene and partial gene for the translation *tef1*-α), this family presumably includes *Protomycocladus*. These authors classified a subclade formed by *Fennellomyces*, *Phascolomyces*, *Protomycocladus*, *Rhizomucor*, *Syncephalastrum*, *Thamnostylum*, *Thermomucor* and *Zychaea* as *incertae sedis*.

Syncephalastrum J. Schröt., in Cohn, Krypt.-Fl. Schlesien (Breslau) 3.1 (9–16): 217 (1886) [1889]; Fig. 83

Index Fungorum Identifier 20556; Index Fungorum (2025) 22 epithets, but Species Fungorum (2025) accepted seven species.

The generic description is similar to the family description above.

Type species – *Syncephalastrum racemosum* Cohn ex J. Schröt., Krypt.-Fl. Schlesien (Breslau) 3.1 (9–16): 217 (1886) [1889]

Notes – After the description of *S. racemosum*, other species and one variety were later proposed: *S. nigricans* Vuillemin (1887), *S. elegans* Marchal (1892), *S. cinererum*, *S. fuliginosum* Bainier (1907), *S. javanicum* Raciborski (1909), *S. rhizopi* Vuillemin (1922), and *S. racemosum* var. *paucisporum* Moreau (1949, without a Latin diagnosis). However, none of these taxa were recognized by Benjamin (1959), Hesseltine & Ellis (1973) and Benny (2010), who only accepted *S. racemosum* as a valid species. According to Benjamin (1959), some morphological criteria used in other studies to differentiate *Syncephalastrum* species, such as pattern of merosporangiophore branching, colony colour, presence or absence of septa in the merosporangiophore, presence or absence of stolons, dimensions of the vesicles subtending the merosporangia, dimensions of the merosporangia, and number, shape, and size of the spores, are not sufficiently informative for delimitation of species in this genus. Misra (1975) proposed a new species, *S. verruculosum*, which was synonymized with *S. racemosum* by Schipper & Stalpers (1983). Zheng et al. (1988) described *S. monosporum* Zheng, G-q Chen & Hu., with four varieties no longer considered valid (www.speciesfungorum.org). The last new species, *S. contaminum* was proposed by Urquhart & Idnurm (2020), who showed that *S. verruculosum* should be treated as a separate species from *S. racemosum*. Currently, *Syncephalastrum* comprises four species (*S. contaminum*, *S. monosporum*, S. *racemosum*, and S. *verruculosum*). Urquhart & Idnurm (2020) have indicated that there is a potential for new *Syncephalastrum* species in culture collections still to be described, including some assigned to *S. racemosum*.

Syncephalastrum species are saprobes, commonly observed on soil and dung, or endophytic (Rahmawati et al. 2021). There are reports of this genus causing mucormycosis in immunocompromised patients (Singh et al. 2021b, Armaki et al. 2022). The pathogenic nature of *Syncephalastrum* sp. in gardens of leaf-cutting ants was studied by Barcoto et al. (2017). *Syncephalastrum* has shown potential to produce antimicrobial and cytotoxic metabolites (Bakhtra et al. 2022), chitosan (Batista et al. 2020), lipids (Hashem et al. 2020), and biosurfactants (Bione et al. 2022). This fungus seems to have anti-diabetic (Teynampet 2015) and anti-HCV (Fu et al. 2013) properties. *Syncephalastrum* has been investigated for its capacity to biotransform trachyloban-19-oic acid (Santos et al. 2018), laxogenin (Wang et al. 2019), and isorhodeasapogenin (Wang et al. 2020b), and some of the biotransformationed metabolites showed anti-neuroinflammatory activity

and inhibition of acetylcholinesterase, an enzyme linked to the symptomatic control of Alzheimer's disease. *Syncephalastrum* could remove iron ions present in aqueous matrices (Martins et al. 2019) and Cr (VI) from tannery effluent, in combination with rice husk (Srivastava & Sharma 2013).

Other genus included

Neofennellomyces Hyang B. Lee & T.T.T. Nguyen, Stud. Mycol. 109: 302 (2024)

Index Fungorum Identifier 900613; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species: *Neofennellomyces jeongsukae* Hyang B. Lee & T.T.T. Nguyen 2023



Figure 83 – *Syncephalastrum* sp. a Colony surface on PDA, at 25°C. b Colony reverse on PDA, at 25°C. c, d Merosporangiophre with merosporangia. e, f Merosporangiophore with columela. g Rhizoid. h Merospores. Scale bars: a–g = 20 µm.

Syzygitaceae H. Zhao, Y.C. Dai, B.K. Cui, F. Wu, Yuan Yuan & X.Y. Liu, Fungal Diversity 123(1): 55 (2023)
Index Fungorum Identifier 571006

Sporangiophores arising directly from substrate hyphae, umbel or dichotomously branched. Sporangia subglobose to globose, columellate, few- or multi-spored, deliquescent-walled. Sporangiospores globose to ovoid, spinose-walled. Zygospores ornamented, with opposed suspensors; homothallic (Zhao et al. 2023).

Family type – *Syzygites* Ehrenb., Sylv. mycol. berol. (Berlin): 25 (1818)

Ecology & life modes – The representatives of *Syzygites* parasitize mushrooms (Kovacs & Sundberg 1999). Their known occurrences are mainly from the northern hemisphere (gbif.org). *Sporodiniella* was described based on a specimen isolated from remnants of Microlepidoptera in Sumatra (Boedijn 1958) and was reported as a facultative parasite on insect larvae in the tropics (Evans & Samson 1977).

Notes – *Syzygitaceae* is sister to *Rhizopodaceae* clade in phylogenetic and divergence time analyses (Zhao et al. 2023).

Syzygites Ehrenb., Sylv. mycol. berol. (Berlin): 25 (1818)
Index Fungorum Identifier 20561; Index Fungorum (2025) lists five epithets, and Species Fungorum (2025) accepted one species.

Type species – *Syzygites megalocarpus* Ehrenb., Sylv. mycol. berol. (Berlin): 25 (1818)

Notes – The asexual form of *Syzygites* was known as *Sporodinia grandis* Link. The genus was previously classified within *Mucoraceae* (O'Donnell et al. 2001, Kirk et al. 2008). In the phylogeny of Walther et al. (2013), *Syzygites megalocarpus* clustered among *Rhizopus* species. However, only *Syzygites megalocarpus* forms dichotomously branched sporangiophores.

Other genera in *Syzygitaceae*

Sporodiniella Boedijn, Sydowia 12(1–6): 336 (1959) [1958]
Index Fungorum Identifier 20547; Index Fungorum (2025) has one epithet, and Species Fungorum (2025) accepted one species.

Type species – *Sporodiniella umbellata* Boedijn, Sydowia 12(1–6): 336 (1959) [1958]; Fig. 84

Notes – *Sporodiniella* differs from *Rhizopus* mostly by forming umbel-branched and spinose sporangiophores (Boedijn 1958). Strain CBS RS 618 was designated as the neotype by Evans & Samson (1977). The genus was previously classified within *Mucoraceae* (O'Donnell et al. 2001, Kirk et al. 2008).

Thermomucoraceae H. Zhao, Y.C. Dai, B.K. Cui, F. Wu, Yuan Yuan & X.Y. Liu, Fungal Diversity 123(1): 57 (2023)
Index Fungorum Identifier 571007

Sporangiophores arising from stolons and rhizoids, branched. Sporangia globose, columellate, multispored, and apophysate. Sporangiospores subglobose, smooth-walled. Zygospores produced from aerial hyphae, smooth-walled, with opposed suspensors. Homothallic and thermophilic (Zhao et al. 2023).

Family type – *Thermomucor* Subrahm., B.S. Mehrotra & Thirum., Georgia J. Sci. 35(1): 1 (1977)

Ecology & life modes – Isolated from compost, on decaying leaves. Reported from India and Malaysia.

Notes – *Thermomucoraceae* is sister to *Lichtheimiaceae* clade in phylogenetic and divergence time analyses (Zhao et al. 2023). However, in our phylogenetic analyses (Fig. 3), *Thermomucoraceae* is sister to *Rhizomucoraceae*.

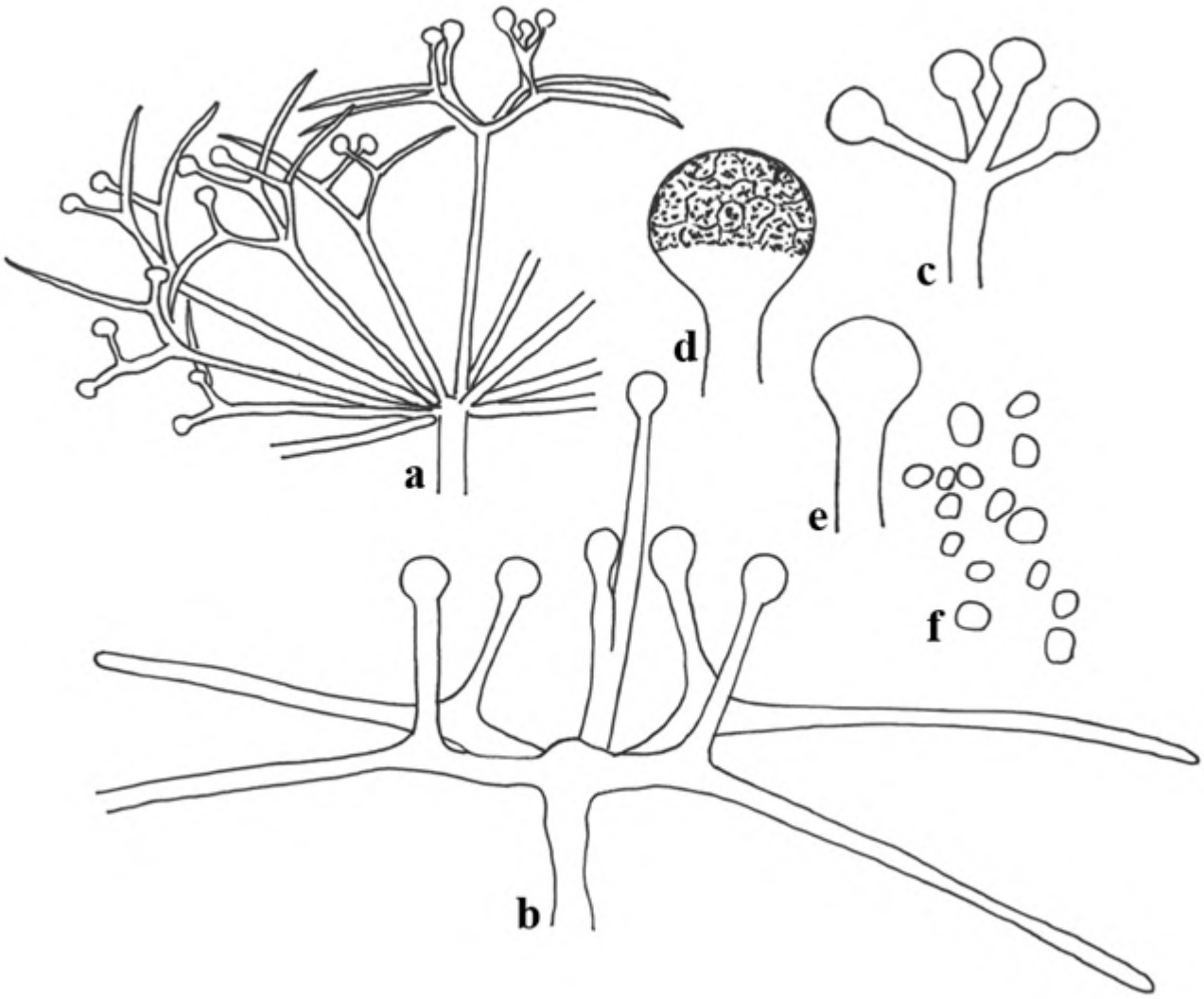


Figure 84 – *Sporodiniella umbellate*. a Top of plant, semidiagrammatic. b End of a branch. c Aberrant branch. d Sporangium. e Columella. f Sporangiospores (Redrawn from Boedijn 1958).

Thermomucor Subrahm., B.S. Mehrotra & Thirum., Georgia J. Sci. 35(1): 1 (1977)
Index Fungorum Identifier 20573; Index Fungorum (2025) lists three epithets, but Species Fungorum (2025) accepted one species.

The generic description is similar to the family description above.

Type species – *T. indicae-seudaticae* Subrahm., B.S. Mehrotra & Thirum., Georgia J. Sci. 35(1): 1 (1977)

Notes – *Thermomucor* is closely related to *Rhizomucor* but differs by producing apophysate sporangia and unusually smooth zygospores. The genus comprises only the type species (Schipper 1979).

Umbelopsidomycetes Tedersoo, Sanchez-Ramirez, Kõljalg, Bahram, M. Döring, Schigel, T.W. May, M. Ryberg & Abarenkov (2018)
Umbelopsidales Spatafora & Stajich & Bonito, Mycologia 108(5): 1035 (2016)
Pygmaeomycetaceae E. Walsh & N. Zhang, Mycologia 113(1): 141 (2020)
Index Fungorum Identifier 832250

Produce hyaline microchlamydospores, a distinctive characteristic from other families in *Mucoromycotina*. Hyphae hyaline, coenocytic, forming subglobose vesicles. No sporangia or

sexual reproduction observed. The two species are distinguished based on a combination of phylogeny and colony/mycelium morphology.

Family type – *Pygmaeomyces* E. Walsh & N. Zhang, Mycologia 113(1): 141 (2020)

Ecology & life modes – Members of the family were reported from vascular plant root-associated; no negative effects on host plants were observed, possibly endophytic (isolated after surface sterilization). Culturable, i. e. capable of saprobic growth, at least in culture.

Notes – The family was erected by Walsh et al. (2021) to encompass the monophyletic genus, *Pygmaeomyces*, with two species, *P. thomasii* E. Walsh & N. Zhang (type species, holotype RUTPP-PP16K26) and *P. pinuum* E. Walsh & N. Zhang (holotype RUTPP-PP16P16A). Based on the combined 18S, 28S, and *rpb2* phylogeny, the family forms a monophyletic clade sister to *Umbelopsidaceae* within the order *Umbelopsidales*. According to Walsh et al. (2021), this clade could correspond to Clade GS23 from the sequence-only global soil survey (Tedersoo et al. 2017). ITS sequences of these species are closely related to several environmental ITS sequences from various ecosystems in USA, Japan, Australia, Guyana and Malaysia. The most similar sequences share affinity for acidic soils or plants typically associated with acidic/oligotrophic soils (*Ericaceae*, conifers), which could hint towards general ecological preferences of the *Pygmaeomycetaceae*.

Pygmaeomyces E. Walsh & N. Zhang, Mycologia 113(1): 141 (2020)
Index Fungorum Identifier 832252; Index Fungorum (2025) and Species Fungorum (2025) accepted two species.

The generic description is similar to *Pygmaeomycetaceae*

Type species – *Pygmaeomyces thomasii* E. Walsh & N. Zhang, Mycologia 113(1): 141 (2020)

Notes – Walsh et al. (2021) introduced this genus with *P. thomasii* E. Walsh & N. Zhang as the type species. The genus comprises two species (CBS 146528 – ex-type (*P. thomasii*), CBS 146529 – ex-type (*P. pinuum*)), which have been reported from the roots of *Pinus rigida*.

Umbelopsidaceae W. Gams & W. Mey., in Meyer & Gams, Mycol. Res. 107(3): 348 (2003) Julia
Index Fungorum Identifier 82139

Flat colonies are rather slow-growing. Slender hyphae are initially non-septate, but often form chlamydospores with abundant lipid droplets. Sporangiophores are dense, with branches commonly arising from inflation of the hyphae, forming a velvety layer, often with septa near the branching and at some distance below the sporangium. The columella is strongly reduced. Sporangiospores are variously shaped, often reddish or ochraceous. Sexual reproduction was not observed (Meyer & Gams 2003).

Family type – *Umbelopsis* Amos & H.L. Barnett, Mycologia 58(5): 807 (1966)

Ecology & life modes – Members of the family are common soil saprotrophs. However, they are also often reported as endophytes or root symbionts (e.g. Qin et al. 2018).

Notes – *Umbelopsidaceae* was introduced by Meyer & Gams (2003) to accommodate taxa previously classified within *Micromucor*, *Mortierella*, *Mucor*, and *Umbelopsis*. The authors also proved that *Umbelopsidaceae* is distantly related to *Mucoraceae* but not to *Mortierellaceae*. *Umbelopsidaceae* is a monogeneric family within *Mucoromycotina*.

Umbelopsis Amos & H.L. Barnett, Mycologia 58(5): 807 (1966); Fig. 85
Index Fungorum Identifier 10350; Index Fungorum (2025) 34 epithets, but Species Fungorum (2025) accepted 31 species.

Representatives of this genus are forming relatively flat colonies of reddish or ochraceus colour. Hyphae are slender and initially non-septate. Chlamydospores with oil droplets are often abundant. Sporangiophores form a velvety layer, often with septa near the branching and at some distance below the sporangium. The columella is strongly reduced. Sporangiospores are variously shaped, often reddish or ochraceous. Sexual reproduction was not observed (Meyer & Gams 2003).

Notes – *Umbelopsis* was originally described as a deuteromycete (Amos & Barnett 1966), and it was transferred to *Zygomycota* by von Arx (1982). The type strain was isolated from the roots of red oak in West Virginia, U.S.A., in 1960. Several other *Umbelipsis* taxa were initially described as *Mortierella.* Gams (1977) described the subgenus *Micromucor* with *Mortierella* to accommodate six species with distinct morphology (i. e. coloured sporangia). Later, *Micromucor* was elevated to the generic level by von Arx (1982). The family consisted of two genera, *Umbelopsis* and *Micromucor*. However, some authors claimed that morphological differences between these two genera are not clear (Yip 1986, Kendrick et al. 1994). Meyer & Gams (2003), using RFLP of the ITS region and ITS1 sequence comparison, transferred all *Micromucor* taxa to *Umbelopsis*. There are 23 *Umbelopsis* species listed in Index Fungorum. Some representatives of *Umbelopsis* are used in biotechnology for polyunsaturated fatty acids (PUFAs) synthesis (Somacal et al. 2020).

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

NEOCALLIMASTIGOMYCOTA M.J. Powell
Neocallimastigomycetes M.J. Powell
Neocallimastigales J.L. Li, I.B. Heath & L. Packer
Anaeromycetaceae Doweld, Index Fungorum 103: 1 (2014)
Index Fungorum Identifier 550425

Obligate anaerobic fungi that produce monoflagellated zoospores, monocentric or polycentric thalli, and filamentous rhizoidal systems.

Family type – *Anaeromyces* Breton, Bernalier, Dusser, Fonty, B. Gaillard & J. Guillot

Ecology & life modes – Anaerobic gut fungi

Notes – Doweld (2014w) introduced *Anaeromycetaceae* as a novel family to encompass the genus *Anaeromyces*. Hanafy et al. (2023) used phylogenetic analysis of the Internal transcribed spacer region 1 (ITS-1), D1/D2 region of the large ribosomal subunit (D1/D2 LSU), and RNA polymerase II large subunit (*rpb1*); phylogenomic analysis, and whole genome/transcriptome average amino acid identity (AAI) values to emend the family to encompass *Capellomyces*, *Liebetanzomyces*, and *Oontomyces*. Estimates for family evolution using molecular dating approaches are 29 Mya (Pratt et al. 2024).

Anaeromyces Breton, Bernalier, Dusser, Fonty, B. Gaillard & J. Guillot (1990); Fig. 86 (a– f)
Index Fungorum Identifier. 27188

On solid media, *Anaeromyces* forms circular white colonies. In liquid, it forms thick growth with pearl-like beads. *Anaeromyces* produces monoflagellated zoospores, exhibits polycentric thallus development, and filamentous rhizoidal growth pattern. Zoospores are always monoflagellated (uniflagellated). Terminal sporangia are typically mucronate with an acuminate apex. *Anaeromyces* produces wide and narrow hyphae, with frequent constrictions in the wide hyphae resulting in a unique sausage-like appearance (Fig. 86a–f).

Notes – The first *Anaeromyce* species, *A. mucronatus* was isolated from the cow rumen in 1990 (Breton et al. 1990). A highly similar strain was reported (also from cow rumen) shortly thereafter, for which the name *Ruminomyces elegans* was proposed (Ho et al. 1990). Precedence was given to the genus name *Anaeromyces* over *Ruminomyces* (Ho et al. 1995).

Four species of *Anaeromyces* have been reported, but only three are currently recognized: *A. mucronatus* (Breton et al. 1990), *A. elegans* (Ho et al 1990), and *A. contortus* (Hanafy et al 2018a). *Anaeromyces robustus* (Li et al. 2016), has conclusively been shown to be misclassified (Hanafy et al. 2022), but Species Fungorum (2025) accepted it as a valid species.

Other genera in the family

Capellomyces Hanafy, Lanjekar, Dhakephalkar, T.M. Callaghan, Dagar, G.W. Griff., Elshahed & N.H. Youssef, Mycologia 112(6): 1231 (2020)
Index Fungorum Identifier: 830739; Index Fungorum (2025) and Species Fungorum (2025) accepted two species.

Type species – *Capellomyces foraminis*, Hanafy, Lanjekar, Dhakephalkar, T.M. Callaghan, Dagar, G.W. Griff., Elshahed & N.H. Youssef, Mycologia 112(6): 1231 (2020).

Notes – Isolates representing two species (*C. foraminis* and *C. elongatus*) were isolated from faecal samples of a wild boar goat (USA) and a domesticated goat (India), respectively (Hanafy et al. 2020b). While displaying a high level of ITS1 and D1/D2 LSU sequence identity, multiple growth and microscopic differences were identified, justifying their accommodation into two distinct species. Only the two species are known, *C. foraminis* and *C. elongatus.*

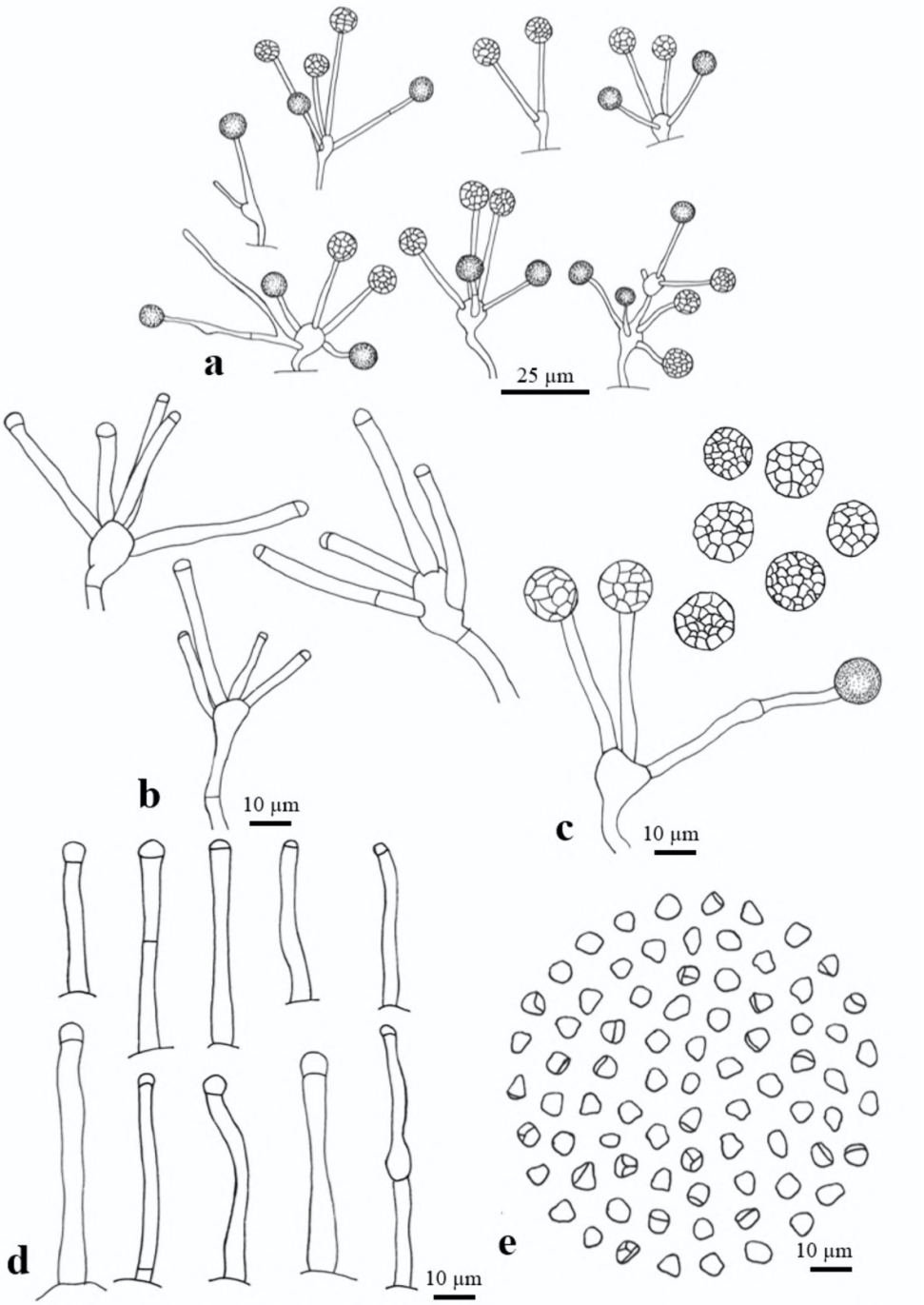


Figure 85 – *Umbelopsis changbaiensis.* a Sporangiophores showing different branching types. b, c Details of branching on vesicles and sporangia. d Sporangiophores with different sizes and shapes of columellae at their tips after the sporangia have been dissolved or detached. e Sporangiospores (redrawn from Wang et al. 2014).

Liebetanzomyces Joshi, G.W. Griff. & Dagar, MycoKeys 40: 104 (2018)

Index Fungorum Identifier 554794; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Liebetanzomyces polymorphus* A. Joshi, G.W. Griff. & Dagar, MycoKeys 40: 104 (2018)

Notes: The single known species, *L. polymorphus*, was isolated from goat rumen (Joshi et al. 2018).

Oontomyces Dagar, Puniya & G.W. Griff., Fungal Biology 119(8): 736 (2015)
Index Fungorum identifier: IF550795; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Oontomyces anksri* Dagar, Puniya & G.W. Griff., Fungal Biology 119(8): 736 (2015)

Caecomycetaceae R.A. Hanafy, Yan Wang, Stajich, C.J. Pratt, N.H. Youssef & Elshahed, Int J Syst Evol Microbiol 73(2, no. 005735): 15 (2023)
Index Fungorum Identifier IF844401

Obligate anaerobic fungi producing monoflagellated zoospores, monocentric or polycentric thalli that are either uni- or multisporangiate, and a bulbous rhizoidal system with spherical holdfasts. Currently accommodates the genera *Caecomyces* (Gold et al. 1988), and *Cyllmayces* (Ozkose et al. 2001). The clade circumscribed by phylogenomic analysis, evolutionary time estimates, AAI values, and confirmed by LSU and *rpb1* phylogenetic analyses.

Family type – *Caecomyces* J.J. Gold 1988

Ecology & life modes – Anaerobic gut fungi

Notes – Hanafy et al. (2023) proposed *Caecomycetaceae* to accommodate *Caecomyces* and *Cyllamyces* based on their unique microscopic character (producing bulbous rhizoidal system), ITS-1, D1/D2 LSU, *rpb1* phylogeny), phylogenomic analysis, and whole genome/transcriptome AAI values. Pratt et al. (2024) estimated that the family evolved 29 Mya.

Caecomyces J.J. Gold, BioSystems 21(3–4): 411 (1988); Fig. 86 (g–j)
Index Fungorum Identifier IF25287

On solid media, *Caecomyces* produces small white granular colonies. In liquid media, it exhibits sandy-like growth. *Caecomyces* produces monoflagellated zoospores, and exhibits a bulbous rhizoidal system with spherical holdfasts, and monocentric thalli that are either uni- or multisporangiate (Gold 1988).

Notes – Microscopic observation of zoospore characteristics of the now-described genus *Caecomyces* was first observed by Liebetanez (1910) and Braune (1913). These structures were erroneously identified as protozoan members of the rumen, for which the name *Sphaeromonas* was proposed. Orpin's seminal research demonstrated that these structures represent the spore phase of a zoosporic fungus (Orpin 1976), and its isolation in pure culture was achieved by Orpin (1981). The genus was formally described by Gold et al. (1988). A name change from *Sphaeromonas* to *Sphaeromyces* to emphasize its fungal nature was unfeasible since the name *Sphaeromyces* was already in use. *Caecomyces* was hence proposed for the genus based on the habitat from which the isolates were obtained (horse caecum).

Four species of *Caecomyces* have been reported, but only three are recognized: *C. communis* (Orpin 1981), *C. equi* (Gold et al. 1988), and *C. sympodialis* (Chen et al. 2007). The fourth species, *C. churrovis* (Henske et al. 2017) has recently been assessed as synonymous with *C. communis*, and the variety designation (referring to *C. churrovis* as *C. communis* var. *churrovis*) has been proposed (Hanafy et al. 2022).

Other genera in *Caecomycetacea*e

Cyllamyces Ozkose, B.J. Thomas, D.R. Davies, G.W. Griff. & Theodorou 2001

Index Fungorum Identifier IF28540; Index Fungorum (2025) listed two epithets but Species Fungorum (2025) accepted only one species

Type species – *Cyllamyces aberensis* Ozkose, B.J. Thomas, D.R. Davies, G.W. Griff. & Theodorou, Canadian Journal of Botany 79(6): 668 (2001)

Notes – Two species are known, *C. aberensis* from cow faeces (Ozkose et al. 2001) and *C. icaris* from the faeces of a water buffalo (Sridhar et al. 2014).

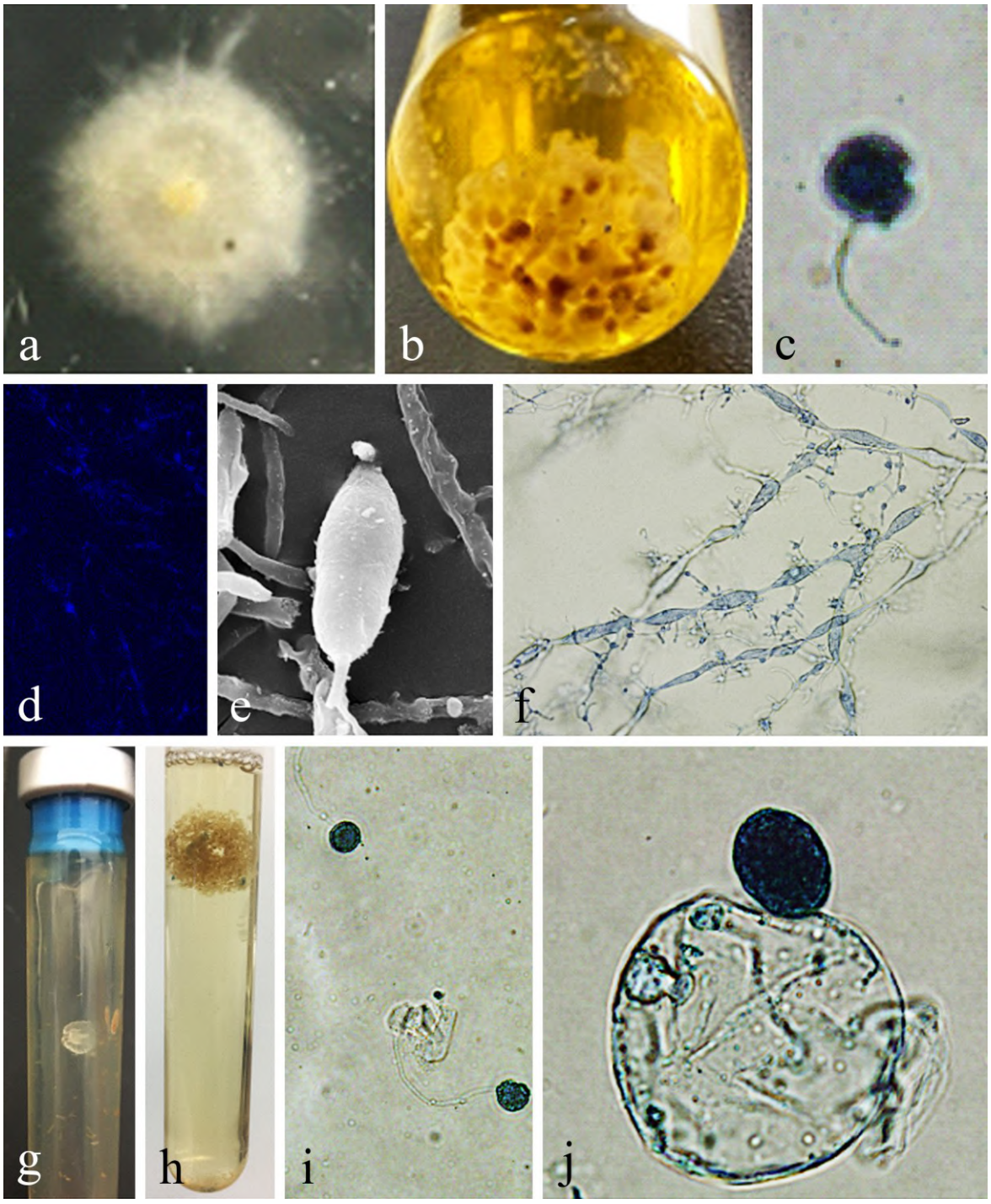


Figure 86 – a–f General characteristics of the genus *Aneromyces.* a Peral-like growth in liquid media. b A monoflagellated zoospores. c DAPI stain thallus exhibiting a polycentric pattern i. e. with nuclei present in the hyphae. d A mucronate sporangium with an acuminate apex. e and wide and narrow hyphae, with frequent constrictions in the wide hyphae resulting in a unique sausage-like appearance. f Figures a, b are from *Anaeromyces* strain xy20, while figures d, e, f are from A. *controtus* strain O2. g–j General characteristics of the genus *Caecomyces*, the type genus of the

family *Caecomycetaceae*. g Small white colonies. h Sandy liquid growth. i monoflagellated zoospores. j Bulbous rhizoial growth, with an ovoid sporangium.

Neocallimastigaceae I.B. Heath, Bauchop & Skipp, Canadian Journal of Botany 61(1): 304 (1983) emended: Y. Hanafy, Y Wang, J. Stajich, N. H. Youssef & M.S. Elshahed

Index Fungorum: IF81063

Obligate anaerobic fungi with monocentric or polycentric thalli and filamentous rhizoidal system. Zoospores are polyflagellated in all genera, except for the monoflagellated genus *Pecoramyces*. The clade is defined by phylogenomic, phylogenetic and morphological characteristics. Currently accommodates the genera *Neocallimastix* (Braune 1913, Vávra & Joyon 1966, Heath et al. 1983), *Ghazallomyces* (Hanafy et al. 2020a), *Orpinomyces* (Breton et al. 1989, Barr et al. 1989, *Pecoramyces* (Hanafy et al. 2017), *Feramyces* (Hanafy et al. 2018b) and *Aestipascuomyces* (Stabel et al. 2020).

Family type – *Neocallimastix* Vávra & Joyon ex I.B. Heath, in Heath, Bauchop & Skipp, Canadian Journal of Botany 61(1): 304 (1983)

= *Neocallimastix* Vávra & Joyon, Protistologica 2(no. 4): 15 (1966) (Nom. inval., Art. 39.1 (Melbourne)

Ecology & life modes – Anaerobic gut fungi

Notes – *Neocallimastigaceae* was proposed by Health et al. (1983) to accommodate all taxa of anaerobic gut fungi. Subsequently, all newly proposed taxa were assigned to the family. Recently, recognition of clear supra-genus relationships between several genera based on morphology (number of zoospore flagella, thallus morphology, rhizoidal system morphology) and sequence data necessitated the creation of multiple families to acknowledge such relationships. Hanafy et al. (2022) proposed three new families, while circumscribing *Neocallimastigaceae* to include only those genera related to the type genus *Neocallimastix*, a proposal that led to a reduction of the number of genera belonging to *Neocallimastigaceae* from 20 to only 6.

All genera produce polyflagellated zoospores (7–20 flagella), except *Pecoramyces* species, which produce monoflagellated zoospores (1–4 flagella). All members of the family exhibit monocentric thallus development, except for *Orpinomyces,* which develops polycentric thalli. All members of the family produce filamentous rhizoids that penetrate plant fibers by their tapering ends. Estimates for family evolution are 52 Mya (Pratt et al. 2024).

Wijayawardene et al. (2022) listed *Agriosomyces*, *Akhlioshbmyces*, *Buwchfawromyces*, *Joblinomyces,* and *Khoyollomyces* under *Neocallimastigaceae*. However, Hanafy et al (2023) excluded them from the family and placed them in *Neocallimastigales* genus *incertae sedis.* In this study, we agree with Hanafy et al. (2023).

Neocallimastix Vávra & Joyon ex I.B. Heath, Canadian Journal of Botany 61(1): 304 (1983); Fig. 87 (a–f)

Index Fungorum: IF542966

On solid agar media, *Neocallimastix* species produce beige circular colonies with a dark center of sporangial structure. In liquid media, *Neocallimastix* strains usually exhibit thin biofilm growth. Members produce polyflagellated zoospores (7-30 flagella), monocentric thalli, and filamentous rhizoids, with both endogenous and exogenous sporangial development patterns (Heath et al. 1983, Wubah & Fuller 1991, Ho & Barr 1995) (Fig. 87a-f).

Type species – *Neocallimastix frontalis* (R.A. Braune) Vávra & Joyon ex I.B. Heath

Notes – The name "*Neocallimastix*" predates the discovery of the fungal nature of "rumen flagellates" by Orpin (Orpin 1975). Polyflagellated structures similar to *Neocallimastix* zoospores were observed by Braune (1913), for which the name *Callimastix frontalis* was proposed. Vavra & Joyon proposed that the *Callimastix* flagellate *C. cyclopsis* represents the dispersal phase of zoosporic fungi and renamed it as *Neocallimastix* with *N. frontalis* as the type species (Vavra & Joyon 1966). Isolates belonging to the genus *Neocallimastix* were first reported in 1981 (Joblin 1981), and the formal description of the first isolate (*N. frontalis*, strain PN1) was provided by Heath et al. (1983).

The following names have been proposed for various *Neocallimastix* isolates: *N. frontalis* (Vavra & Joyon 1966, Heath et al. 1983), *N. patriciarum* (Orpin & Munn 1986), *N. hurleyensis* (Webb & Theodorou 1991), *N. variabilis* (Ho et al. 1993), *N. cameroonii* (Ariyawansa 2015), *N. californiae* (Li 2016), and *N. lanati* (Wilken et al. 2021). The potential synonymy between *N. frontalis*, *N. hurleyensis*, *N. patriciarum*, and *N. variabilis* (Ho et al. 1993) has been debated based on a lack of morphological differences, and has been recently confirmed through phylogenetic analysis (Hanafy et al. 2022). Synonymy has also been proposed for *N. cameroonii*, *N. californiae*, and *N. lanati* based on molecular sequence data and the lack of morphological differences (Hanafy et al. 2022). Accordingly, the following *Neocallimastix* species are retained: *N. frontalis* (synonyms *N. hurleyensis*, *N. variabilis*, *N. patriciarum* (Orpin 1975), and *N. cameroonii* (Syn. *N. californiae*, *N. cf. patriciarum* and *N. lanati*) (Hanafy et al. 2022).

Other genera in *Neocallimastigaceae*

Aestipascuomyces Stabel, R. Hanafy, Schweitzer, Greif, Aliyu, Flad, D. Young, Lebuhn, Elshahed, Ochsenreither & N.H. Youssef 2020

Index Fungorum Identifier 837524; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Aestipascuomyces dupliciliberans* Stabel, R. Hanafy, Schweitzer, Greif, Aliyu, Flad, D. Young, Lebuhn, Elshahed, Ochsenreither & N.H. Youssef, Microorganisms 8(11): 13 (2020)

Feramyces R.A. Hanafy, Elshahed & N.H. Youssef, Mycologia 110(3): 521 (2018)

Index Fungorum Identifier 823650; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Feramyces austinii* R.A. Hanafy, Elshahed & N.H. Youssef, Mycologia 110(3): 521 (2018)

Notes: Hanafy et al. (2018b) introduced this monotypic genus.

Ghazallomyces Hanafy, Lanjekar, Dhakephalkar, T.M. Callaghan, Dagar, G.W. Griff., Elshahed & N.H. Youssef, Mycologia 112(6): 1232 (2020)

Index Fungorum Identifier 830733; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Ghazallomyces constrictus* Hanafy, Lanjekar, Dhakephalkar, T.M. Callaghan, Dagar, G.W. Griff., Elshahed & N.H. Youssef, Mycologia 112(6): 1233 (2020)

Orpinomyces D.J.S. Barr, H. Kudo, Jakober & K.J. Cheng, Canadian Journal of Botany 67(9): 2819 (1989)

Index Fungorum Identifier 25326; Index Fungorum (2025) and Species Fungorum (2025) accepted three species.

Type species – *Orpinomyces bovis* D.J.S. Barr, H. Kudo, Jakober & K.J. Cheng, Canadian Journal of Botany 67(9): 2819 (1989)

Notes – The first polycentric isolate was reported by Breton et al. (1989) from the rumen of sheep. Despite its polycentric nature, the isolate was nevertheless described as a new species of *Neocallimastix* (the first isolated AGF and exhibiting monocentric thallus development pattern). Barr et al. (1989) isolated a closely related strain from cow rumen and reasoned that the observed polycentric thallus merits the proposition of a new genus to accommodate this strain.

Two *Orpinomyces* species are recognized, *O. joyonii* (Barr et al. 1989, Breton et al. 1989), and *O. intercalaris* (Ho et al. 1994). *Orpinomyces joyonii* (Breton et al. 1989) was mistakenly named *Neocallimastix joyonii*. Shortly thereafter, Barr et al. (1989) isolated another strain from the rumen of a Holstein steer for which the name *Orpinomyces bovis* was first proposed. A detailed comparison between *O. bovis* and *N. joyonii* was conducted by Li et al. (1991), who concluded that both isolates represented the same species based on their morphological similarities. The

combination *Orpinomyces joyonii* was hence proposed: *Orpinomyces* for the genus name to recognize these strains as the first representative of a new genus, and *joyonii* for the species name to recognize the priority of Breton et al. Over Barr et al (1989). The second species *Orpinomyces intercalaris* was subsequently isolated and characterized by Ho et al. (1994).

Paucimyces R.A. Hanafy, N.H. Youssef & Elshahed, Int. J. Syst. Evol. Microbiol. 71(6, no. 004832): 7 (2021)

Index Fungorum Identifier 838953; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Paucimyces polynucleatus* R.A. Hanafy, N.H. Youssef & Elshahed 2021

Pecoramyces Hanafy, N.H. Youssef, G.W. Griff. & Elshahed, Mycologia 109(2): 240 (2017)

Index Fungorum Identifier 552530; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Pecoramyces ruminantium* Hanafy, Noha Youssef, G.W. Griff. & Elshahed 2017

Notes – The first isolate (strain C1A) was erroneously classified as a member of the genus *Orpinomyces*. However, subsequent analysis identified clear morphological and microscopic differences when compared to *Orpinomyces*, and phylogenetic analysis using ITS1 and D1/D2 LSU loci further affirmed its phylogenetic distinction. Such results hence justified its accommodation in a new genus, for which the name *Pecoramyces* was proposed (Hanafy et al. 2021).

Piromycetaceae R.A. Hanafy, Yan Wang, Stajich, C.J. Pratt, N.H. Youssef & Elshahed, Int. J. Syst. Evol. Microbiol. 73(2, no. 005735): 16 (2023)

Index Fungorum: IF844402

Obligate anaerobic fungi that produce monoflagellated zoospores, monocentric thalli, and filamentous rhizoidal systems. Currently accommodates the genus *Piromyces*[12]. The clade is circumscribed by phylogenomic analysis, AAI values, and confirmed by LSU and *rpb1* phylogenetic analyses, as well as morphological characteristics.

Family type – *Piromyces* J.J. Gold, I.B. Heath & Bauchop

Ecology & life modes – Obligate anaerobic fungi

Notes – This family was proposed to accommodate all taxa phylogenetically affiliated with the first described monocentric, monoflagellated, and filamentous isolate, *Piromyces communis* (Gold et al. 1988), based on phylogenomic analysis, evolutionary time estimates, AAI values, and confirmed by LSU and *rpb1* phylogenetic analyses. Estimates for family evolution is 45 Mya.

Piromyces J.J. Gold, I.B. Heath & Bauchop, BioSystems 21(3–4): 411 (1988); Fig. 87 (g–m)

Index Fungorum Identifier IF25332

On solid agar media, *Piromyces* produces small circular colonies with a dark center of sporangial structure. In liquid, it exhibits thin biofilm-like growth. Biofilms firm attachment to the glass walls of the tube is characteristic to members of the genus. Members of the genus *Piromyces* produce monocentric thalli (with both endogenous and exogenous sporangial development), filamentous rhizoidal system, and monoflagellated zoospores (occasionally bi- to tetra-flagellated).

Notes – Monoflagellated spores morphologically distinct from *Sphaeromonas communis* (larger and more elongate) were reported by Liebetanez et al. (1910) and Braune (1913), and named *Piromonas communis*. Orpin (1977) obtained a mixed bacterial-fungal culture with *P. communis* as the sole fungal strain, and the name *Piromyces* was later suggested by Gold et al. (1988) to emphasize the fungal, rather than protozoan, nature of members of this genus. The genus was first defined to encompass all phenotypes with monocentric thalli, filamentous rhizoidal systems, and monoflagellated zoospores (Gold et al. 1988). However, subsequent isolation efforts demonstrated that such a phenotype is prevalent in several phylogenetically disparate genera across the *Neocallimastigomycota* (Callaghan et al. 2015, Dagar et al. 2015, Hanafy et al. 2020a, b).

Type species – *Piromyces communis* C.G. Orpin 1977

OLPIDIOMYCOTA Doweld
Olpidiomycetes Doweld
Olpidiales Caval.-Sm.
Olpidiaceae J. Schröt. [as 'Olpidiacei'], in Cohn, Krypt.-Fl. Schlesien (Breslau) 3.1(1–8): 180 (1886) [1889]
Index Fungorum Identifier 81080

Without any mycelium or rhizoids. The swarming spores penetrate into the interior of living cells and develop here into plasmodia, which either become swarming sporangia or permanent sporangia. Zygospore formation not observed. A single sporangium or a permanent spore form directly from the penetrated swarm spore. *Thallus* monocentric, holocarpic or eucarpic; Sporangium and resting spore developed exogenous to the zoospore cyst; usually endobiotic. Zoosporic, single flagellum; thallus monocentric, holocarpic or eucarpic; two parallel centrioles linked to nucleus by shared, tapering, striated rhizoplast; sporangium single, endobiotic (*fide* Schröter 1886, Kirk et al. 2001, Naranjo-Ortiz & Gabaldón 2019)

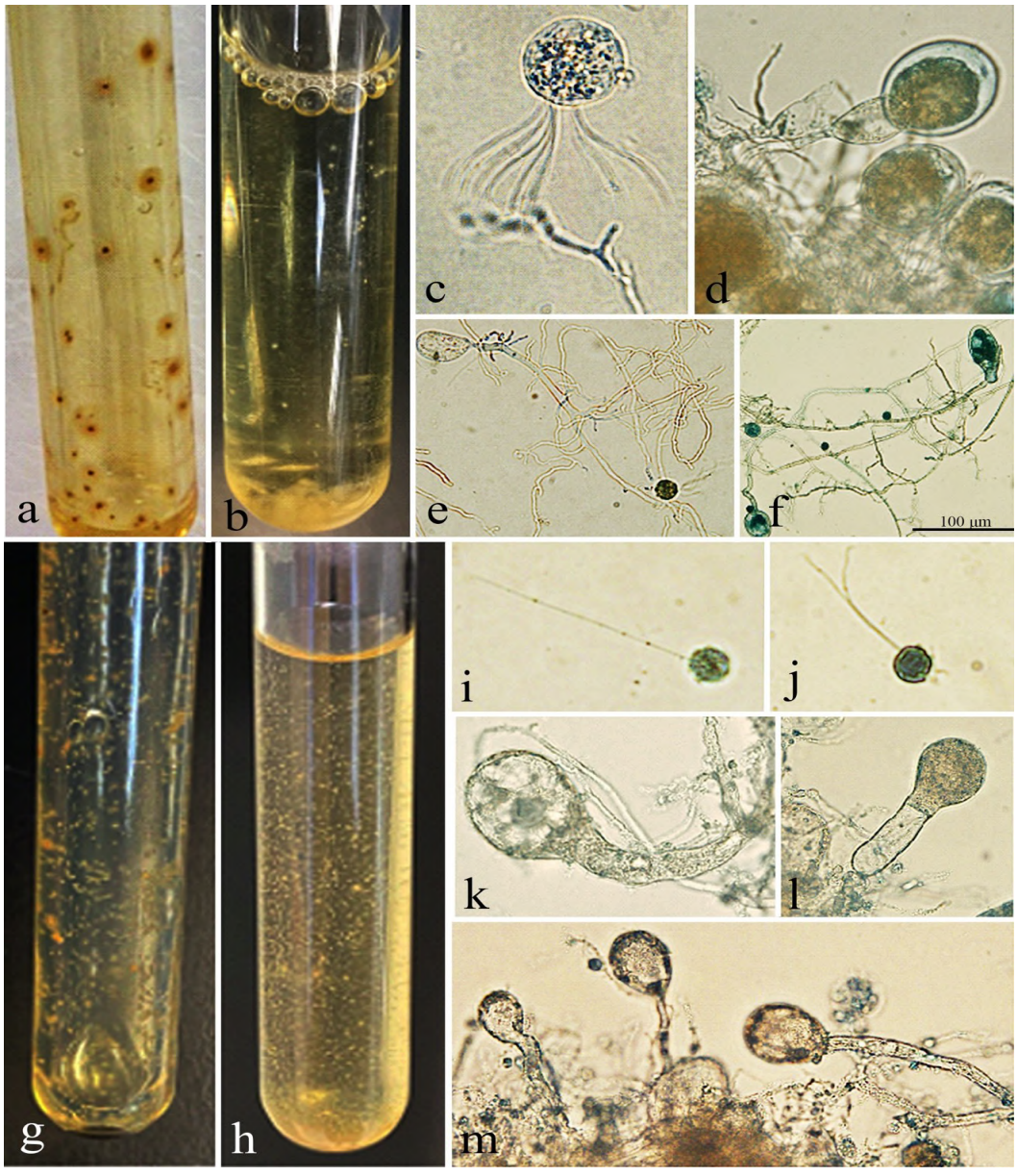


Figure 87 – a–f General characteristics of *Neocallimastix*. Beige circular colonies with a dark centre of sporangial structure. a thin biofilm growth in liquid media. b Polyflagellated zoospores. c Monocentric thalli with filamentous rhizoids showing sporangiophores. d Pleomorphic sporangia.

g–m General characteristics of *Piromyces*. g colony. h Liquid growth. i, j Spores of *Piromyces communis* strain jen1. k–m Filamentous growth showing sporangiophores and pleomorphic sporangia of *Priomyces finnis* strain DonB11.

Ecology & life modes – Obligate biotrophic plant pathogen (Grogan et al. 1958, Stanghellini et al. 2010, Powell & Letcher 2014b, Lay et al. 2018, Naranjo-Ortiz & Gabaldón 2019), vectors of plant pathogenic viruses (Dijkstra & Jager 1998, Rochon et al. 2003, Meresa & Gebremedhin 2020).

Family type – *Olpidium* (A. Braun) J. Schröt. 1886 (An isonym, see Art. 6.3 Note 2); Fig. 88

Obligate synonym: *Olpidium* (A. Braun) Rabenh. 1868

Notes – *Olpidiaceae* Schröt. (Schröter 1886) was introduced to accommodate *Olpidium* (A. Braun) J. Schröt. (1886) under *Chytridiales*, *Chytridiomycota*. Later, Barr (1980) reclassified *Olpidiaceae* under *Spizellomycetales*, *Spizellomycetes*, *Chytridiomycota*. *Olpidiales* was first introduced in *Zygomycota* (Cavalier-Smith (2013). However, Doweld (2013d) placed *Olpidiaceae* under a new phylum *Olpidiomycota*.

While proposing the high-level classification of the fungi and a tool for evolutionary ecological analyses, Tedersoo et al. (2018) confirmed *Olpidiomycota*. Recently, Chang et al. (2021) confirmed the 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 *EF-2*, *rpb1*, *rpb2* and *actin*.

Olpidium (A. Braun) J. Schröt., in Cohn, Krypt.-Fl. Schlesien (Breslau) 3.1(1–8): 180 (1886) (An isonym, see Art. 6.3 Note 2)

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

Index Fungorum Identifier 20382

Plasmodium is motionless from the start. Sporangia are rounded or elongate, living inside a plant cell or an animal structure, which empties the swarm spores to the outside through a cylindrical excretory duct. Swarm spores are globular, elliptic or ovate with a single flagellum at the anterior pole. *Danersporangia* formed from adult Plasmodium with a firm smooth membrane (fide Schröter 1886)

Notes – *Olpidium* has about 50 species recorded and has a cosmopolitan distribution. *Olpidium* species were reported as parasites of economically important crop plants, algae and rotifers (Grogan et al. 1958, Raghukumar 1987, Kirk et al. 2008, Stanghellini et al. 2010, Powell & Letcher 2014b, Lay et al. 2018, Naranjo-Ortiz & Gabaldón 2019). Chang et al. (2021) resolved the phylogeny of *Olpidium* through whole-genome data as the closest living zoosporic fungus to the non-flagellated, terrestrial fungi. Cultures and sequences are available in GenBank.

Type species – *O. endogenum* (A. Br.) Schroet., in Cohn, Krypt.-Fl. Schlesien (Breslau) 3.1(1–8): 180 (1886) [1889

Other genera in *Olpidiaceae*

Chytridhaema Moniez, C. r. hebd. Séanc. Acad. Sci., Paris 104: 184 (1887)

Index Fungorum Identifier 20122; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Chytridhaema cladocerarum* Moniez, C. r. hebd. Séanc. Acad. Sci., Paris 104: 183 (1887)

Cibdelia Juel, Ark. Bot. 19(no. 20): 9 (1925)

Index Fungorum Identifier 27484; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Cibdelia infestans* Juel, Ark. Bot. 19(no. 20): 9 (1925)

Leiolpidium Doweld, Index Fungorum 126: 1 (2014)

Index Fungorum Identifier 550480; Index Fungorum (2025) and Species Fungorum (2025) accepted five species.

Type species – *Leiolpidium cucurbitacearum* (D.J.S. Barr & Dias) Doweld, Index Fungorum 126: 1 (2014)

Notes – Members of the genus have been reported as intracellular parasites of roots and show cosmopolitan distribution.

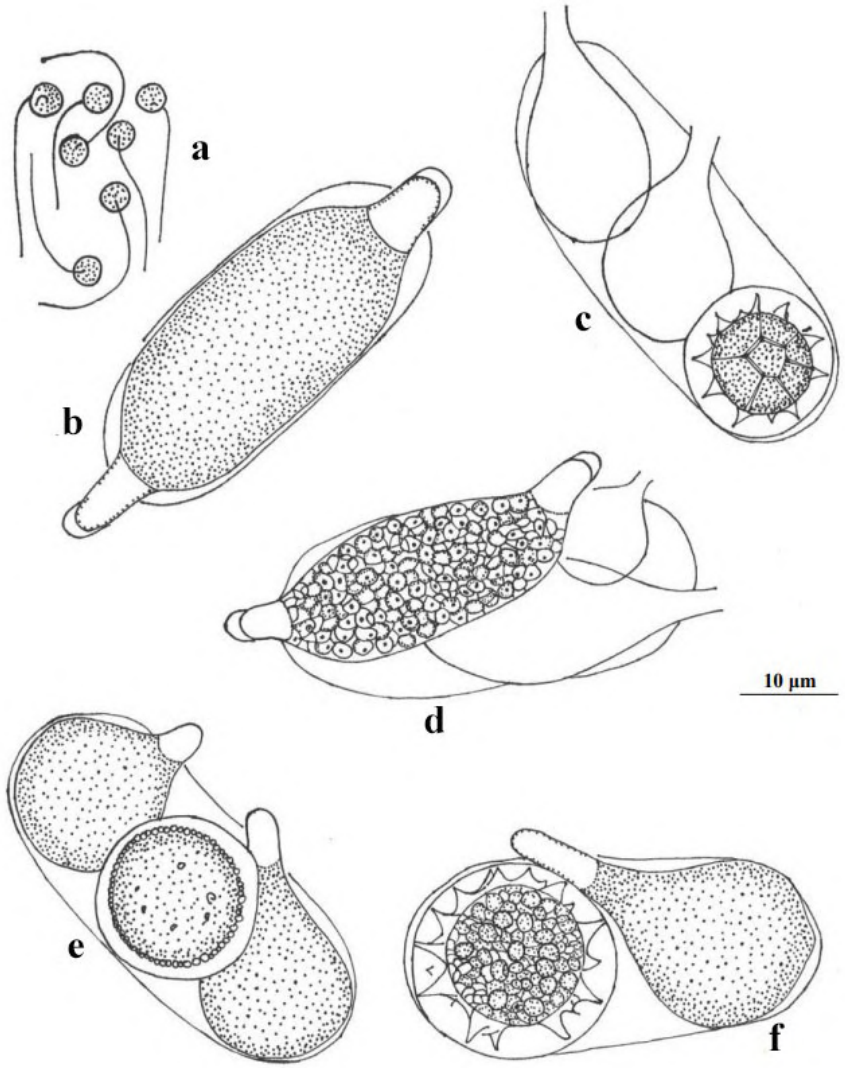


Figure 88 – *Olpidium vermicola*. a Posterially flagellate Zoospore. b Zoosporangium with evacuation tubes. c Mature resting spores. d Zoosporangium with encysted spores. e Zoosporangia. f Mature resting spore and sporangium. Scale bars: a–f = 10 µm (Redrawn from Barron & Szuarto 1986).

ROZELLOMYCOTA Doweld
Rozellidea T. Cavalier-Smith 2013, stat. nov.
Rozellida T. Cavalier-Smith 2013
Rozellidae T. Cavalier-Smith, T. Europ. J. Protistol. 49(2): 155 (2013)
Index Fungorum Identifier 622201

According to Cavalier-Smith (2013), posteriorly unicilliate naked cells of rozellids that bore through the cell walls of fungi or pseudofungi, enter their cytoplasm and phagocytose it from

within. Therefore, unlike in *Aphelidium*, their intracellular phase is not surrounded by host cell membrane.

The original diagnosis needs to be clarified and detailed in terms of the interface between the parasite and host cells. It varies depending on the rozellid species. The intracellular stages of *Rozella polyphagi* are surrounded by scattered patches of the host's smooth and rough endoplasmic reticulum (Powell 1984). *Rozella allomycis* and *R. rhizoclosmatii* are surrounded by two membranes of the smooth endoplasmic reticulum of the host (Letcher et al. 2017a, Powell et al. 2017). It was shown that aphelids and rozellids have the same mode of penetration of the host and a similar mode of trophont development in the host regarding their interface (Karpov & Paskerova 2020).

Due to the expansion of *Rozellomycota*, the diagnosis given by Doweld (2013e) for the phylum can be used nowadays to detail the description of the family *Rozellidae*: "Intracellular obligate parasites phagocytize host organelles, penetration of the host via a germ tube. Cells amoeboid, multinucleate, protoplast surrounded 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. Zoospores bilaterally symmetrical, posteriorly uniflagellate, flagellum inserted at the base of a lateral, posteriorly directed canal, smooth, with a striated, fibrous, cone-shaped, solid rhizoplast associated with the functional kinetosome; single large mitochondrion displaces the helmet-shaped nucleus anteriorly; kinetosome relatively long, transitional zone not well-defined, possesses struts to the plasma membrane; with two centrioles, vesicular mitochondrial cristae as flattened, finger-like lobes with constricted attachment at the inner membrane; ribosomes scattered throughout the cytoplasm. Resting spores thick-walled".

Family type – *Rozella* M. Cornu, Annls Sci. Nat., Bot., sér. 5 15: 148 (1872)

Ecology & life modes – The representatives of the family are obligate intracellular parasites (parasitoids) of lower fungi, *Oomycetes* and green algae. They are described from hosts collected in Europe, North and South America, and Africa (Sparrow 1960).

Notes – rRNA gene sequences are available for three species of *Rozella* and for several unclassified *Rozella* sp. Two genome assemblies for *Rozella allomycis* are available (11.86 Mb, 6350 protein-coding genes, GCA_000442015.1 – James et al. 2013; GCA_003614725.1 - Ahrendt et al. 2018).

Rozella M. Cornu, Annls Sci. Nat., Bot., sér. 5 15: 148 (1872)
Index Fungorum Identifier 20493

The members of the genus exhibit the characters of the family with the following additions: they are either mono- or polysporangiate. In polysporangiate forms, the parasite induces host hyphae to produce septa, compartmentalizing the parasite plasmodia as they develop into unwalled sporangial plasmodia or thick-walled resting spores, smooth or with spiny ornamentations; in monosporangiate forms, the parasite induces host hypertrophy (Letcher & Powell 2018c).

Type species – *Rozella septigena* M. Cornu, Annls Sci. Nat., Bot., sér. 5 15: 148 (1872); Fig. 89

Notes – *Rozella septigena* Cornu 1872 was designated as the type of the genus by Clements and Shear (1931). It parasitizes *Achlya*, *Saprolegnia* (*Oomycota*). The last revision of the genus was provided by Letcher & Powell (2018c). It includes twenty-seven species infecting fungi (*Chytridiomycota*, *Blastocladiomycota*, *Monoblepharomycota*, *Basidiomycota*), *Oomycetes* and green alga (*Coleochaete*).

Chytridiopsea J. Weiser 1974, stat. nov.
Chytridiopsida J. Weiser 1974
Chytridiopsidae V. Sprague, R. Ormières & J.F. Manier, J. Invert. Path. 20(2): 228–231 (1972), emend. J.I.R. Larsson, in Microsporidia: Pathogens of Opportunity,1st ed. Weiss L.M. and Becnel J.J. (Eds). John Wiley & Sons, pp. 605–634 (2014)

Index Fungorum Identifier 90212

All stages are with isolated nuclei (monokaryotic). Presporogonial reproduction is probably lacking. Sporogonial reproduction is endogenous by vacuolation and sometimes in addition by plasmotomy. The life cycle includes two sporogonies, free and enveloped. Enveloped sporogony occurs in polysporophorous spore sacs incorporating the plasma membrane of the sporont. Spores are small, spherical or oval, uninucleate, with thin exospore. Endospore is thick, thin, or absent. Polar filament is short, untilted, arranged in a few coils. Surface layer of the polar filament is alveolar. Polar sac lacks an anchoring disk. The central posterior surface of the polar sac is shaped like a socket, to which the collar-like anterior part of the polar filament attaches. Only the central part of the polar filament enters the polar sac. Typical polaroplast is absent.

Family type – *Chytridiopsis* A. Schneider, Arch. Zool. Exp. Gén., 2e Sér., 2: 1–36 (1884)

Ecology & life modes – They are obligate intracellular parasites of insects (*Coleoptera*, *Trichoptera*, *Siphonaptera*), myriapods and arachnids (*Acari*). They are described from the hosts collected in Europe and in North America.

Phylogeny – SSU rRNA gene sequence is available for one species only – *Chytridiopsis typographi*, a parasite of the bark beetle *Ips typographus*. There is no genomic data. An analysis of the rRNA gene sequence of *Ch. typographi* placed it in the phylogenetic tree as a sister group to canonical Microsporidia + Metchnikovellida (Corsaro et al. 2019). The overall structure of *Ch. typographi* rRNA is more similar to typical eukaryotic rRNA than to a microsporidian one. In some SSU rDNA trees, *Ch. typographi* occurs to be in the "cryptomycotan" clade LKM15 (the clade X *sensu* Lazarus &James 2015), which also includes *Mitosporidium daphniae*, *Morellospora saccamoebae* and a parasite of *Lamproderma* sp. (Frolova et al. 2021, Mikhailov et al. 2022b).

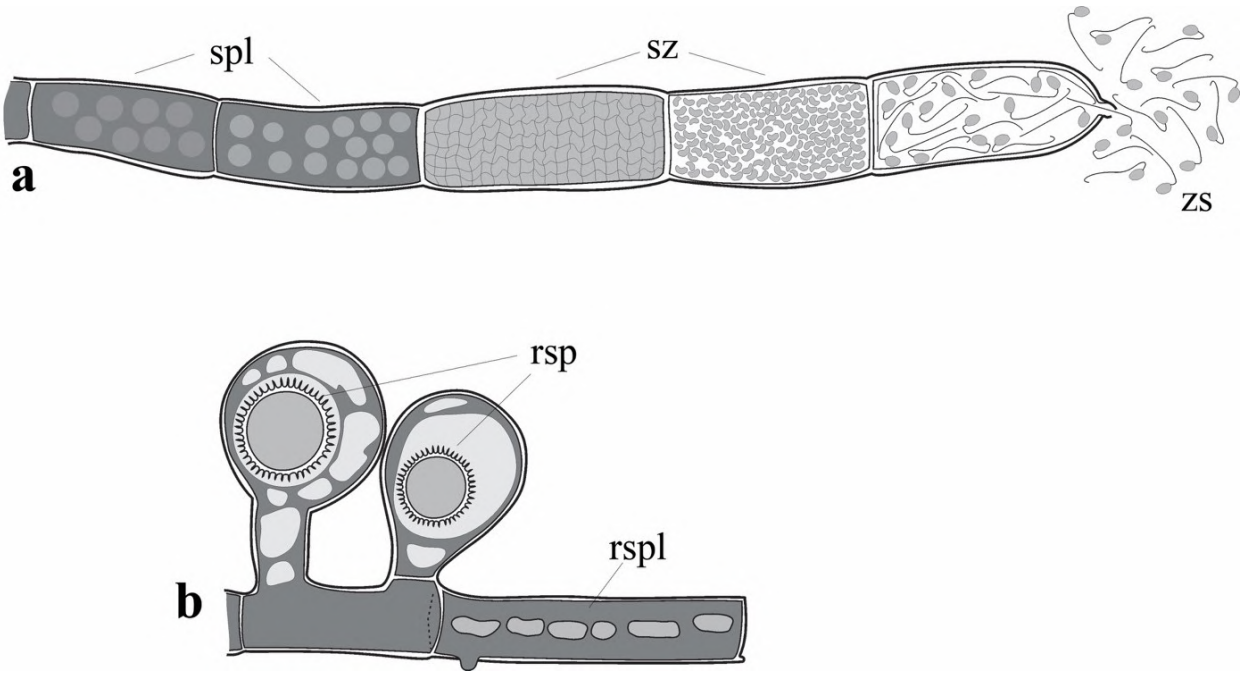


Figure 89 – Developmental stages of *Rozella septigena* parasitizing the oomycete *Saprolegnia* sp. a Subsequent stages of parasite development: unwalled sporangial plasmodia (spl) developing within host hypha; sporogenesis (sz), zoospore (zs) formation, zoospores are posteriorly uniflagellate (flagella are not shown), discharging from apical part of the hypha. b Parasite resting spores with spiny walls (rsp) and resting spore plasmodia (rspl). Redrawn from Cornu 1872 (Plate 6, Fig. 1 and 17) and from Fischer 1892 (Fig. 11), with modifications.

Chytridiopsis A. Schneider, Archs Zool. exp. gén., sér. 2: 1–36 (1884), emend. J.I.R. Larsson, in Microsporidia: Pathogens of Opportunity,1st ed. Weiss L.M. and Becnel J.J. (Eds). John Wiley & Sons, pp. 605–634 (2014); Fig. 90a
Index Fungorum Identifier 20127

Chytridiopsis species exhibit typical morphological characters of the *Chytridiopsidae***.** In addition to that, they undergo enveloped sporogony within thick-walled spore sacs. Endospore is thin. Polar filament is isofilar, with only 1–2 turns, made up of a dense core surrounded by an alveolate (honeycomb-like) sheath. Only the central part of the polar tube, not the honeycomb layer, continues into the polar sac (Canning & Vavra 2000). There is no polaroplast of the traditional type. Sprague with co-authors (1992) suggested that the alveolate ornamentation of the filament sheath is an analogue of the polaroplast. Sporogony occurs in close association with the nucleus of the host cell, proceeding in an invagination of the nucleus.

Type species – *Chytridiopsis socia* A. Schneider, Archs Zool. Exp. Gén., sér. 2: 1–36 (1884)

Notes – A total of eleven species of *Chytridiopsis*, parasitizing in the intestinal epithelium; rDNA sequence is available for *Chytridiopsis typographi*.

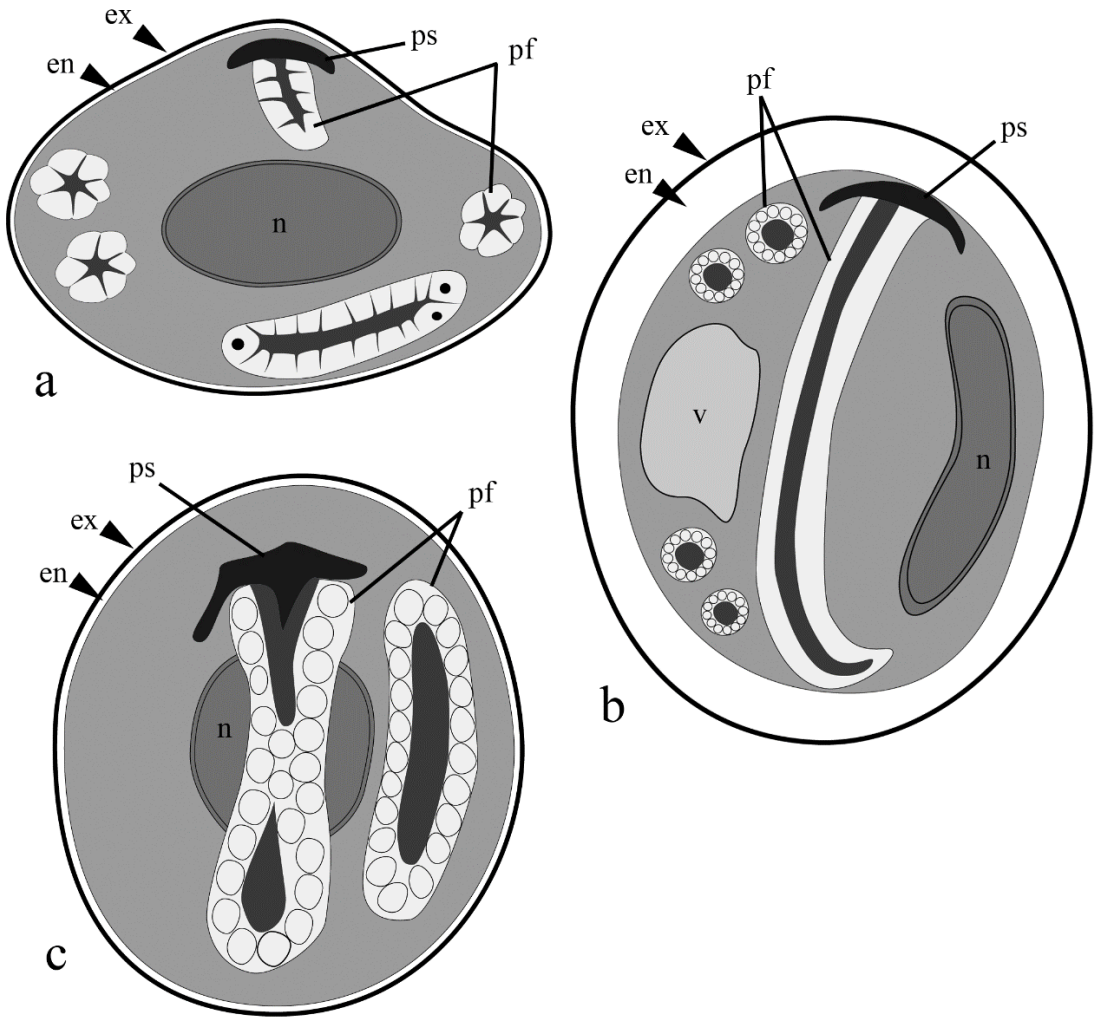


Figure 90 – Schematic drawings of the mature spores of the members of the family *Chytridiopsidae* from the following genera. a *Chytridiopsis*, b *Intexta*, c *Nolleria*. Abbreviations: ex = exospore; en = endospore; n = nucleus; pf = polar filament; ps = polar sac; v = posterior vacuole. Drawing is based on Issi 1986 (a), Canning & Vavra 2000 (b, c), with some modifications.

Other genera in *Chytridiopsidae*

Acarispora R. Radek, M. Kariton, J. Dabert & G. Alberti, Acta Parasitol 60(2): 200–210 (2015)
Index Fungorum Identifier 92529

Type species – *Acarispora falculifera* R. Radek, M. Kariton, J. Dabert & G. Alberti, Acta Parasitol 60(2): 200–210 (2015)

Notes – *Acarispora* is a monotypic genus. Its only representative is an obligate intracellular parasite of the feather mites collected in Europe. No sequences are available.

Intexta R. Larsson, M.Y. Steiner & S. Bjørnson, Acta Protozool. 36(4): 295–304 (1997)
Index Fungorum Identifier 30503

Type species – *Intexta acarivora* R. Larsson, M.Y. Steiner & S. Bjørnson, Acta Protozool. 36(4): 295–304 (1997); Fig. 90b

Notes – *Intexta* is a monotypic genus. The only described species is an obligate intracellular parasite of the forage mites, collected in Europe. No sequences are available.

Nolleria B.B. Beard, J.F. Butler & J.J. Becnel, J. Protozool. 37: 90–99 (1990)
Index Fungorum Identifier 30535

Type species – *Nolleria pulicis* B.B. Beard, J.F. Butler & J.J. Becnel, J. Protozool. 37: 90–99 (1990); Fig. 94c

Notes – *Nolleria* is a monotypic genus, described from the fleas in North America. No sequences are available.

Sheriffia J.I.R. Larsson Microsporidia: Pathogens of Opportunity,1st ed. Weiss L.M. and Becnel J.J. (eds). John Wiley & Sons, pp. 605–634 (2014)
Index Fungorum Identifier IF 92530

Type species – *Sheriffia brachynema* C.S. Richards & H.G. Sheffield, Soc. Invertebr. Pathol. Newsl. 2: 12 (1970), emend. J.I.R. Larsson Microsporidia: Pathogens of Opportunity,1st ed. Weiss L.M. and Becnel J.J. (eds). John Wiley & Sons, pp. 605–634 (2014)

Synonyms – *Coccospora brachynema* Richards & Sheffield, 1971; *Steinhausia brachynema* Sprague, Ormières & Manier, 1972

Notes – *Sheriffia* is a monotypic genus, which includes parasites of freshwater gastropods (snails) from South America. No sequences are available.

Buxtehudiidae J.I.R. Larsson, Protistologica 16(1): 85–101 (1980)
Index Fungorum Identifier 90144

According to Larsson (1980, 2014), all stages of the life cycle contain isolated nuclei (monokaryotic). Presporogonial reproduction is probably lacking. Sporogonial reproduction is endogenous by vacuolation, and sometimes in addition by plasmotomy. There are two sporogonies, free and enveloped. Enveloped sporogony occurs in thin-walled polysporophorous spore sacs formed by the plasma membrane of the sporont. Spores are spherical or lightly lenticular, uninucleate, with endo- and exospore layers. Polar filament is long, coiled, and tilted. Polar sac devoid of an anchoring disk. The central posterior surface of the polar sac shaped like a socket, to which the collar-like anterior part of the polar filament attaches. Only the central part of the polar filament enters the polar sac. The surface layer of the polar filament is a folded membrane, giving the transversely sectioned filament a stellate appearance. Development is not associated with the nucleus of the host cell.

Family type – *Buxtehudea* J.I.R. Larsson, Protistologica 16(1): 85–101 (1980)

Ecology & life modes – The representatives of the family are described as obligate intracellular parasites of terrestrial insects and annelids from Europe.

Phylogeny – No sequences are available.

Buxtehudea J.I.R. Larsson, Protistologica 16(1): 85–101 (1980)
Index Fungorum Identifier 30456

The representatives of the genus *Buxtehudea* exhibit typical morphological characters of the *Buxtehudiidae*. In addition, they possess endospore of equal thickness over the whole spore, rudimentary polaroplast and well-developed posterior vacuole. Sporogonial plasmodia with unpaired nuclei develop within membrane-bound vacuoles and give rise to 50–100 uninucleate sporoblasts and spores. Spores are 2.5–3.5 µm in size, spherical or lenticular with one U-shaped nucleus. Polar filament is isofilar, with 9–11 coils arranged in two disorderly rows. The outer membrane of filament is raised in spirally wound ridges, giving a stellate appearance to the polar filament in cross sections (Canning & Vavra 2000). They are primarily parasites of terrestrial insects.

Type species – *Buxtehudea scaniae* J.I.R. Larsson, Protistologica 16(1): 85–101 (1980); Fig. 91a

Notes – It is a monotypic genus; the only species is described from Zygentomain Europe. No sequences are available.

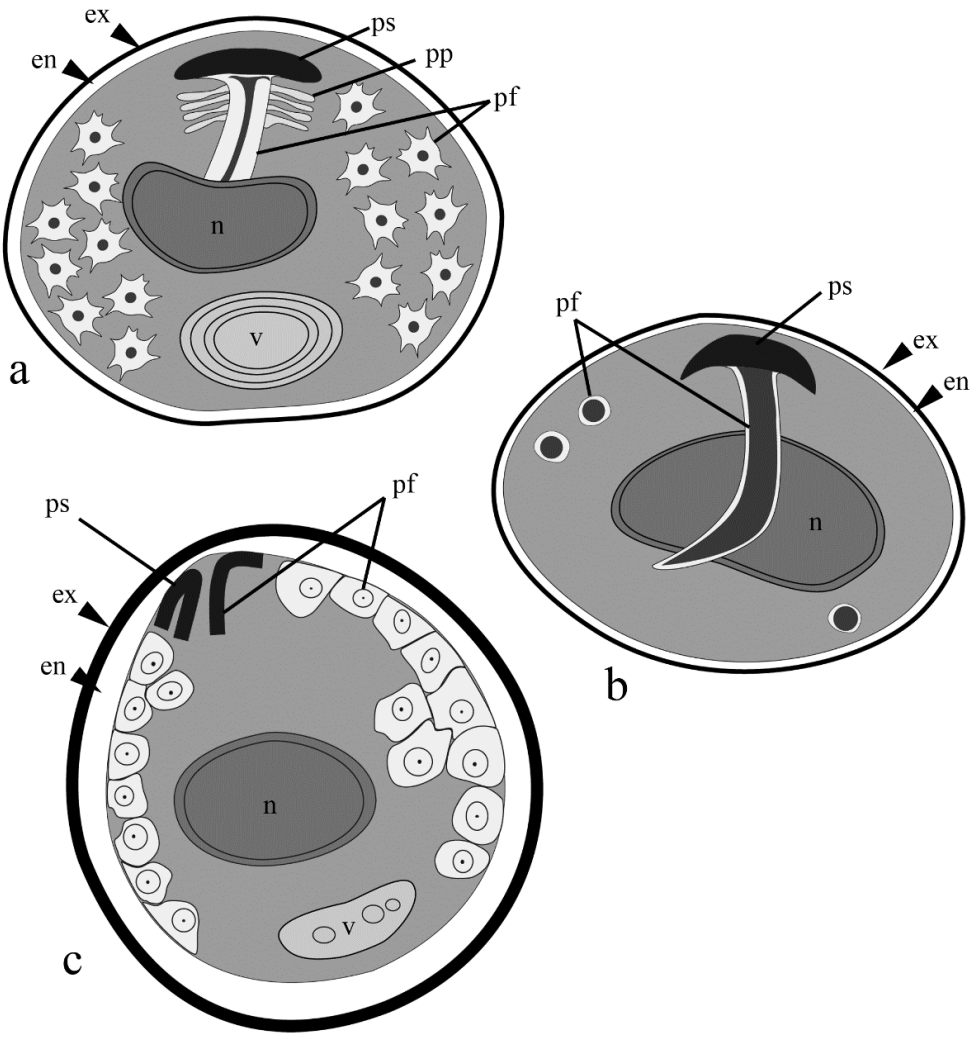


Figure 91 – Schematic drawings of mature spores of the members of the following families. a *Buxtehudiidae.* b *Hesseidae*. c *Burkeidae*. Abbreviations: ex = exospore; en = endospore; n = nucleus; pf = polar filament; pp = polaroplast; ps = polar sac; v = posterior vacuole. In *Buxtehudea scaniae* (a) polar filament in cross-sections has octagonal stellate appearance, posterior vacuole is surrounded by the multilayered membrane. In *Hessea squamosa* (b) the mature spores possess a thick exospore and rudimentary endospore, a short polar filament (2–3 coils) and no polaroplast. In *Burkea gatesi* (c) the polar tube isofilar with about 10 coils in two ranks, the posterior vacuole with

large electron-dense inclusions, the spore wall seems to have a thick exospore. Redrawn from Canning & Vavra 2000 with some modifications.

Other genera in *Buxtehudiidae*:

Jiroveciana J.I.R. Larsson, Protistologica 16(1): 85–101 (1980)

Index Fungorum Identifier 30508

Type species – *Jiroveciana limnodrili* O. Jírovec Arch. Protistenkd. 94: 80–92 (1940), emend. J.I.R. Larsson, Protistologica 16(1): 85–101 (1980)

Synonym – *Chytridiopsis limnodrili* Jírovec, 1940

Notes – It is a monotypic genus, the only species is described from oligochaetes in Europe (Jírovec 1940). No sequences are available.

Hesseidae R. Ormières & V. Sprague J. Invert. Path. 21(3): 224–240 (1973)

Index Fungorum Identifier 90513

According to the diagnosis, emended by Sprague (1977), the merogony sequence is present in the disporoblastic, monomorphic (referred to as 'monosporous' by Sprague) life cycle of representatives of this family. Spore sacs (referred to as ‘sporocysts’ in the terminology of Sprague) possess a thick-walled envelope. Encysting stage seems to be something earlier than a sporont. Parasite with no special relation to host cell nucleus.

Family type – *Hessea* R. Ormières & V. Sprague, J. Invert. Path. 21(3): 224–240 (1973); Fig. 91b

Ecology & life modes – The members of this family are obligate intracellular parasites of *Diptera*. They are described from Europe.

Phylogeny – No sequences are available.

Hessea R. Ormières R. & V. Sprague, J. Invert. Path. 21(3): 224–240 (1973)

Index Fungorum Identifier 30494

The representatives of the genus *Hessea* exhibit typical morphological characters of the family *Hesseidae*. In addition, they are characterized by merogony, which occurs through binary or multiple fission. They are diplo- and monokaryotic. Sporogonial plasmodia become enclosed in ornate, thick-walled spore sacs (10–15 µm), which are externally ornamented by a mosaic of polygonal plaques from which lamellate projections extend. The spore sacs contain about 16–30 spores. The nuclei are paired in the sporont, but are not closely appressed as diplokaryon. Each sporont divides to produce one normal and one abortive sporoblast. Spores are usually monokaryotic, spherical or oval, 1.5–2.5 µm, with a thick exospore and rudimentary endospore. Typically, they possess one nucleus, sometimes two. The polar filament has 2–3 coils. The polaroplast is probably missing (Ormières & Sprague 1973; Canning & Vavra 2000).

Type species – *Hessea squamosa* R. Ormières R. & V. Sprague, J. Invert. Path. 21(3): 224–240 (1973); Fig. 91b

Notes – Only one species was described. It was discovered in the gut epithelium of a larva *Sciara* sp. (*Diptera*), collected in Europe. No sequences are available.

Burkeidae V. Sprague, in Bulla et al. (Eds), Comparative Pathobiology (New York) 2: 1–510 (1977)

Index Fungorum Identifier 90112

Merogony is unknown. The sporogony is likely to proceed through vacuolation. Parasite is not isolated during sporulation but it develops in direct contact with the host cell cytoplasm. Infected cell undergoes hypertrophy, with the cell membrane involving in the cyst production. This process resembles a xenoma formation.

Family type – *Burkea* V. Sprague, in Bulla et al. (Eds), Comparative Pathobiology (New York) 2: 1–510 (1977)

Ecology & life modes – These organisms are obligate intracellular parasites of annelids (Oligochaetes). They are known from Hawaiian Islands, Pacifica (Sprague 1977).

Phylogeny – No sequences are available.

Burkea V. Sprague, in Bulla et al. (Eds), Comparative Pathobiology (New York) 2: 1–510 (1977)
Index Fungorum Identifier 30455

The members of the genus *Burkea* exhibit typical morphological characters of the family *Burkeidae*. The two described species are characterized by sporogony resulted in production of large spore sacs ('cysts'), which are up to 1.5 mm wide. The sac is formed around a sporogonial plasmodium with isolated nuclei. The spherical spores are measured 2.5–3 μm in size in fixed preparations. The spores exhibit a long, tilted polar filament, with slightly reduced diameter towards the rear end. The polar filament is arranged in two coils. The transversely sectioned filament is layered, and the external layer is membranous and separated from the dense central part by a wide, lucent space. Aggregated flat vesicles, partly surrounding the nucleus, are believed to be the equivalent of a polaroplast. There is a posterior vacuole with a large electron-dense inclusion. The spore wall has a thick exospore layer separated from the plasma membrane by a wide, lucent space. The wall of the spore sac appears as a comparatively thin, membranous layer. Each spore is believed to be surrounded by an individual fold of the membrane (De Puytorac & Tourret 1963).

Type species – *Burkea gatesi* (P. De Puytorac & M. Tourret, Ann. Parasitol. (Paris) 38: 861–874 (1963)) V. Sprague, in Bulla et al. (Eds), Comparative Pathobiology (New York) 2: 1–510 (1977); Fig. 91c

Synonym – *Coccospora gatesi* De Puytorac & Tourret, 1963

Notes – Two species were described from the terrestrial oligochaetes. They are developing in the musculature and epidermis of the worms. The infected tissue is reorganized into a syncytium (Fig. 1 in De Puytorac & Tourret 1963; Fig. 1 in Burke 1970). They were isolated in Hawaiian Islands, Pacifica. No sequences are available.

Rudimicrosporea V. Sprague 1977
Metchnikovellida E. Vivier 1975
Amphiacanthidae J.I.R. Larsson, in Microsporidia: Pathogens of Opportunity,1st ed. Weiss L.M. and Becnel J.J. (Eds). John Wiley & Sons, pp. 605–634 (2014)
Index Fungorum Identifier 90052

The diagnosis of the family proposed by Larsson (2014): "Presporogonial development not observed, presumed absent. Free sporogony yielding a small number of sporoblasts together with polysporoblastic enveloped sporogony in elongated spore sacs. Spore sacs spindle-shaped, terminating as threadlike prolongations, and lacking polar plugs. The plasma membrane of the sporont is incorporated into the envelope of the spore sac. Enveloped spores produced by vacuolation. At least a part of the life cycle with coupled nuclei. Both spore types rounded to pyriform, with a characteristic extrusion apparatus comprising a polar sac devoid of an anchoring disk, a polar filament with manubroid and bulbous parts, and a posterior membranous more or less folded prolongation following the spore wall and in sections partly visible as rounded or tubular structures. Polar filament only partially coupled to the polar sac. Typical polaroplast and posterior vacuole absent. Spores with polyribosomes. Parasites of gregarines".

Family type – *Amphiacantha* M. Caullery & F. Mesnil, C. r. Séanc. Soc. Biol. 77: 527–532 (1914), emend. J.I.R. Larsson in Microsporidia: Pathogens of Opportunity,1st ed. Weiss L.M. and Becnel J.J. (Eds). John Wiley & Sons, pp. 605–634 (2014)

Ecology & life modes – The representatives are obligate hyperparasites of lecudinid gregarines from intestines of marine polychaetes of the family *Lumbrineridae* (Caullery & Mesnil 1914, Stubblefield 1955, Larsson 2000).

Phylogeny – The family is supported in SSU rRNA phylogenetic reconstructions (Mikhailov et al. 2017, Corsaro et al. 2019, Nassonova et al. 2021, Frolova et al. 2021, 2022). *Metchnikovella spiralis* and environmental clone p1–44 (GenBank KX214677) are branching together with *Amphiacantha* spp. (Frolova et al. 2021, 2022) with high support that indicates the need to revise the frames of the family in the future.

Amphiacantha M. Caullery & F. Mesnil, C. r. Séanc. Soc. Biol. 77: 527–532 (1914), emend. J.I.R. Larsson in Microsporidia: Pathogens of Opportunity,1st ed. Weiss L.M. and Becnel J.J. (Eds). John Wiley & Sons, pp. 605–634 (2014); Fig. 92
Index Fungorum Identifier 30442

According to Larsson (2014), the diagnosis of the genus includes the characters of the family and the following additions: "free spores bluntly pyriform, enveloped spores irregularly rounded. Enveloped sporogony involves sporoblast mother cells. Both spore types with the extrusion apparatus at the wider pole, coupled nuclei at the narrower end. The coat and the surface layer of the manubrium penetrate the polar sac. A collar-like section is intersected between manubrium and bulb".

Type species – *Amphiacantha longa* M. Caullery & F. Mesnil, C. r. Séanc. Soc. Biol. 77: 527–532 (1914), emend. J.I.R. Larsson in Microsporidia: Pathogens of Opportunity,1st ed. Weiss L.M. and Becnel J.J. (Eds). John Wiley & Sons, pp. 605–634 (2014)

Notes – Three species were described in Europe and North America. The sequences of SSU rDNA are available in GenBank for two non-described isolates of *Amphiacantha* sp.

Metchnikovellidae M. Caullery & F. Mesnil, C. r. Séanc. Soc. Biol. 77: 528 (1914), emend. J.I.R. Larsson in Microsporidia: Pathogens of Opportunity,1st ed. Weiss L.M. and Becnel J.J. (Eds). John Wiley & Sons, pp. 605–634 (2014)
Index Fungorum Identifier 90585

The diagnosis of the family proposed by Larsson (2014): "Presporogonial development not observed, presumed absent. Polysporoblastic free sporogony together with polysporoblastic enveloped sporogony in spore sacs of characteristic shapes. Spore sacs with rounded ends, one or both with a polar plug. The plasma membrane of the sporont is incorporated into the envelope of the spore sac. Enveloped spores produced by vacuolation. All stages with isolated nuclei, spores uninucleate. Free spores rounded, sac-bound spores rounded or elongated. If both sporogonies produce rounded spores, the free spores are slightly larger, having a thinner spore wall. Both spore types with a characteristic extrusion apparatus comprising of a polar sac devoid of an anchoring disk, a polar filament with manubroid and bulbous parts, and a posterior membranous more or less folded prolongation, following the spore wall and in sections partly visible as rounded or tubular structures. Polar filament only partially coupled to the polar sac. Typical polaroplast and posterior vacuole absent. Spores with free ribosomes, but lacking polyribosomes. Parasites of gregarines".

Family type – *Metchnikovella* M. Caullery & F. Mesnil, C. r. hebd. Séanc. Acad. Sci., Paris 125: 789 (1897), emend. J.I.R. Larsson R. in Microsporidia: Pathogens of Opportunity,1st ed. Weiss L.M. and Becnel J.J. (Eds). John Wiley & Sons, pp. 605–634 (2014)

Ecology & life modes – The representatives of the family are obligate parasites of archi- and eugregarines from intestines of marine polychaetes (Errantia: *Nereididae, Phyllodocidae, Eunicidae*; Sedentaria: *Spionidae, Opheliidae, Travisiidae, Capitellidae, Cirratulidae*; *Echiurida*), sipunculids and oligochaetes (Caullery & Mesnil 1914, Vivier 1975, Larsson 2014).

Phylogeny – SSU rDNA phylogenetic and phylogenomic analyses demonstrated the heterogeneity of the genus *Metchnikovella* (Nassonova et al. 2021, Frolova et al. 2021, 2022) and an obvious need for revision of the genus and the family *Metchnikovellidae* when a robust and representative phylogenetic tree is constructed.

Metchnikovella M. Caullery & F. Mesnil, C. r. hebd. Séanc. Acad. Sci., Paris 125: 789 (1897), emend. J.I.R. Larsson R. in Microsporidia: Pathogens of Opportunity,1st ed. Weiss L.M. and Becnel J.J. (Eds). John Wiley & Sons, pp. 605–634 (2014); Fig. 93a–c, e–f, 94a
Index Fungorum Identifier: 30610

The diagnosis of the genus provided by Larsson (2014) includes the characters of the family and the following additions: "spore sacs cylindrical or fusiform, more or less curved, with rounded

ends containing polar plugs. Length not exceeding 10 times the width. Spores are oval. Both sporogonies produce spores of approximately the same shape".

Type species – *Metchnikovella spionis* M. Caullery & F. Mesnil, C. r. hebd. Séanc. Acad. Sci., Paris 125: 789 (1897); Fig. 97 (e).

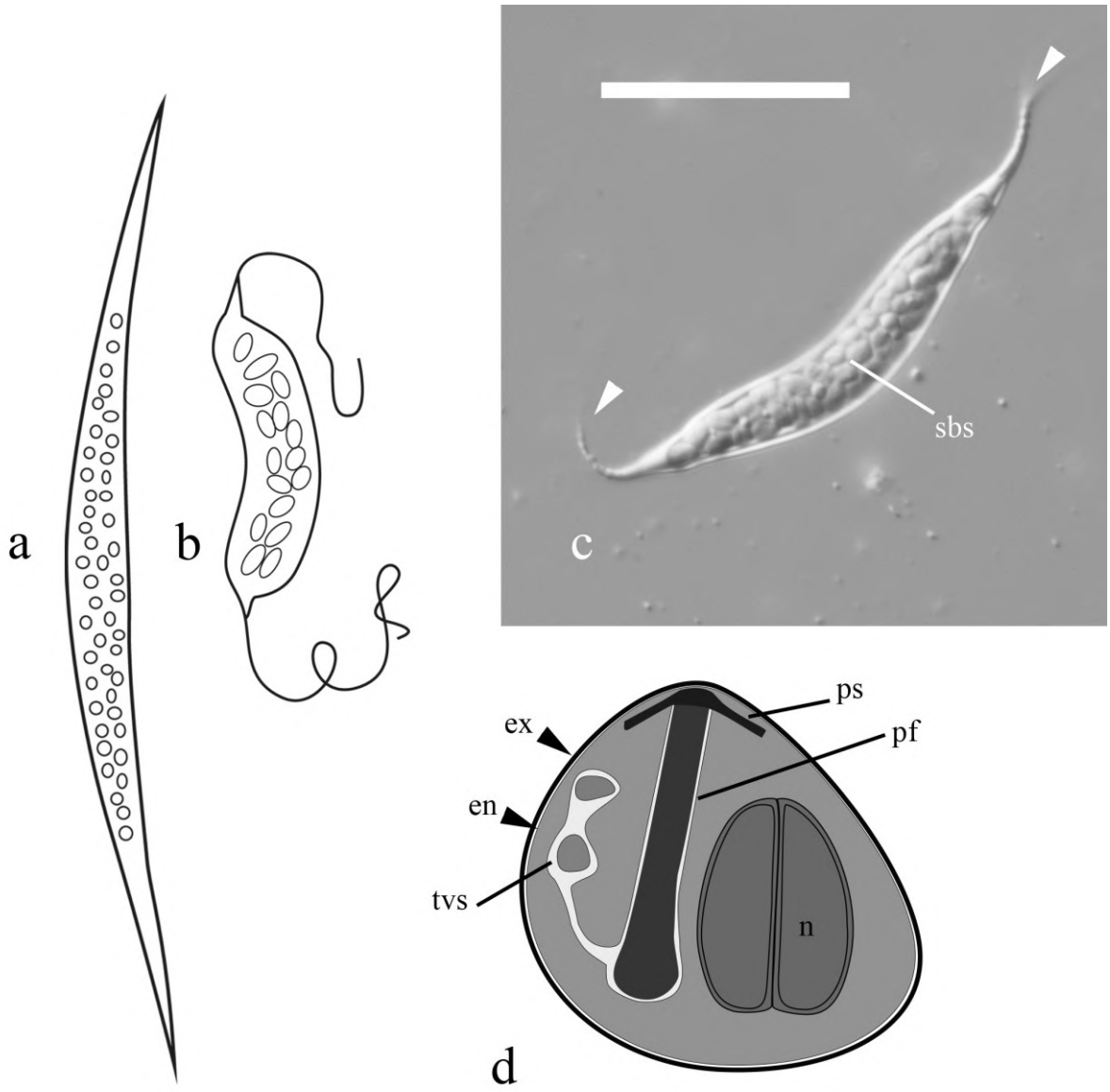


Figure 92 – The morphological features of the representatives of the genus *Amphiacantha*. a–b Schematic drawings showing general morphology of the spore sacs of *A. longa* (a, after Caullery & Mesnil 1919) and *A. ovalis* (b, after Stubblefield 1955, Vivier 1975). c Live spore sac of *Amphiacantha* sp., a parasite of the gregarine *Lecudina* sp. from the polychaete *Lumbrineris fragilis*, arrowheads indicate the thread-like extensions at the both ends of the spore sac, scale bar is 30 μm. d Schematic drawing of fine structure of the mature spore of *Amphiacantha* spp. based on morphological description and Figs. 14–15 from Larsson 2000; the generalized scheme shows longitudinal section through the longest axis of a free spore; it is important to note that the coupled nuclei are usually visible not in longitudinal sections but in ones taken perpendicularly to the longitudinal axis). Abbreviations: ex = exospore; en = endospore; n = nucleus; pf = polar filament; ps = polar sac; sbs = sac-bound spores; tvs = tubulovesicular system, a posterior membranous more or less folded prolongation of polar filament following the spore wall and in sections partly visible as rounded or tubular structures ('membraneous coat' and 'circular elements' according to terminology applied by Larsson 2000).

Notes – SSU rDNA phylogenetic and phylogenomic analyses demonstrated that the genus is a paraphyletic group of species, indicating the need for a future revision as more phylogenomic data becomes available for a wider range of representatives. SSU rDNA and protein-coding sequences are available in GenBank for a number of species; the genome of *M. incurvata* is sequenced and annotated (5.84 Mb; QXFS00000000.1 – Galindo et al. 2018); 19 species were described within the genus (see Table 1 in Paskerova et al. 2016, Frolova et al. 2021, 2023), the validity of two of them were questioned (Larsson 2014). Seven species sporulating in oval spore sacs with one polar plug were transferred to the genus *Caulleryetta* in the revision of Larsson (2014). Currently, ten species are classified within the genus *Metchnikovella*. They were described from archi- and eugregarines inhabiting intestines of polychaetes (Sedentaria: *Spionidae*, *Opheliidae*, *Cirratulidae*; Errantia: *Nereididae*) and oligochaetes (*Fridericia polychaete*), isolated in Europe (summarized from Larsson 2014, Frolova et al. 2023).

Other genera in *Metchnikovellidae*

Amphiamblys Caullery M. & Mesnil F., C. r. Séanc. Soc. Biol. 77: 527–532 (1914); Figs. 93d, h & 94b

Index Fungorum Identifier 30443

Type species – *Amphiamblys capitellides* M. Caullery & F. Mesnil, C. r. hebd. Séanc. Acad. Sci., Paris 125: 789 (1897)

Notes – Seven species are described, all of them are obligate intracellular parasites of gregarines from polychaetes (Sedentaria: *Capitellidae*, *Spionidae*; Errantia: *Eunicidae*, *Phyllodocidae*; *Echiurida*) isolated in Europe. Ribosomal RNA and protein-coding gene sequences are available in GenBank; the genome of *Amphiamblys* sp. (5.62 Mb; 3642 protein-coding genes; MKPU00000000.1 – Mikhailov et al. 2017) is sequenced and annotated.

Caulleryetta V.A. Dogiel, Ann. Inst. Pasteur. 36: 574–577 (1922)

Index Fungorum Identifier 30460

Type species – *Caulleryetta mesnili* V.A. Dogiel, Ann. Inst. Pasteur. 36: 574–577 (1922); Fig. 93f

Notes – Seven species sporulating in oval spore sacs with one polar plug were transferred to the genus *Caulleryetta* in the revision of Larsson (2014). They are obligate intracellular parasites of gregarines from polychaetes (*Travisiidae*, *Spionidae*, *Nereididae*) and sipunculids (*Phascolion strombus strombus*) isolated in Europe (summarized from Larsson 2014). No rDNA sequences are available.

Desportesia I.V. Issi & V.N. Voronin in Issi IV, Protozoologiya (Leningrad) 10: 6–136 (1986)

Index Fungorum Identifier 30475

Type species – *Desportesia laubieri* (I. Desportes & J. Théodoridès, Protistologica 15: 435–457 (1979)) I.V. Issi & V.N. Voronin in Issi IV, Protozoologiya (Leningrad) 10: 6–136 (1986); Fig. 94c

Synonym – *Amphiamblys laubieri* Desportes & Théodoridès, 1979

Notes – the monotypic genus was established on the basis of the distinct morphology of the spores of *Amphiamblys laubieri*. They resemble in structure the cylindrical spores of canonical microsporidia (*Helmichia*, *Baculea*, *Striatospora*). Additionally, the discovery of structures akin to a simplified polaroplast, represented by a few membranous lamellae, also supported the classification. However, Larsson did not support the validity of the genus *Desportesia* (Larsson 2014).

Metchnikovellida genera *incertae sedis*

Mesnilivella (Frolova et al. 2023) E.V. Frolova & E.S. Nassonova **nom. nov.**

Basionym: *Mesnilia* E.V. Frolova, M.P. Raiko, N.I. Bondarenko, G.G. Paskerova, T.G. Simdyanov, A.V. Smirnov, E.S. Nassonova, Protistology 17(4): 244–258 (2023) (Nom. illegit., Art. 53.1);

Index Fungorum Identifier IF 92531

This genus is characterised by elongated spore sacs with one polar plug. Both sporogonies are in direct contact with the host cytoplasm. Spore sacs non-accompanied by free spores may be observed in the host cytoplasm.

Type species – *Mesnilivella travisiae* (Frolova et al. 2023) Frolova & Nassonova **nom. nov**.; Fig. 95.

Note – *Mesnilivella* is introduced as **a** new genus name as a basionym to *Mesnilia*. The genus *Mesnilia* (Frolova et al. 2023), is preoccupied by the copepod genus described earlier (Canu 1898) and by an invalid nowadays genus of microsporidian parasite with the type species *Mesnilia legeri* (Paillot 1941) transferred to the genus *Cystosporogenes* (Kleespies et al. 2003). SSU rRNA gene sequences of *M. travisiae* are available in the GenBank under the accession numbers OR887354–OR887355.

Microsporidea Corliss & Levine
Amblyosporida Y.S. Tokarev & Issi
Amblyosporidae Weiser, Vest Cesk Spol Zool 41(4): 308–321 (1977) emend. Y.S. Tokarev & Issi, in Wijayawardene et al. Mycosphere 11(1): 1060–1456 (2020)
Index Fungorum Identifier 90040

One sporulation sequence "*Thelohania*-like", sporogony being octosporoblastic and accompanied by meiosis, the 8 uninucleate spores (meiospores) in a vesicle. Another sporulation sequence "*Nosema*-like", being diplokaryotic and disporous, the spores binucleate and isolated. A third sporulation sequence ends with uninucleate-lanceolate spores; these are haploid and usually develop in an intermediate host. Different variants of life cycles are present in this monophyletic group (Sprague et al. 1992).

Family type – *Amblyospora* Hazard & Oldacre 1975

Ecology & life modes – obligate biotrophic parasites of aquatic arthropods, predominantly mosquitoes and copepods as intermediate hosts. Distributed worldwide (Andreadis et al. 2012).

Notes – The only species infecting a host other than mosquitoes and copepods is allocated to this family based on ultrastructure only (Tonka & Weiser 2000) and may not constitute a single phylogenetic lineage with other members of this family. Referred to as highly specialized parasites of mosquitoes, all taxa examined using the molecular phylogeny approach show associations with mosquitoes and/or copepods, which are supposed to originate from an ancestor with a complex life cycle involving both hosts (Andreadis et al. 2012).

Amblyospora (Kellen & Lipa) Hazard & Oldacre, Tech. Bull. U.S. Dep. Agric. 1530: 16 (1975)
Index Fungorum Identifier 30440

Predominantly dimorphic with two developmental sequences in their hosts: one only in immature males or in both immature males and females, producing octospores enclosed by a pansporoblastic membrane; and another in adult females, producing a variable number of free spores. The pansporoblasts are oval. Living octospores are oval, having broadly rounded posterior ends and somewhat narrow anterior ends. The octospores have a thick exospore, a long polar filament consisting of a broad basal portion abruptly constricting near the middle to a narrow distal portion, and a prominent lamellar polaroplast. The living octospores of most species are covered by a mucous envelope. The multinucleate sporonts associated with female hosts and transovarial transmission produce free spores (4 to 12 in number), thin-walled, with a large, prominent vacuole and a polar filament of uniform diameter (Hazard & Oldacre 1975).

Type species – *Amblyospora californica* (Kellen & Lipa) Hazard & Oldacre

Notes – Up to 90 species are described, of which a reliable proportion is genotyped (Andreadis et al. 2012)

Other species in *Amblyosporidae*
Aedispora P.J. Kilochitskii, Věstník Zoologii 31: 15–23 (1997).

Index Fungorum Identifier 30463; two epithets are listed in Index Fungorum (2025)

Type species – *Aedispora dorsalis* Kilochitskii 1997

Notes – Species are reported as obligate intracellular parasites of mosquitoes and are distributed in Europe. No sequences are available.

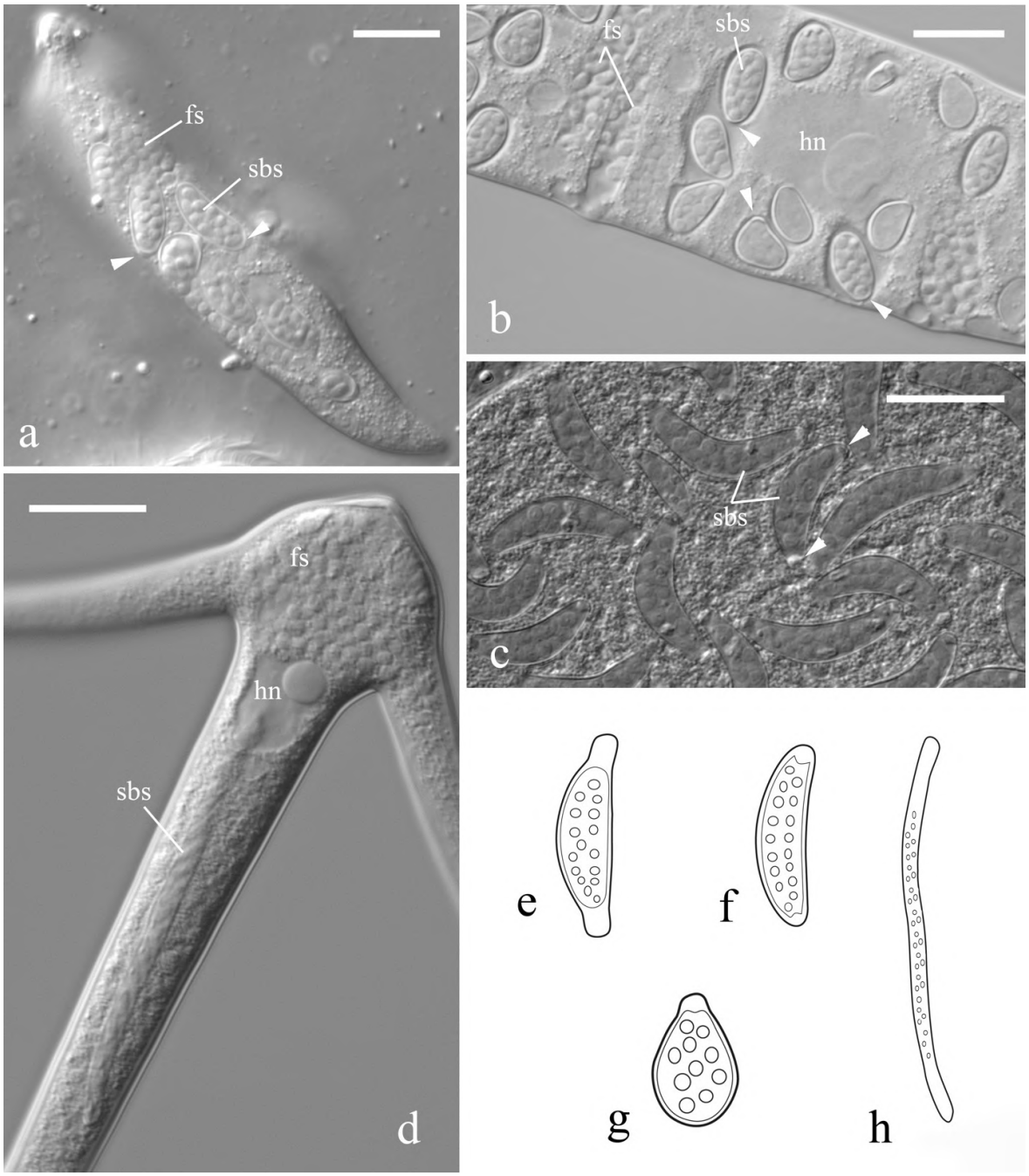


Figure 93 – The morphological features of the representatives of the family *Metchnikovellidae*. a–d The spore sacs (arrowheads) and free spores (fs) of metchnikovellids in the cytoplasm of gregarines: *Metchnikovella dogieli* ex *Selenidium pygospionis* from the gut of the polychaete *Pygospio elegans* (a); *M. dobrovolskiji* ex *Selenidium pygospionis* ex *P. elegans* (b); *M. incurvata* ex *Polyrhabdina pygospionis* ex *P. elegans* (c); *Amphiamblys* sp. ex *Ancora sagittata* infecting *Capitella capitata* (d). Abbreviations: fs = free spores; hn = host nucleu; sbs = sac-bound spores; DIC, scale bars: 20 μm (a, c, d), 10 μm (b); e–h Schematic drawings showing general morphology of the spore sacs of the representatives of the family: *M. spionis*, the type species (e), *M. incurvata* (f), *Caulleryetta mesnili* (g), *Amphiamblys* sp. (h). Redrawn from Caullery & Mesnil 1919 (e, f); Dogiel 1922 (g). Original drawing by E.V. Frolova (h).

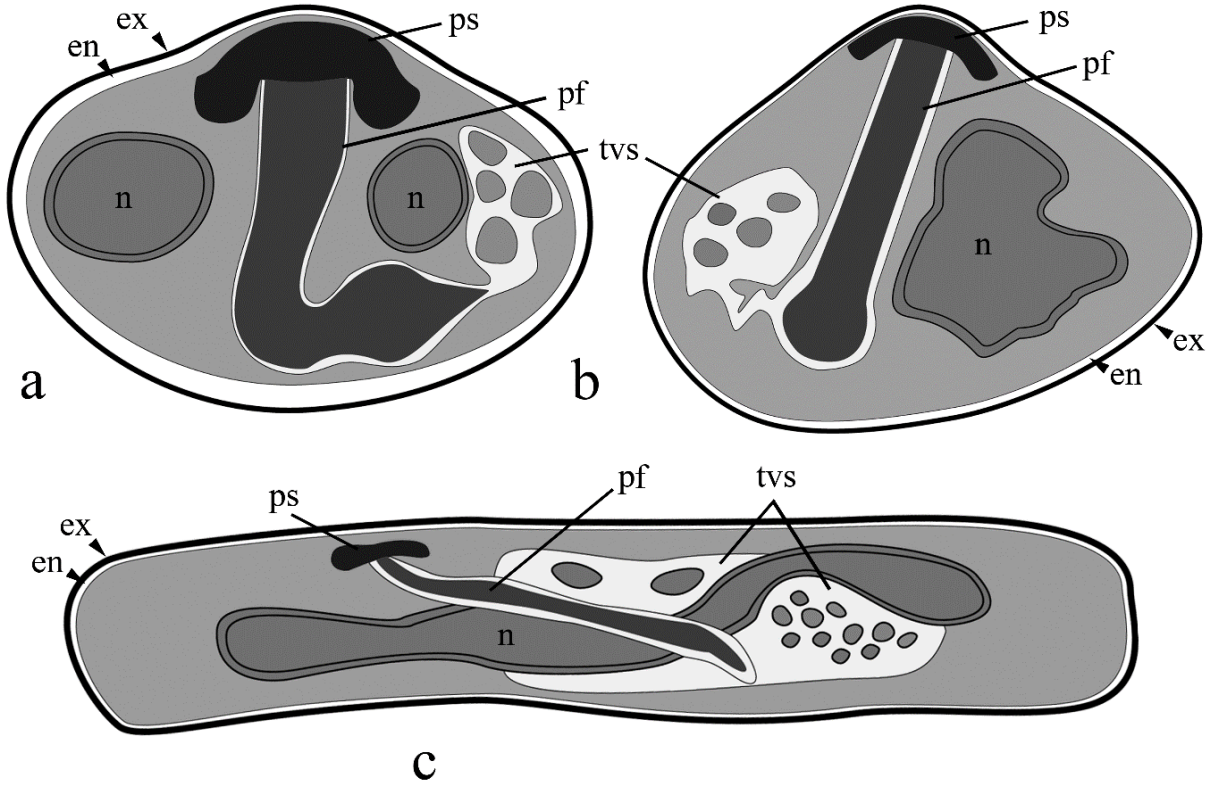


Figure 94 – Schematic drawings of mature spores of the genera comprising the family *Metchnikovellidae*. a *Metchnikovella.* b *Amphiamblys.* c *Desportesia*. Abbreviations: ex = exospore; en = endospore; n = nucleus; pf = polar filament; ps = polar sac; tvs = tubulovesicular system. Redrawn from Vivier 1975 (a), Issi 1986 (c) with some modifications. Schematic drawing of the spore of *Amphiamblys* (b) is based on the TEM micrographs from Larsson & Køie (2006).

Andreanna A.V. Simakova, C.R. Vossbrinck & Andreadis, J. Invert. Path. 99(3): 302–311 (2008).
Index Fungorum Identifier 531758; one epithet is listed in Index Fungorum (2025)

Type species – *Andreanna caspii* Simakova, Vossbrinck & Andreadis 2008.

Notes – Species are reported as obligate intracellular parasites of mosquitoes and are distributed in Asia. rDNA sequences are available in GenBank.

Becnelia T. Tonka & J. Weiser, Acta Protozool. 39: 251 (2000).
Index Fungorum Identifier 30086; two epithets are listed in Index Fungorum (2025)

Type species – *Becnelia sigarae* Tonka & Weiser 2000

Notes – Species are reported as obligate intracellular parasites of water bugs and are distributed in Europe. No sequences are available in GenBank.

Crepidulospora A.V. Simakova, T.F. Pankova & I.V. Issi, Parazitologiya 38(5): 477–478 (2004).
Index Fungorum Identifier 30468; one epithet is listed in Index Fungorum (2025)

Type species – *Crepidulospora beklemishevi* Simakova, Pankova, & Issi.

Notes – Species are reported as obligate intracellular parasites of mosquitoes in Asia, no sequences are available.

Cristulospora Khodzhaeva & Issi, (1989).
Index Fungorum Identifier 30469; three epithets are listed in Index Fungorum (2025)

Type species – *Cristulospora sherbani* Khodzhaeva & Issi 1989.

Notes – Species are reported as an obligate intracellular parasite of mosquitoes, Asia, no sequences are available.

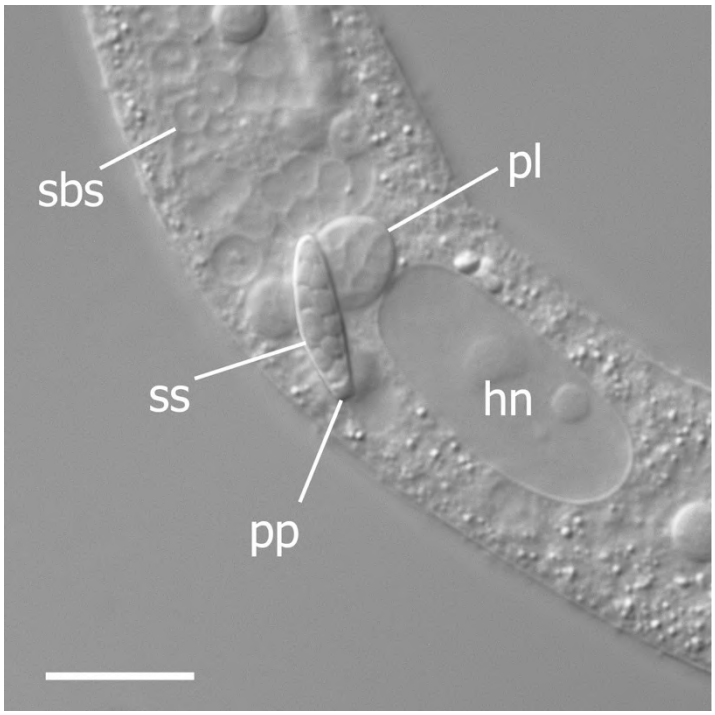


Figure 95 – *Mesnilivella travisiae*, a parasite of archigregarines *Selenidium* sp. from the polychaete *Travisia forbesii*. Abbreviations: hn = host nucleus; pl = plasmodium; pp = polar plug; sbs = sporoblasts; ss = spore sac. Scale bar: 10 µm. Reproduced with permission of the publisher from: Frolova et al. 2023.

Culicospora J. Weiser (1977)
Index Fungorum Identifier 30471; two epithets are listed in Index Fungorum (2025)

Type species – *Culicospora magna* (Kudo) Weiser 1977.

Notes – Species are reported as obligate intracellular parasites of mosquitoes in Europe, rDNA sequences are available in GenBank.

Culicosporella Weiser (1977).
Index Fungorum Identifier 30472; one epithet is listed in Index Fungorum (2025)

Type species – *Culicosporella lunata* (Hazard & Savage) Hazard & Savage 1977.

Notes – Species are reported as obligate intracellular parasites of mosquitoes; in Europe, rDNA sequences are available.

Dimeiospora A.V. Simakova, T.F. Pankova & I.V. Issi, Parazitologiya 37(2): 145–153 (2003).
Index Fungorum Identifier 30083; one epithet is listed in Index Fungorum (2025)

Type species – *Dimeiospora palustris* Simakova, Pankova & Issi 2003.

Notes – Species are reported as obligate intracellular parasites of mosquitoes in Asia, no sequences are available.

Edhazardia Becnel, Sprague & Fukuda, in: Becnel, Sprague, Fukuda & Hazard, (1989).
Index Fungorum Identifier 30478; one epithet is listed in Index Fungorum (2025)

Type species – *Edhazardia aedis* (Kudo) Becnel, Sprague & Fukuda 1989.

Notes – Species are reported as obligate intracellular parasites of mosquitoes, North America; rDNA sequences are available in GenBank. The genome of *Edhazardia aedis* is sequenced (51.35 Mb; 4190 protein-coding genes; AFBI00000000.3).

Hyalinocysta E.I. Hazard & Oldacre, Tech. Bull. U.S. Dep. Agric. 1530: 52 (1975).
Index Fungorum Identifier 30500; two epithets are listed in Index Fungorum (2025)

Type species – *Hyalinocysta chapmani* Hazard & Oldacre 1975.

Notes – Species are reported as obligate intracellular parasites of mosquitoes in North America. rDNA sequences are available in GenBank.

Intrapredatorus W.J. Chen, T.L. Kuo & S.T. Wu, Parasitol. Internat. 47(3): 183–193 (1998).
Index Fungorum Identifier 30504; two epithets are listed in Index Fungorum (2025)

Type species – *Intrapredatorus barri* W.J. Chen, T.L. Kuon & S.T. Wu 1998.

Notes – Species are reported as obligate intracellular parasites of mosquitoes in North America. rDNA sequences are available in GenBank.

Novothelohania T.G. Andreadis, A.V. Simakova, C.R. Vossbrinck, J.J. Shepard & Y.A. Yurchenko, J. Invert. Path. 109: 74 (2012).
Index Fungorum Identifier 92228; one epithet is listed in Index Fungorum (2025)

Type species – *Novothelohania ovalae* Andreadis, Simakova, Vossbrinck, Shepard & Yurchenko 2012.

Notes – Species are reported as an obligate intracellular parasite of mosquitoes in Asia. rDNA sequences are available in GenBank.

Parastempellia Khodzhaeva (1988).
Index Fungorum Identifier 30552; one epithet is listed in Index Fungorum (2025)

Type species – *Parastempellia odagmiae* Khodzhaeva 1988.

Notes – Species are reported as an obligate intracellular parasite of blackflies in Asia. No sequences are available.

Parathelohania Codreanu, Proceedings of the First International Congress of Parasitology: 602 (1966).
Index Fungorum Identifier 30553; 25 epithets are listed in Index Fungorum (2025)

Type species – *Parathelohania legeri* (E. Hesse) Codreanu 1966.

Notes – Species are reported as obligate intracellular parasites of mosquitoes in Europe and Asia. rDNA sequences are available in GenBank.

Trichoctosporea J.I.R. Larss., Arch. Protistenk. 144: 147–161 (1994).
Index Fungorum Identifier 30590; one epithet is listed in Index Fungorum (2025)

Type species – *Trichoctosporea pygopellita* Larss. 1994.

Notes – Species are reported as obligate intracellular parasites of mosquitoes in Europe and Asia. rDNA sequences are available in GenBank.

Tricornia J.K. Pell & E.U. Canning (1992)
Index Fungorum Identifier 30594; one epithet is listed in Index Fungorum (2025)

Type species – *Tricornia muhezae* J.K. Pell & E.U. Canning 1992.

Notes – Species are reported as obligate intracellular parasites of mosquitoes in Europe. No sequences are available.

Caudosporidae Weiser 1958
Index Fungorum Identifier 90175

Interfacial envelope either absent or present in sporulation but very delicate and ephemeral. Sporont produces 8 or 16 spores. Exospore with or without ornamentation (Sprague et al. 1992).

Family type – *Caudosporina* (Weiser 1946) Y.S. Tokarev & Issi

Basionym: *Caudospora* J. Weiser, Věstn. Česk. Spol. Zool. 10: 262 (1946) (Nom. illegit., Art. 53.1); Fig. 96

Ecology & life modes – Parasites of aquatic arthropods, predominately of black flies. A cosmopolitan parasite (Adler et al. 2000).

Notes – The phylogeny depicts the North American members of *Caudosporidae* as generally falling into eastern (*Caudospora pennsylvanica*, *C. polymorpha*, *C. simulii*, and *C. palustris*) and western groups (*C. alaskensis*, *C. stricklandi*, and *Weiseria sommermanae*), reflecting the geographic distribution of their hosts (Adler et al. 2000).

Caudosporina (J. Weiser) Y.S. Tokarev & Issi **nom. nov.**
Index Fungorum Identifier: IF903241

Basionym – *Caudospora* J. Weiser, Věstn. Česk. Spol. Zool. 10: 262 (1946) (Nom. illegit., Art. 53.1); Index Fungorum Identifier 30604.

Microsporidia form an arbitrary number of diplokarya (30–50) during sporogony. Spores are binucleate, oval with a caudal process. Spores of some species have outgrowths on the lateral surfaces and anterior pole (Canning & Vavra 2000).

Type species – *Caudosporina simulii* (J. Weiser) Y.S. Tokarev & Issi
Index Fungorum Identifier: IF903242

Note – Wijayawardene et al. (2020, 2024) included *Microsporidia* as a part of *Rozellomycota*. It is necessary to avoid *Caudospora* J. Weiser synonymy with the fungal taxon, *Caudospora* Starbäck 1889 (see Starbäck 1889). Thus, a new name is herewith introduced, *Caudosporina* (J. Weiser) Y.S. Tokarev & Issi. (Fig. 96). All species are specific to blackflies *Simuliidae*.

Other genera in *Caudosporidae*

Binucleospora A.M. Bronnvall & J.I.R. Larss., Eur. J. Protist. 31: 63–72 (1995).
Index Fungorum Identifier 30450; one epithet is listed in Index Fungorum (2025)

Type species – *Binucleospora elongata* Bronnvall & Larsson 1995.

Notes – Species are reported as obligate intracellular parasites of ostracods in Europe. No sequences are available.

Flabelliforma E.U. Canning, R. Killick-Kendrick & M. Killick-Kendrick, (1991).
Index Fungorum Identifier 30485; three epithets are listed in Index Fungorum (2025)

Type species – *Flabelliforma montana* Canning, R. Killick-Kendrick & M. Killick-Kendrick 1991.

Notes – Species are reported as obligate intracellular parasites of sandflies in Europe. rDNA sequences are available in GenBank.

Myrmecomorba R.M. Plowes, J.J. Becnel, E.G. LeBrun, D.H. Oi, S.M. Valles, N.T. Jones & L.E. Gilbert, J. Invert. Path. 129: 45–56 (2015).
Index Fungorum Identifier 622240; one epithet is listed in Index Fungorum (2025)

Type species – *Myrmecomorba nylanderiae* Plowes, Becnel, LeBrun, Oi, Valles, Jones & Gilbert 2015.

Notes – Species are reported as obligate intracellular parasites of the tawny crazy ant Nylanderia fulva in North America. rDNA sequences are available in GenBank.

Neoflabelliforma D.J. Morris & M.A. Freeman, Intern. J. Parasitol. 40: 367 (2010).
Index Fungorum Identifier 92227; three epithets are listed in Index Fungorum (2025)

Type species – *Neoflabelliforma aurantiae* Morris & Freeman 2010.

Notes – Species are reported as obligate intracellular parasites of oligochaetes, myxozoans and ctenopods in Europe and Asia. DNA sequences are available in GenBank.

Octosporea Flu, Centbl. Bakt. Parasitenk, Abt. I 57: 524 (1911).
Index Fungorum Identifier 30541; 19 epithets are listed in Index Fungorum (2025)

Type species – *Octosporea muscaedomesticae* Flu 1911.

Notes – Species are reported as obligate intracellular parasites of Diptera, Ephemeroptera, Hemiptera, Lepidoptera, Amphipoda and Cladocera in North America and Europe. rDNA sequences are available in GenBank.

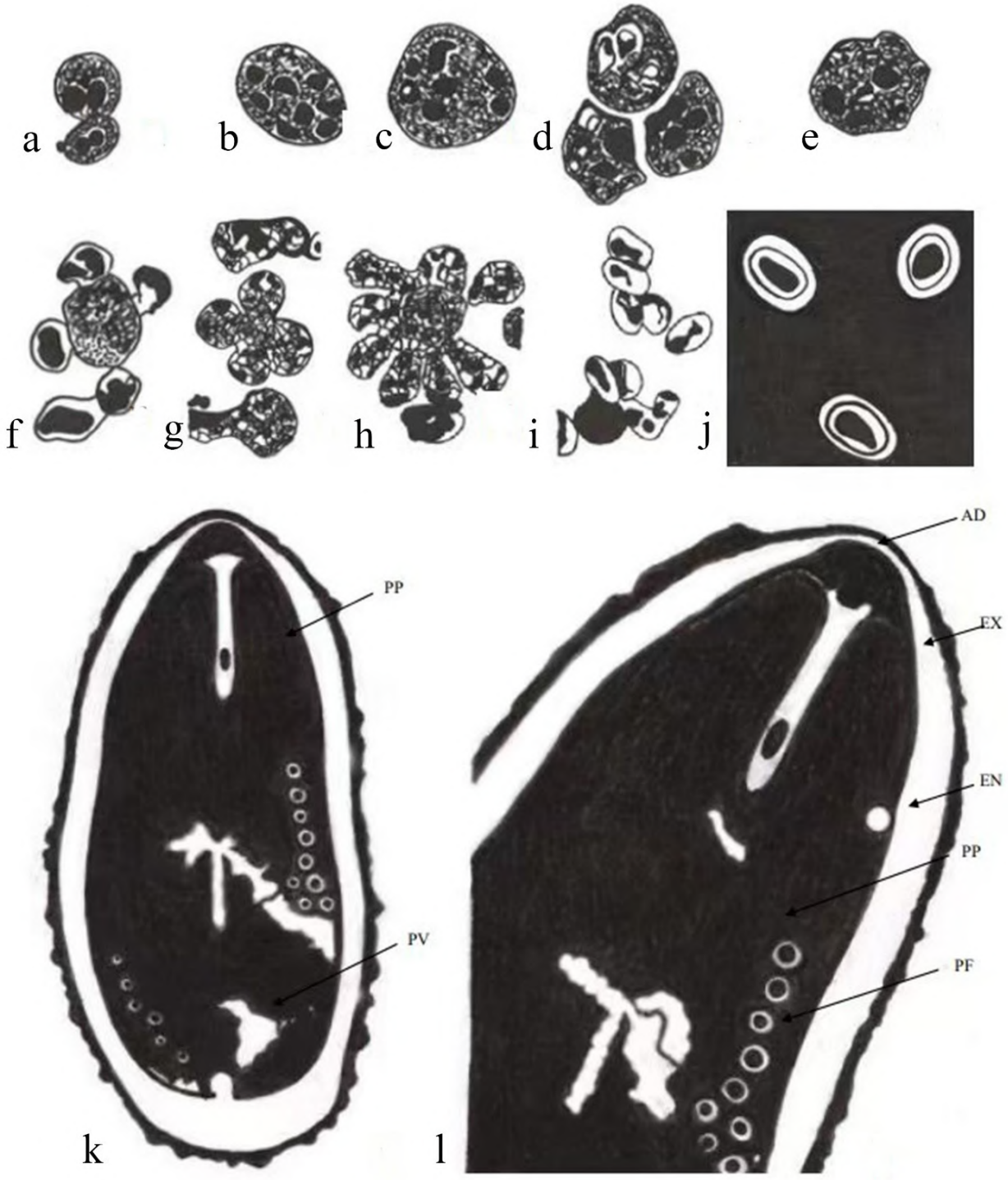


Figure 96 – Light (a–j) and transmission electron microscopy (k, l) of *Caudosporina* (*Caudospora*) *palustris*, including Giemsa-stained prespore developmental stages (a–h) and spores (i), fresh mount of spores in phase-contrast (j), and ultrathin TEM sections of spores (k, l) showing anchoring disc (AD), exospore (EX), endospore (EN), polaroplast (PP), posterior vacuole (PV), and polar filament (PF). Drawn according to Adler et al. (2000).

Polydispyrenia E.U. Canning & E.I. Hazard, (1982).
Index Fungorum Identifier 30560; two epithets are listed in Index Fungorum (2025)

Type species – *Polydispyrenia simulii* (Lutz & Splendore) Canning & Hazard 1982.

Notes – Species are reported as obligate intracellular parasites of blackflies in the family Simuliidae and are cosmopolitan parasites. rDNA sequences are available.

Ringueletium J.J. Garcia, (1990).
Index Fungorum Identifier 30568; one epithet is listed in Index Fungorum (2025)

Type species – *Ringueletium pillosa* Garcia 1990.

Notes – Species are reported as obligate intracellular parasites of blackflies in the family Simuliidae in South America. Sequence data is unavailable.

Scipionospora E.K.C. Bylén & J.I.R. Larss., Eur. J. Protist. 32: 104–115 (1995).
Index Fungorum Identifier 30570; one epithet is listed in Index Fungorum (2025)

Type species – *Scipionospora tetraspora* (Léger & Hesse) Bylén & Larss. 1995.

Notes – Species are reported as obligate intracellular parasites of Diptera, *Chironomidae* in Europe. Sequence data is unavailable.

Weiseria J.M. Doby & F. Saguez, C. r. hebd. Séanc. Acad. Sci., Paris 259: 3614 (1964)
Index Fungorum Identifier 30602; three epithets are listed in Index Fungorum (2025)

Type species – *Weiseria laurentii* Doby & Saguez 1964.

Notes – Species are reported as obligate intracellular parasites of blackflies in the family Simuliidae in Europe. Sequence data is unavailable.

Gurleyidae **(**Thelohan 1892) Sprague, Comparative Pathobiology (New York) 2: 1–510 (1977)
Index Fungorum Identifier 90509

A delicate interfacial envelope is present, produced by the parasite, sometimes becoming a delicate sporophorous vesicle. Sporogony polysporoblastic (disporoblastic?). Conspicuous xenoma formed, distinctive for genus (Sprague et al. 1992).

Family type – *Gurleya* Doflein, Zoologisches Jahrbuch Abteilungen Anat. 11: 281–350 (1898)

Ecology & life modes – obligate biotrophic parasites of aquatic arthropods. Distributed in Europe, Asia

Notes – Parasites are the sister group to Amblyosporidae (Refardt et al. 2002).

Gurleya Doflein, Zoologisches Jahrbuch Abteilungen Anat. 11: 281–350 (1898)
Index Fungorum Identifier 30490

Sporogony occurs in the sporphorus vesicle with the formation of four spores.

Notes – Fifteen species have been described from crustacea Branchiopoda, Europe (Frederich et al. 1996).

Other genera in *Gurleyidae*

Agglomerata J.I.R. Larss. & N.D. Yan, Arch. Protistenk. 135: 271–288 (1988).
Index Fungorum Identifier 30435; five epithets are listed in Index Fungorum (2025)

Type species – *Agglomerata sidae* (Jírovec) Larss. & Yan 1988.

Notes – *Agglomerata* species are reported as obligate intracellular parasites of Branchiopoda in Europe and Asia. rDNA sequences are available in GenBank.

Binucleata D. Refardt, E. Decaestecker, P.T.J. Johnson & Vávra, J. Eukary. Microbiol. 55(5): 393–408 (2008).
Index Fungorum Identifier 530374; one epithet is listed in Index Fungorum (2025)

Type species – *Binucleata daphniae* Refardt, Decaestecker, Johnson & Vávra 2008.

Notes – Species are reported as obligate intracellular parasites of Branchiopoda, in Europe and Asia. rDNA sequences are available in GenBank.

Conglomerata I. Vávra, P. Fiala, Krylová, Petrusek & Hyliš, J. Invert. Path. 159: 102 (2018).
Index Fungorum Identifier 633950; one epithet is listed in Index Fungorum (2025)

Type species – *Conglomerata obtusa* (Moniez) Vávra, Fiala, Krylová, Petrusek & Hyliš 2018.

Notes – Species are reported as obligate intracellular parasites of Branchiopoda in Europe. rDNA sequences are available in GenBank.

Episeptum J.I.R. Larss., Arch. Protistenk. 131: 257–279 (1986).
Index Fungorum Identifier 30482; six epithets are listed in Index Fungorum (2025)

Type species – *Episeptum inversum* Larss. 1986.

Notes – Species are reported as obligate intracellular parasites of caddisflies (Trichoptera) in Europe. rDNA sequences are available in GenBank.

Lanatospora Voronin, (1986).
Index Fungorum Identifier 30513; four epithets are listed in Index Fungorum (2025)

Type species – *Lanatospora macrocyclopis* (Voronin) Voronin 1986.

Notes – Species are reported as obligate intracellular parasites of Copepoda in Europe. rDNA sequences are available in GenBank.

Larssonia S.S. Vidtmann & Y.Y. Sokolova, Parasitologija 28: 202–314 (1994).
Index Fungorum Identifier 30514; two epithets are listed in Index Fungorum (2025)

Type species – *Larssonia obtusa* (Moniez) Vidtmann & Sokolova 1994

Notes – Species are reported as obligate intracellular parasites of Branchiopoda in Europe. rDNA sequences are available in GenBank.

Marssoniella Lemmerm., (1900)
Index Fungorum Identifier 30607; seven epithets are listed in Index Fungorum (2025)

Type species – *Marssoniella elegans* Lemmermann 1900.

Notes – Species are reported as obligate intracellular parasites of *Copepoda* in Europe. rDNA sequences are available in GenBank.

Norlevinea Vávra, J. Protozool. 31(4): 508–513 (1984).
Index Fungorum Identifier 30536; one epithet is listed in Index Fungorum (2025)

Type species – *Norlevinea daphniae* (Weiser) Vávra 1984.

Notes – Species are reported as an obligate intracellular parasite of *Branchiopoda* in Europe. rDNA sequences are available.

Paraepiseptum M. Hyliš, Oborník, J. Nebesářová & Vávra, Eur. J. Protist. 43(3): 221 (2007).
Index Fungorum Identifier 30085; four epithets are listed in Index Fungorum (2025)

Type species – *Paraepiseptum plectrocnemia*e Hyliš, Oborník, Nebesářová & Vávra 2007.

Notes – Species are reported as obligate intracellular parasites of the caddisfly (*Trichoptera*) in Europe. rDNA sequences are available.

Pseudoberwaldia Vávra, I. Fiala, P. Krylová, Petrusek & Hyliš, J. Invert. Path. 162: 46 (2019).
Index Fungorum Identifier 633952; one epithet is listed in Index Fungorum (2025) and no epithet is accepted in Species Fungorum (2025).

Type species – *Pseudoberwaldia daphniae* Vávra, Fiala, Krylová, Petrusek & Hyliš 2019.

Notes – Species are reported as obligate intracellular parasites of *Branchiopoda* in Europe. rDNA sequences are available in GenBank.

Senoma A.V. Simakova, T.F. Pankova, Y.S. Y.S. Tokarev & I.V. Issi, Protistology (Stuttgart) 4(2): 143 (2005).
Index Fungorum Identifier 30572; one epithet is listed in Index Fungorum (2025)

Type species – *Senoma globulifera* (Issi & Pankova) Simakova, Pankova, Y.S. Tokarev & Issi 2005.

Notes – Species are reported as obligate intracellular parasites of blood-sucking mosquitoes (Diptera, Culicidae) in Asia. rDNA sequences are available in GenBank.

Zelenkaia M. Hyliš, Oborník, J. Nebesářová & Vávra, J. Invert. Path. 114(1): 11–21 (2013).
Index Fungorum Identifier 581558; one epithet is listed in Index Fungorum (2025)

Type species – *Zelenkaia trichopterae* Hyliš, Oborník, Nebesářová & Vávra 2013.

Notes – Species are reported as obligate intracellular parasites of the caddisfly (*Trichoptera*) in Europe. rDNA sequences are available in GenBank.

Order *Neopereziida* Y.S. Tokarev & Issi
Berwaldiidae Simakova, Y.S. Tokarev & Issi, Parasitol. Res. 117: 1301 (2018)
Index Fungorum Identifier

All stages are in direct contact with the host cell cytoplasm. Sporogonial division presumably by binary fission. Surface of sporoblasts and exospore of immature spores bear additional ornamentation: coated bundles of fibrils or tight rows of thin tubular structures. Polaroplast bipartite with lamellar anterior and globular posterior parts. Polar tube slightly anisofilar (Simakova et al. 2018a).

Family type – *Berwaldia* Larsson 1981

Ecology & life modes – Obligate biotrophic pathogens of aquatic crustaceans (Vávra et al. 2017, Simakova et al. 2018a). *Fibrillanosema crangonycis* is vertically transmitted in its invasive amphipod host and is selectively retained during the invasion process (Galbreath et al. 2004).

Notes – *Berwaldiidae* is a monophyletic group including *Berwaldia* (family type) and sister to *Fibrillanosema* in Tubulinosematidae. The family comprises two genera, *Berwaldia* Larsson and *Fibrillanosema* Galbreath et al. A new genus *Fibrillaspora* was erroneously established despite its higher-level ultrastructural similarity to *Berwaldia*, as this new microsporidium was not related to the taxon annotated as *Berwaldia schaefernai* in GenBank under accession number AY090042 (Simakova et al. 2018a). However, the sequence was derived from a microsporidium that is not *Berwaldia* (Vávra et al. 2017). After the correctly annotated sequences of *Berwaldia* derived from the type specimens were compared to *Fibrillaspora*, it became evident that the respective species are congeneric and *Fibrillaspora* was a synonym of *Fibrillanosema* (Simakova et al. 2018b).

Berwaldia Larsson, Parasitology 83: 325–342 (1981)
Index Fungorum Identifier 30449

Merogony and sporogony stages with single, large nuclei. Disporoblastic. Spores are elongate oval or ovoid, monokaryotic, with conspicuously large nuclei and a posterior vacuole located terminally in some species or shifted to the spore side in some species. Spore covered by a thick endospore and a thin, single-layer exospore. Polar filament isofilar, coils forming a single row (except last 2–3 imperfect coils). Polaroplast bipartite, anterior lamellae closely arranged, posterior part less orderly and vesicular-like. Spores in individual sporophorous vesicles form a blister-like or chamber-like sachet around the spore. Sporophorous vesicle wall formed with material of variable structure (Vávra et al. 2017).

Type species – *Berwaldia singularis* Larsson

Notes – Five species are described from *Daphnia* spp. in Eurasia, for three of which rDNA sequences are available (Vávra et al. 2017, Simakova et al. 2018a).

Other genus in *Berwaldiidae*
Fibrillanosema G.M.J. Slothouber Galbreath, J.E. Sm., R.S. Terry, J.J. Becnel & A.M. Dunn, Intern. J. Parasitol. 34(2): 235–244 (2004).

Index Fungorum Identifier 30484; one epithet is listed in Index Fungorum (2025)

Type species – *Fibrillanosema crangonycis* G.M. Johanna, S. Galbreath, J.E. Sm., R.S. Terry, J.J. Becnel & A.M. Dunn 2004.

Notes – Species are reported as obligate intracellular parasites of amphipod crustaceans in North America and the UK. rDNA sequences are available in GenBank.

Neopereziidae Voronin emend. Issi, Y.S. Tokarev, Seliverstova & Voronin, Eur. J. Protistol. 48: 17–29 (2012)

Index Fungorum Identifier 904515

Microsporidia are either monomorphic, producing only one spore type: monokaryotic or diplokaryotic, or dimorphic, with two sporogonies and two spore types (monokaryotic and diplokaryotic), occurring within the same host. All developmental stages possess large nuclei. Meronts and meront/sporont transitional stage are diplokaryotic. The inner structure of monokaryotic and diplokaryotic spores in all genera is similar. Polaroplast is bipartite. Its anterior part is bounded by a membrane and covers the posterior one in a bell-like manner. The isofilar polar tube possesses numerous coils arranged in one to four rows; the additional rows are disposed alongside the middle coils of the first row. Diplokaryotic spores possess an additional coating on the exospore (Issi et al. 2012).

Family type – *Neoperezia* Issi & Voronin

Ecology & life modes – obligate biotrophic pathogens of moss-inhabiting animals (Canning et al. 2002), and dipteran insects (Issi et al. 2012). All species have been described in Europe.

Notes – Host specificity is excluded from the family diagnosis because it is an elusive taxonomic character, and the ability to switch hosts is widespread in microsporidia (Issi 2020). Though listed among the family representatives in some studies (Wijayawardene et al. 2020), *Bacillidium* has a strikingly different morphology and is clustered with *Janacekia* and *Jirovecia* (Weng et al. 2021). An independent family should be assigned to this group after further studies.

Neoperezia Issi & Voronin Parazitologiia 13: 150–158 (1979)

Index Fungorum Identifier 30534

Either monomorphic, producing only one monokaryotic spore type, or dimorphic, with two sporogonies and two spore types (monokaryotic and diplokaryotic) occurring within the same host and the same cell. All developmental stages possess large nuclei. Merogony is diplokaryotic, division by multiple fission. The meront/sporont transitional stage is diplokaryotic. The transition to monokaryotic sporogony proceeds with meiosis. The polaroplast is bipartite; its anterior part is filled with wavy-fibrillar structures, while the posterior one is lamellar. The sheath of the sporophorous vesicle is a thin membrane, single or folded, made up of thin parallel structures. The anchoring disc is fungiform. The polar tube is isofilar, the diameter of the first and the last coil is equal and the posterior three to four coils with the inner content of higher electron density (Issi et al. 2012).

Type species – *Neoperezia chironomi* Issi & Voronin

Notes – Due to their variable life cycles, two distinct species found in chironomid larvae were introduced as *Neoperezia* and *Semenovaia.* However, further morphological studies of the type species of these genera showed high-level similarity of the inner structure of the spores, and phylogenetic analyses based on SSU rRNA gene confirmed both genera are congeneric (Issi et al. 2012). Hence, Issi et al. (2012) suggested to synonymize the latter genus under the former (Issi et al. 2012). Both species are parasites of *Chironomus plumosus* (Insecta: Diptera) in Europe.

Other genera in *Neopereziidae*

Bryonosema E.U. Canning, D. Refardt, C.R. Vossbrinck, B. Okamura & A. Curry, Eur. J. Protist. 38(3): 264 (2002)

Index Fungorum Identifier 30453; two epithets are listed in Index Fungorum (2025)

Type species – *Bryonosema plumatellae* Canning, Refardt, Vossbrinck, Okamura & Curry.

Notes – Species are reported as obligate intracellular parasites of moss animals in Europe. rDNA sequences are available in GenBank.

Pseudonosema E.U. Canning, D. Refardt, C.R. Vossbrinck, B. Okamura & A. Curry, Eur. J. Protist. 38(3): 264 (2002).
Index Fungorum Identifier 30562; one epithet is listed in Index Fungorum (2025)

Type species – *Pseudonosema cristatellae* (Canning, Okamura & Curry) Canning, Refardt, Vossbrinck, Okamura & Curry 2002.

Notes – Species are reported as obligate intracellular parasites of moss-inhabiting animals in Europe. rDNA sequences are available in GenBank.

Schroedera D.J. Morris & A. Adams, Acta Protozool. 41(4): 395 (2002).
Index Fungorum Identifier 30569; two epithets are listed in Index Fungorum (2025)

Type species – *Schroedera plumatellae* Morris & Adams 2002.

Notes – Species are reported as obligate intracellular parasites of moss-inhabiting animals in Europe. rDNA sequences are available in GenBank.

Trichonosema E.U. Canning, D. Refardt, C.R. Vossbrinck, B. Okamura & A. Curry, Eur. J. Protist. 38(3): 264 (2002).
Index Fungorum Identifier 30592; two epithets are listed in Index Fungorum (2025)

Type species – *Trichonosema pectinatellae* Canning, Refardt, Vossbrinck, Okamura & Curry 2002.

Notes – Species are reported as obligate intracellular parasites of moss-inhabiting animals in Europe. rDNA sequences are available in GenBank.

Tubulinosematidae C. Franzen, S. Fisch., Schröd., J. Schölmerich & S. Schneuwly emend. Y.S. Tokarev & Issi in Wijayawardene et al. Mycosphere 11(1): 1060–1456 (2020)
Index Fungorum Identifier 90619

The parasites develop in direct contact with the host cell cytoplasm. The nuclei possess diplkaryotic arrangement. The plasmodia are not formed. The spores are typical of canonical microsporidia. The polar tube is slightly anisofilar, the last coils are slightly smaller in diameter. The polar tube coils are arranged in 1–3 layers on both sides of the spore.

Family type – *Tubulinosema* C. Franzen, S. Fisch., Schröd., J. Schölmerich & S. Schneuwly

Ecology & life modes – Obligate biotrophic pathogens of insects of the orders Orthoptera, Diptera, Lepidoptera, Hymenoptera, and Coleoptera (Franzen et al. 2006, Issi et al. 2008, Sokolova & Fuxa 2008, Bjørnson et al. 2011, Malysh et al. 2013), as well as *Crustacea* (Y.S. Tokarev et al. 2018). Cases of human infections are described in *Anncaliia* (Visvesvara et al. 1999) and *Tubulinosema* (see below).

Notes – The family includes three genera comprising a monophyletic lineage based upon SSU rRNA gene sequences (Franzen et al. 2005) in a sister position to *Berwaldiidae*, both families share a morphological trait of fine tubules or fibrils composing an outer layer of developmental stages.

Tubulinosema C. Franzen, S. Fisch., Schröd., J. Schölmerich & S. Schneuwly, Journal of Eukaryotic Microbiology. 52(2): 141–152 (2005)
Index Fungorum Identifier 30595

Spores are ovoid or slightly pyriform. The polar tube coils are arranged in 1–2 layers. The exospore is thick, thinner over the anchoring disc. The genus name reflects the presence of small tubuli on the surface of late meronts (Franzen et al. 2006b), also found on the spore surface (Issi et al. 2008).

Type species – *Tubulinosema ratisbonensis* Franzen, Fisch., Schröd., Schölmerich & Schneuwly

Notes – Members of this family have been described from locusts (Franzen et al. 2006b, Issi et al. 2008), moths (Malysh et al. 2013), ladybeetles (Bjørnson et al. 2011), fruit flies (Franzen et al. 2005, Biganski et al. 2021) and parasitoid wasps (Franzen et al. 2006a). The parasites display high prevalence rates during lepidopteran host outbreaks in nature (Malysh et al. 2018) and induce fruit fly colony collapse in the lab (Niehus et al. 2012). Two cases of infection in immunocompromised human patients were reported induced by a microsporidium most closely related to *T. acridophagus* from locusts (Choudhary et al. 2011, Meissner et al. 2012). Draft genome sequence of 7.5 Mb, including a total of 3082 protein-encoding genes and an array of transposable elements, is available for the type species (RCSS00000000.1 *fide* Polonais et al. 2019).

Other genera in *Tubulinosematidae*

Anncaliia I.V. Issi, S.V. Krylova & V.M. Nikolaeva, Parazitologiya 27(2): 127–133 (1993).
Index Fungorum Identifier 30444; seven epithets are listed in Index Fungorum (2025)

Type species – *Anncaliia meligethi* (Issi & Radishcheva) Issi, Krylova & Nikolaeva 1993.

Notes – Species are reported as obligate intracellular parasites of insects, crustaceans, and mammals, including humans (Index Fungorum 2025). Distribution is cosmopolitan. Sequences are available, including complete annotated genome sequences of three strains of *A. algerae* (reference genome of *A. algerae* PRA339 isof 12.1623 Mb in size with 3661 protein-encoding genes - GCA_000385875.2).

Kneallhazia Sokolova & Fuxa, Parasitology 135: 924 (2008).
Index Fungorum Identifier 529081; two epithets are listed in Index Fungorum (2025), and no epithet is accepted in Species Fungorum (2025).

Type species – *Kneallhazia solenopsae* (Knell, Allen & Hazard) Sokolova & Fuxa 2008.

Notes – Species are reported as obligate intracellular parasites of ants in North America. rDNA sequences are available in GenBank.

Order *Ovavesiculida* Y.S. Tokarev & Issi

Ovavesiculidae Sprague, Becnel & Hazard emend. Y.S. Tokarev & Issi, in Wijayawardene et al. Mycosphere 11(1): 1060–1456 (2020)
Index Fungorum Identifier 90601

An interfacial envelope of uncertain origin is present during sporulation, more or less persistent as a polysporophorous vesicle. Distinguishing characters: after nuclear dissociation, 4 nuclear divisions produce a sporogonial plasmodium with 32 nuclei; plasmodium divides into 32 sporoblasts (extracted from Sprague et al. 1992).

Family type – *Ovavesicula* Andreadis & Hanula

Ecology & life modes – obligate biotrophic pathogens of insects (Andreadis & Hanula 1987)

Notes – At the time when the monotypic family and genus were established, molecular data for this and related species were not available. When the SSU rRNA sequence information was acquired, three genera showed monophyly, one of them belonging to the currently established family. The priority of this higher rank taxonomy was respected. This taxon was further used as the type for the establishment of the order of *Ovavesiculida* in a recent re-classification (Wijayawardene et al. 2020).

Ovavesicula Andreadis & Hanula 1987, J. Protozool. 34(1): 15–21 (1987)
Index Fungorum Identifier 30548

Meronts with diplokaryotic nuclei and in direct contact with the host cell cytoplasm. Merogony by binary fission of diplokaryotic cells. Sporonts are surrounded by a thick sporophorous vesicle and at maturity contain 32 unpaired nuclei. Karyokinesis of sporont nuclei is synchronous and cytokinesis of sporogonial plasmodia does not take place until nuclear division is

complete. Spores are uninucleate and are regularly formed in groups of 32 (extracted from Andreadis & Hanula 1987).

Type species – *Ovavesicula popilliae* Andreadis & Hanula.

Notes – Based upon analysis of the SSU rRNA gene sequence, *Ovavesicula* is a distant sister group to *Paranosema* and *Antonospora* that corresponds to the original morphological description, as both species are distinguished from *Ovavesicula* according to structure and life cycle (Vossbrinck & Andreadis 2007).

Other genera in *Ovavesiculidae*

Antonospora I. Fr., R.J. Paxton, J. Tengö, J.A. da Silva, S.B. Slemenda & N.J. Pieniazek, Eur. J. Protist. 35: 183–193 (1999).

Index Fungorum Identifier 30445; three epithets are listed in Index Fungorum (2025)

Type species – *Antonospora scoticae* Fr., Paxton, Tengö, da Silva, Slemenda & Pieniazek 1999.

Notes – Species are reported as obligate intracellular parasites of hymenopterans. Distribution is cosmopolitan (Fries et al. 1999). rDNA sequences are available in GenBank.

Paranosema Y.Y. Sokolova, V.V. Dolgikh, E.V. Morzhina, E.S. Nassonova, I.V. Issi, R.S. Terry, J.E. Ironside, J.E. Sm. & C.R. Vossbrinck, J. Invert. Path. 84(3): 159–172 (2003).

Index Fungorum Identifier 30550; three epithets are listed in Index Fungorum (2025) and no epithet is accepted in Species Fungorum (2025).

Type species – *Paranosema grylli* (Sokolova, Selezniov, Dolgikh & Issi) Sokolova, Dolgikh, Morzhina, Nassonova, Issi, Terry, Ironside, Sm. & Vossbrinck 2003.

Notes – Species are reported as obligate intracellular parasites of hymenopterans, cosmopolitan, rDNA sequences are available in GenBank.

Glugeida Gurley emend. Y.S. Tokarev & Issi

Facilisporidae Jones, Prosperi-Porta & Kim, Journal of Eukaryotic Microbiology. 99(3): 206–217 (2012)

Index Fungorum Identifier 549434

All developmental stages are monokaryotic. Merogonic and sporogonic replication by binary fission. Developmental stages are in direct contact with the host cell cytoplasm. Diplosporoblasts produce ovoid spores. Polar filament with 3–5 coils in one rank.

Family type – *Facilispora* Jones, Prosperi-Porta & Kim

Ecology & life modes – Obligate biotrophic hyperparasite of sea lice from fishes in North America (Jones et al. 2012).

Notes – The host specificity is excluded from the family diagnosis because it is an elusive taxonomic character, as host switch ability is underestimated in microsporidia. A phylogenetic analysis resolved the SSU rDNA sequence in a unique lineage most similar to microsporidia from marine and brackish water crustaceans (Jones et al. 2012).

Facilispora Jones, Prosperi-Porta & Kim, Journal of Eukaryotic Microbiology. 99(3): 206–217 (2012)

Index Fungorum Identifier 549432

With characteristics of the family.

Type species – *Facilispora margolisii*;

Glugeidae Gurley Bull. US Fish Commiss. 11: 407–402 (1891) emend. Y.S. Tokarev & Issi, in Wijayawardene et al. Mycosphere 11(1): 1060–1456 (2020)

Index Fungorum Identifier 90417

A delicate interfacial envelope is present, produced by the parasite, sometimes becoming a delicate sporophorous vesicle. Sporogony polysporoblastic. Conspicuous xenoma formed, distinctive for genus (Sprague et al. 1992).

Family type – *Glugea* Thélohan

Ecology & life modes – Obligate biotrophic pathogens of fish, amphibians, insects, and crayfish (Paperna & Lainson 1995, Lange et al. 1996, Sanders et al. 2012, Bojko et al. 2020b, Liu et al. 2021).

Notes – Bojko et al. (2022) recently revised the family and accepted *Glugea*, *Loma*, *Pseudoloma*, and *Ichthyosporidium* based on molecular data analyses.

Glugea Thélohan, C. r. hebd. Séanc. Acad. Sci., Paris 112: 168 (1891)
Index Fungorum Identifier 30487

Spores are elongated or ovoid. The polar tube coils are isofilar, arranged in 1–4 layers. The exospore is thin. Polaroplast lamellate is bipartite, and the posterior vacuole generally occupies nearly half of the spore volume.

Type species – *Glugea microspora* Thélohan 1891

Notes – Several species of *Glugea* have been reported as parasites of cultured fish, including *Glugea plecoglossi* in cultured ayu, *Plecoglossus altivelis altivelis* in Japan and China, and unidentified species in groupers, *Epinephelus* spp.

Other genera in *Glugeidae*

Alloglugea I. Paperna & R. Lainson, Dis. Aquat. Org. 23: 13 (1995).
Index Fungorum Identifier 523096; six epithets are listed in Index Fungorum (2025)

Type species – *Alloglugea bufonis* Paperna & Lainson 1995.

Notes – Species are reported as obligate intracellular parasites of amphibia. Sequence data are unavailable.

Amazonspora C. Azevedo & E. Matos, J. Parasit. 89(2): 336–341 (2003).
Index Fungorum Identifier 30439; one epithet is listed in Index Fungorum (2025)

Type species – *Cercospora lupini* Narayan, Kharwar & Singh 2001.

Notes – Species are reported as obligate intracellular parasites of fish. Sequences are unavailable.

Cambaraspora Bojkoa, Behringer, Molere, Strattond & Reisingerd, J. Invert. Path. 171(no. 107345): 8 (2020).
Index Fungorum Identifier 636241; one epithet is listed in Index Fungorum (2025)

Type species – *Cambaraspora floridanus* Bojkoa, Behringer, Molere, Strattond & Reisingerd 2020.

Notes – Species are reported as obligate intracellular parasites of crayfish.

Ichthyosporidium Caullery & Mesnil, C. r. Séanc. Soc. Biol. 58: 640 (1905).
Index Fungorum Identifier 20279; six epithets are listed in Index Fungorum (2025)

Type species – *Ichthyosporidium giganteum* (Thélohan) Swarczewsky in need of revision as suggested by researchers (Sander et al. 2012).

Notes – Species are reported as obligate intracellular parasites of fish. Sequences are available, including the complete annotated genome sequences of *P. neurophilia* of 5.25 Mb.

Johenrea C.E. Lange, J.J. Becnel, E. Razafindratiana, J. Przybyszewski & H. Razafindrafara, J. Invert. Path. 68(1): 28–40 (1996).
Index Fungorum Identifier 30509; one epithet is listed in Index Fungorum (2025)

Type species – *Johenrea locustae* Lange, Becnel, Razafindratiana, Przybyszewski & Razafindrafara 1996.

Notes – Species are reported as obligate intracellular parasites of insects. Sequences are unavailable.

Loma C.M. Morrison & R. Sprague, Journal of Fish Diseases 4(1): 30 (1981)
Index Fungorum Identifier 30517; 31 epithets are listed in Index Fungorum (2025), and eight epithets are accepted in Species Fungorum (2025).

Type species – *Loma morhuae* Morrison & Sprague 1981.

Notes – Species are reported as obligate intracellular parasites of fish. Sequences are available.

Parapleistophora Issi, Kadyrova, Pushkar, Khodzhaeva & Krylova, (1990).
Index Fungorum Identifier 30551; one epithet is listed in Index Fungorum (2025)

Type species – *Parapleistophora ectospora* Issi, Kadyrova, Pushkar, Khodzhaeva & Krylova 1990.

Notes – Species are reported as obligate intracellular parasites of fish. Sequences are unavailable.

Pseudoloma J.L. Matthews, A.M.V. Br., K. Larison, J.K. Bishop-Stewart, P. Rogers & M.L. Kent, Journal of Eukaryotic Microbiology. 48(2): 227–233 (2001).
Index Fungorum Identifier 30561; one epithet is listed in Index Fungorum (2025), and no epithet accepted in Species Fungorum (2025).

Type species – *Pseudoloma neurophilia* Matthews, Br., Larison, Bishop-Stewart, Rogers & Kent 2001.

Notes – Species are reported as obligate intracellular parasites of fish. Sequences are available, including the complete annotated genome sequences of *P. neurophilia* of 5.25 Mb.

Myosporidae Stentiford, Bateman, Small, Moss, Shields, Reece & Tuck, Int. J Parasitol. 10:1443 (2010)
Index Fungorum Identifier 900402

Microsporidian parasites, diplosporoblastic, diplokaryotic, monomorphic, associated with host cell cytoplasm. Spores are rod-shaped to cylindrical (Stentiford et al. 2010).

Family type – *Myospora* Stentiford, Bateman, Small, Moss, Shields, Reece & Tuck

Ecology & Life modes – obligate biotrophic parasites of crustaceans.

Myospora G.D. Stentiford, K.S. Bateman, H.J. Small, J. Moss, Shields, Reece & I. Tuck, Intern. J. Parasitol. 40(12): 1433–1446 (2010)
Index Fungorum Identifier 584120

Type species – *Myospora metanephrops* Stentiford, Bateman, Small, Moss, Shields, Reece & Tuck, Intern. J. Parasitol. 40(12): 1433–1446 (2010)

Pereziidae Loubes, Maurand, Comps & Campillo, (1977) emend. Y.S. Tokarev & Issi, in Wijayawardene et al. Mycosphere 11(1): 1060–1456 (2020)
Index Fungorum Identifier 90602

Interfacial envelope absent. Sporogonial plasmodium moniliform (Sprague 1977).

Family type – *Perezia* Léger & Duboscq

Ecology & life modes – Obligate biotrophic pathogens of gregarines (Sprague 1992), insects of the orders of *Diptera* (Bylén & Larsson 1994a), and crustaceans (Han et al. 2016, Sokolova & Hawke 2016, Olson et al. 1994, Sokolova et al. 2023). Cases of gregarine infection are described in the type species of *Perezia*, and insect infection occurred only in *Pernicivesicula* (Bylén & Larsson 1994a).

Phylogeny – The family includes four genera comprising a monophyletic lineage based upon SSU rRNA gene sequence (Small et al. 2019, Sokolova et al. 2023).

Perezia Léger & Duboscq, Archs Zool. exp. gén., sér. 5 1: XI (1909)
Index Fungorum Identifier 30555

The parasites develop in direct contact with the host cell cytoplasm. All life stages possess diplokaryotic nucleus. Merogonial plasmodia develop to sporogonial plasmodia by binary division. The plasmodia are not formed. The spores are ovoid. The polar tube is isofilar, coiled with 13– 14 turns. The last coils are slightly smaller in diameter. The polar tube coils are arranged in 1– 3 layers on both sides of the spore (Sprague et al. 1992). Small subunit ribosomal RNA gene sequence of the type species is not available, but *P. nelsoni* (GenBank accession KX856426) and an unidentified species (GenBank accession KP825331) were described with molecular characteristics, which would be helpful for the taxonomy of *Perezia* spp. (Han et al. 2016, Sokolova & Hawke 2016).

Type species – *Perezia lankesteriae* Léger & Duboscq

Notes – The parasites are described from gregarines (Sprague 1992) and crustaceans (Han et al. 2016, Sokolova & Hawke 2016).

Other genera in *Pereziidae*

Ameson V. Sprague, Comparative Pathobiology (New York): 279 (1977).
Index Fungorum Identifier 30441; ten epithets are listed in Index Fungorum (2025)

Type species – *Ameson michaelis* Sprague.

Notes – Species are reported as obligate intracellular parasites of crustaceans, rDNA sequences are available in GenBank, as well as a complete annotated genome sequence of *A. portunus* of 13.7 Mb.

Nadelspora Olson, Tiekotter & Reno, J. Eucaryot. Microbiol. 41(4):359 (1994)
Index Fungorum Identifier 900403; one epithets are listed in Index Fungorum (2025) and one epithet is accepted in Species Fungorum (2025).

Type species – *Nadelspora canceri* Olson, Tiekotter & Reno, J. Eucaryot. Microbiol. 41(4):359 (1994)

Notes – Species are obligate intracellular parasites of crustaceans, and rDNA sequences are available in GenBank

Pernicivesicula E.K.C. Bylén & J.I.R. Larss., Eur. J. Protist. 30: 139–150 (1994).
Index Fungorum Identifier 522826; one epithet is listed in Index Fungorum (2025)

Type species – *Pernicivesicula gracilis* Bylén & Larss. 1994.

Notes – Species are reported as obligate intracellular parasites of *Diptera* species. Sequences are unavailable.

Pleistophoridae Doflein 1901 emend. Y.S. Tokarev & Issi, in Wijayawardene et al. Mycosphere 11(1): 1060–1456 (2020)
Index Fungorum Identifier 90606

Interfacial envelope, consisting mostly or entirely of host material, present on meront; envelope is close-fitting and dividing during merogony, separating at the onset of sporogony, persisting more or less as a polysporophorous vesicle. Sporogony polysporoblastic. Conspicuous xenoma not formed (Sprague 1992).

Ecology & life modes – Obligate biotrophic pathogens of fishes (Sprague 1992, Diamant et al. 2010), insects of the orders of Diptera (Matos et al. 2006), reptiles, crustaceans, trematodes, as well as mammals (Vávra et al. 2011, Bojko et al. 2020a, Stratton et al. 2022a). Human infections are mainly reported in *Trachipleistophora* (Curry et al. 2005).

Family type – *Pleistophora* Gurley

Notes – The family includes seven genera comprising a monophyletic lineage based upon the SSU rRNA gene sequence (Bojko et al. 2022). Genomes are sequenced for *T. hominis* (8.5 Mb; 3253 protein-coding genes) and *Vavraia culicis* (6.12 Mb; 2825 protein-coding genes).

Pleistophora Gurley, Bull. US Fish Commiss. 11: 410 (1893)
Index Fungorum Identifier 30558

All life stages possess monokaryotic nucleus. Numerous whitish xenomas are easily observed in fish. Spores are dimorphic with microspores and macrospores. The polar tube coils are arranged mostly in 1–2 rows, rarely in 2–3 rows (Canning & Nicholas 1980).

Type species – *Pleistophora typicalis* Gurley

Other genera in *Pleistophoridae*

Dasyatispora A. Diamant, M. Goren, M.B. Yokes, B.S. Galil, Y. Klopman, D. Huchon, A. Szitenberg & S.Ü. Karhan, Dis. Aquat. Org. 91(2): 147 (2010).
Index Fungorum Identifier 92221; one epithet is listed in Index Fungorum (2025)

Type species – *Dasyatispora levantinae* Diamant, Goren, Yokes, Galil, Klopman, Huchon, Szitenberg, Karhan 2010.

Notes – Species are reported as obligate intracellular parasites of cartilaginous fishes. rDNA sequences are available.

Heterosporis G. Schub., Z. ParasitenkParasitenkd. 32: 59 (1969).
Index Fungorum Identifier 30495; six epithets are listed in Index Fungorum (2025), and no epithet is accepted in Species Fungorum (2025).

Type species – *Heterosporis finki* G. Schub. 1969.

Notes – Species are reported as obligate intracellular parasites of cartilaginous fishes. Sequences are available.

Myosporidium E. Baquero, M. Rubio, I.N.S. Moura, N.J. Pieniazek & R. Jordana, Journal of Eukaryotic Microbiology. 52(6): 476–483 (2005).
Index Fungorum Identifier 30528; three epithets are listed in Index Fungorum (2025)

Type species – *Myosporidium merluccius* Baquero, Rubio, Moura, Pieniazek & Jordana 2005.

Notes – Species are reported as obligate intracellular parasites of fishes. rDNA sequences are available in GenBank.

Ovipleistophora M. Pekkarinen, Lom & F. Nilsen, Dis. Aquat. Org. 48(2): 133–142 (2002).
Index Fungorum Identifier 30549; four epithets are listed in Index Fungorum (2025)

Type species – *Ovipleistophora mirandellae* (Vaney & Conte) Pekkarinen, Lom & Nilsen 2002.

Notes – Species are reported as obligate intracellular parasites of fishes, crustaceans, and trematodes. rDNA sequences are available in GenBank.

Trachipleistophora W.S. Hollister, E.U. Canning, E. Weidner, A.S. Field, J. Kench & D.J. Marriott, Parasitology 112: 143–154 (1996).
Index Fungorum Identifier 30589; three epithets are listed in Index Fungorum (2025)

Type species – *Trachipleistophora hominis* Hollister, Canning, Weidner, Field, Kench & Marriott 1996.

Notes – Species are reported as obligate intracellular parasites of mammals and insects. rDNA sequences are available in GenBank.

Vavraia J. Weiser 1977
Index Fungorum Identifier 30599; ten epithets are listed in Index Fungorum (2025)

Type species – *Vavraia culicis* (J. Weiser) J. Weiser 1977.

Notes – Species are reported as obligate intracellular parasites of insects (Diptera) and reptiles (salamander). rDNA and protein-coding gene sequences, as well as the genome assembly for *Vavraia culicis* subsp. *floridensis* (AEUG00000000.1) are available in GenBank.

Spragueidae Weissenberg 1976 emend. Y.S. Tokarev & Issi, in Wijayawardene et al. Mycosphere 11(1): 1060–1456 (2020)

Index Fungorum Identifier 90613

Spores of two morphological types occur in some species. Interfacial envelope absent. A distinctive xenoma formed. Parasite develops in a colony confined to a specific location in a host cell, first forming uninucleate (haplophasic) spores, later binucleate (dihaplophasic) spores in centre of colony. The infected host cell is very hypertrophic (Sprague et al. 1992).

Family type – *Spraguea* Weissenberg, Comp. Pathobiol., I, Biology of the Microsporidia: 216 (1976)

Ecology & life modes – obligate biotrophic pathogens of fishes (Casal et al. 2008, Lom et al. 2000, Liu et al. 2019) and crustaceans (Ding et al. 2016, Sokolova & Overstreet 2018).

Notes – The family includes eight genera comprising a monophyletic lineage based upon the SSU rRNA gene sequence (Bojko et al. 2022). The genomes are sequenced for eleven strains of *S. lophii*, revealing the basis of host-microsporidian interactions (Campbell et al. 2013, Williams et al. 2016). Reference genome: *S. lophii* ASM188794v1 (5.76 Mb; LDOQ01000000).).

Spraguea Weissenberg, Comp. Pathobiol., I, Biology of the Microsporidia: 216 (1976)

Index Fungorum Identifier 30577

Spraguea species commonly infect the nervous system of the host and lead to the formation of large assemblages of xenomas. Life stages develop in direct contact with host cell cytoplasm and possess monokaryotic nuclei. The early stages are merogonial plasmodia, which further develop to sporogonial plasmodia. Mature spores are uninucleate and ovoid and possess isofilar polar filaments arranged in one layer (Sprague et al. 1992).

Type species – *Spraguea lophii* (Doflein) R. Weissenb., Comp. Pathobiol., I, Biology of the Microsporidia: 216 (1976)

Notes – A small subunit ribosomal RNA gene sequence of the type species is available (GenBank accession KP825331).

Other genera in *Spragueidae*

Apotaspora Y.Y. Sokolova & R.M. Overstreet, J. Invert. Path. 157: 125–135 (2018).

Index Fungorum Identifier 631992; one epithet is listed in Index Fungorum (2025)

Type species – *Apotaspora heleios* Sokolova & Overstreet 2018.

Notes – Species are reported as obligate intracellular parasites of crustaceans and rDNA sequence is available.

Inodosporus R.M. Overstreet & E. Weidner, Z. Parasitenk. 44: 169 (1974).

Index Fungorum Identifier 30502; three epithets are listed in Index Fungorum (2025), and no epithet is accepted in Species Fungorum (2025).

Type species – *Inodosporus spraguei* R.M. Overstreet & E. Weidner 1974.

Notes – Species are reported as obligate intracellular parasites of crustaceans and fishes. rDNA sequences are available in GenBank.

Kabatana Lom, Dyková & Tonguthai, J. Parasit. 93(3): 655–660 (2000)

Index Fungorum Identifier 30511; five epithets are listed in Index Fungorum (2025)

Type species – *Kabatana arthuri* (Lom, Dyková & Shaharom) Lom, Dyková & Tonguthai 2000.

Notes – Species are reported as obligate intracellular parasites of fishes. RDNA sequences are available in GenBank.

Microgemma J.R. Ralphs & R.A. Matthews, J. Fish Dis. 9: 239 (1986).
Index Fungorum Identifier 30523; six epithets are listed in Index Fungorum (2025)

Type species – *Microgemma hepaticus* Ralphs & Matthews, J. Fish Dis. 9: 239 (1986)

Notes – Species are reported as obligate intracellular parasites of fish (Mansour et al. 2005). rDNA sequences are available.

Potaspora G. Casal, E. Matos, M.L. Teles-Grilo & C. Azevedo, Parasitology 135: 1053–1064 (2008).
Index Fungorum Identifier 30082; three epithets are listed in Index Fungorum (2025)

Type species – *Potaspora morhaphis* Casal, Matos, Teles-Grilo & Azevedo 2008.

Notes – Species are reported as obligate intracellular parasites of crustaceans and fishes. rDNA sequences are available in GenBank.

Pseudokabatana X.H. Liu, G.D. Stentiford, V.N. Voronin, H. Sato, A.H. Li & J.Y. Zhang, Parasitology Research 118(6): 1689–1699 (2019).
Index Fungorum Identifier 649127; one epithet is listed in Index Fungorum (2025)

Type species – *Pseudokabatana alburnus* Liu, Stentiford, Voronin, Sato, Li & Zhang, Parasitology Research 118(6): 1689–1699 (2019).

Notes – Species are reported as obligate intracellular parasites of fishes. rDNA sequences are available in GenBank.

Tetramicra R.A. Matthews & A.B.F. Matthews, J. Fish Diseases 3(6): 495–515 (1980).
Index Fungorum Identifier 30585; one epithet is listed in Index Fungorum (2025), and no epithet is accepted in Species Fungorum (2025).

Type species – *Tetramicra brevifilum* Matthews & Matthews 1980.

Notes – Species are reported as obligate intracellular parasites of fishes. rDNA sequences are available in GenBank.

Thelohaniidae Hazard & Oldacre, US. Dept. Agric. Tech. Bull. 1530: 104 emend. Y.S. Tokarev & Issi, in Wijayawardene et al. Mycosphere 11(1): 1060–1456 (2020)
Index Fungorum Identifier 89007

An interfacial envelope is present during sporulation, elaborated by the sporont, subpersistent as an octosporophorous vesicle. Sporogonial plasmodium various. Spores vary in shape and morphological detail (Sprague et al. 1992).

Family type – *Thelohania* Henneguya

Ecology & life modes – obligate biotrophic pathogens of crustaceans (Brown & Adamson 2006, Ovcharenko et al. 2010) and insects (Larsson 1986, 1990, Bylén & Larsson 1994b).

Notes – Several genera in the family have been transferred to new families based on molecular analyses; *Agmasoma* and *Helmichia* were accommodated in *Mrazekiidae*, *Hyalinocysta* and *Trichoctosporea* were transferred to *Amblyosporidae*, and *Inodosporus* was transferred to *Spragueidae* (Bojko et al. 2022). In addition, freshwater *Thelohania* species were removed to a new genus in a new family, while marine species were retained in the genus (Stratton et al. 2022b).

The family includes 16 genera comprising a monophyletic lineage based upon the present available SSU rRNA gene sequences of species of several genera (Bojko et al. 2022). The genome is sequenced for *Cucumispora dikerogammari* (32.41 Mb, 4599 protein-coding genes) (Cormier et al. 2021b).

Thelohania Henneguy, C. R. hebd. Séanc. Acad. Sci., Paris 114: 1554 (1892)
Index Fungorum Identifier 30586

Thelohania species usually infects the muscle tissue of the host and causes a white appearance and no xenomas are observed. Life stages are diplokaryotic and develop in direct contact with the host cell cytoplasm. Sporogony is octosporoblastic and occurs within the

sporophorous vesicle. Spores are ovoid or pyriform and possess isofilar polar filaments arranging in 1–2 layers (Sprague et al. 1992, Brown & Adamson 2006).

Type species – *Thelohania giardi* Henneguy

Other genera in *Thelohaniidae*

Bohuslavia J.I.R. Larss., Protistologica 21: 235–248 (1985).

Index Fungorum Identifier 30451; one epithet is listed in Index Fungorum (2025)

Type species – *Bohuslavia asterias* (Weiser) Larss. 1985.

Notes – Species are reported as obligate intracellular parasites of insects. Sequences are unavailable.

Chapmanium E.I. Hazard & Oldacre, Tech. Bull. U.S. Dep. Agric. 1530: 46 (1975).

Index Fungorum Identifier 30461; four epithets are listed in Index Fungorum (2025), and no epithets are accepted in Species Fungorum (2025).

Type species – *Chapmanium cirritus* Hazard & Oldacre 1975.

Notes – Species are reported as obligate intracellular parasites of insects. Sequences are unavailable.

Coccospora Wallr., Fl. crypt. Germ. (Norimbergae) 2: 176 (1833)

Index Fungorum Identifier 7717; 16 epithets are listed in Index Fungorum (2025)

Type species – *Coccospora aurantiaca* Wallr. 1833.

Notes – Species are reported as obligate intracellular parasites of insects. Sequences are unavailable.

Cucumispora M.O. Ovcharenko, K. Bacela, T. Wilkinson, J.E. Ironside, T. Rigaud & Wattier, Parasitology 137(2): 191–204 (2010).

Index Fungorum Identifier 565840; three epithets are listed in Index Fungorum (2025)

Type species – *Cucumispora dikerogammari* (Ovcharenko & Kurandina) Ovcharenko, Bacela, Wilkinson, Ironside, Rigaud & Wattier 2010.

Notes – Species are reported as obligate intracellular parasites of amphipods. RDNA sequences and the genome sequence for *C. dikerogammari* are available in GenBank.

Hyperspora G.D. Stentiford, Ramilo, E. Abollo, R. Kerr, K.S. Bateman, Feist, D. Bass & A. Villalba, Parasitology 144: 191 (2017).

Index Fungorum Identifier 626565; one epithet is listed in Index Fungorum (2025)

Type species – *Hyperspora aquatica* Stentiford, Ramilo, Abollo, Kerr, Bateman, Feist, Bass & Villalba 2017.

Notes – Species are reported as obligate intracellular parasites of crustaceans. Sequences are available.

Napamichum J.I.R. Larss. (1990).

Index Fungorum Identifier 30531; two epithets are listed in Index Fungorum (2025)

Type species – *Napamichum dispersum* (J.I.R. Larss.) J.I.R. Larss. 1990

Notes – Species are reported as obligate intracellular parasites of insects. Sequences are unavailable.

Octotetraspora Issi, Kadyrova, Pushkar, Khodzhaeva & Krylova (1990).

Index Fungorum Identifier 30542; one epithet is listed in Index Fungorum (2025)

Type species – *Octotetraspora paradoxa* Issi, Kadyrova, Pushkar, Khodzhaeva & Krylova 1990.

Notes – Species are reported as obligate intracellular parasites of insects. Sequences are unavailable.

Ormieresia C.P. Vivarès, G. Bouix & Manier, J. Protozool. 24(1): 91 (1977).
Index Fungorum Identifier 30545; one epithet is listed in Index Fungorum (2025)

Type species – *Ormieresia carcini* Vivarès, Bouix & Manier 1977

Notes – Species are reported as obligate intracellular parasites of crustaceans. Sequences are unavailable.

Orthothelohania Codreanu & Codr.-Balc., in Henneguy & Thélohan, Proceedings of the Third International Congress of Parasitology 1: 16 (1974).
Index Fungorum Identifier 30547; one epithet is listed in Index Fungorum (2025)

Type species – *Orthothelohania octospora* (Henneguy) Codreanu & Codr.-Balc. 1974

Notes – Species are reported as obligate intracellular parasites of insects. Sequences are unavailable.

Paradoxium G.D. Stentiford, S.H. Ross, R. Kerr, D. Bass & K.S. Bateman, J. Invert. Path. 130: 1–8 (2015).
Index Fungorum Identifier 547993; one epithet is listed in Index Fungorum (2025)

Type species – *Paradoxium irvingi* Stentiford, Ross, Kerr, Bass & Bateman 2015

Notes – Species are reported as obligate intracellular parasites of crustaceans. Sequence is available.

Pegmatheca E.I. Hazard & Oldacre, Tech. Bull. U.S. Dep. Agric. 1530: 79 (1975).
Index Fungorum Identifier 30554; two epithets are listed in Index Fungorum (2025)

Type species – *Pegmatheca simulii* Hazard & Oldacre 1975

Notes – Species are reported as obligate intracellular parasites of insects. Sequences are unavailable.

Resiomeria J.I.R. Larss., Protistologica 22: 379–398 (1986).
Index Fungorum Identifier 30567; one epithet is listed in Index Fungorum (2025)

Type species – *Resiomeria odonatae* Larss. 1986

Notes – Species are reported as obligate intracellular parasites of insects. Sequences are unavailable.

Spherospora J.J. Garcia, (1991).
Index Fungorum Identifier 30575; one epithet is listed in Index Fungorum (2025)

Type species – *Spherospora andinae* Garcia 1991.

Notes – Species are reported as obligate intracellular parasites of insects. Sequences are unavailable.

Systenostrema E.I. Hazard & Oldacre, Tech. Bull. U.S. Dep. Agric. 1530: 87 (1975).
Index Fungorum Identifier 30581; five epithets are listed in Index Fungorum (2025)

Type species – *Systenostrema tabani* Hazard & Oldacre 1975

Notes – Species are reported as obligate intracellular parasites of insects. Sequences are unavailable.

Unikaryonidae Sprague, in: Bulla, L. A., Cheng, T. C., eds. Comparative Pathobiology. Pienum Press, New York. 2: 1–510 (1977) emend. Y.S. Tokarev & Issi
Index Fungorum Identifier 90621

Interfacial envelope lacking. Sporogony disporoblastic or with moniliform plasmodium that is susceptible to interpretation as a stage in either binary or multiple division (Sprague 1977).

Family type – *Unikaryon* Canning

Ecology & life modes – obligate biotrophic pathogens of amphipod crustaceans, insects (Kohlmayr et al. 2003, Weiser et al. 2006), and hyperparasites of Platyhelminthes (Sokolova et al. 2021).

Notes – *Oligosporidium* was reassigned to the family *Nosematidae* based on a phylogenetic analysis (Y.S. Tokarev et al. 2020), and *Orthosomella* was transferred to the *Orthosomella*-like group (Dubuffet et al. 2021). The family includes four genera (*Unikaryon*, *Canningia*, *Larssoniella*, and *Dictyocoela*). The family seems to be a monophyletic lineage based upon the available SSU rRNA gene sequences of *Unikaryon* and *Dictyocoela*. However, more molecular data of *Canningia* and *Larssoniella* are required to completely reveal the phylogenetic relationships within this family (Bojko et al. 2022, Sokolova et al. 2021). Genome sequences of *Dictyocoela mulleri* (41.92 Mb; 6442 protein-coding genes; SDVU00000000.1), and *D. roeselum* (2.21 Mb; 1201 protein-coding genes; SDVW00000000.1), indicate independent evolution of feminization in microsporidia at the molecular genetic level and pave the way to study the evolution of symbiont-mediated feminization (Cormier et al. 2021a).

Unikaryon Canning, Lai & Lie, J. Protozool. 21: 19–25 (1974)
Index Fungorum Identifier 30597

Unikaryon includes exclusively hyperparasites of Platyhelminthes (Sokolova et al. 2021). All life stages are monokaryotic, and the early meronts are in direct contact with host cytoplasm (Azevedo & Canning 1987, Sprague et al. 1992). Sporogony is disporoblastic and sporophorous vesicle forms during these stages (Azevedo & Canning 1987). Spores are ovoid or slightly pyriform. Polar filaments are arranged in 1–2 rows.

Type species – *Unikaryon piriformis* Canning, Lai & Lie, 1974

Other genera in *Unikaryonidae*
Canningia J. Weiser, Wegenst. & Z. Žižka, Folia Parasit. 42: 7 (1995).
Index Fungorum Identifier 30458; two epithets are listed in Index Fungorum (2025)

Type species – *Canningia spinidentis* Weiser, Wegenst. & Žižka 1995.

Notes – Species are reported as obligate intracellular parasites of insects. Sequences are unavailable.

Dictyocoela R.S. Terry, J.E. Sm., R.G. Sharpe, T. Rigaud, D. Littlew., J.E. Ironside, Rollinson, Bouchon, MacNeil, J.T.A. Dick & A.M. Dunn, Proc. R. Soc. Lond., B. Biol. Sci. 271(no. 1550): 1783–1789 (2004).
Index Fungorum Identifier 30476; eight epithets are listed in Index Fungorum (2025), and no epithets are accepted in Species Fungorum (2025).

Type species – not indicated.

Notes – Species are reported as obligate intracellular parasites of amphipoda, rDNA sequences for eight described species, including numerous isolates of *D. berillonum*, *D. cavimanum*, *D. duebenum*, *D. mulleri* and *D. roeselum*, and numerous environmental sequences of unclassified *Dictyocoela* species as well as genome sequences for *D. mulleri* and *D. roeselum* are available in GenBank.

Larssoniella J. Weiser & L. David, Arch. Protistenk. 147(3–4): 405–410 (1997).
Index Fungorum Identifier 30515; two epithets are listed in Index Fungorum (2025), and no epithets are accepted in Species Fungorum (2025).

Type species – *Larssoniella resinellae* Weiser & David 1997.

Notes – Species are reported as obligate intracellular parasites of insects. Sequences are unavailable.

Nosematida Labbe emend. Y.S. Tokarev & Issi
Encephalitozoonidae Voronin, Arch. Protistenk. 137(4): 357–366 (1989)

Index Fungorum Identifier 90369

All developmental stages of the parasite in the vacuole are enveloped by a membrane from the host. Sporogony disporoblastic (Sprague et al. 1992).

Family type – *Encephalitozoon* Levaditi, Nicolau & Schoen 1923

Ecology & life modes – obligate parasites of many vertebrates, particularly mammals, including humans, as well as in insects, ticks, trematodes, cosmopolitan parasites (Canning & Vavra 2000).

Encephalitozoon C. Levaditi, Nicolau & R. Schoen, C. r. hebd. Séanc. Acad. Sci., Paris 177: 987 (1923)

Index Fungorum Identifier 30479

Monomorphic, monokaryotic throughout life cycle. Microsporidia with single nuclei. Development occurs in the parasitophorous vacuole. The spores are small" (Canning & Vavra 2000).

Type species – *Encephalitozoon cuniculi* Levaditi, Nicolau & Schoen 1923

Note – The genus comprises 13 species.

Other species in *Encephalitozoonidae*

Mockfordia Y.Y. Sokolova, I.M. Sokolov & C.E. Carlton, J. Invert. Path. 104(3): 186–194 (2010).

Index Fungorum Identifier 539724; one epithet is listed in Index Fungorum (2025) and no epithet accepted in Species Fungorum (2025).

Type species – *Mockfordia xanthocaeciliae* Sokolova, Sokolov & Carlton 2010.

Notes – Species are reported as obligate intracellular parasite of the insect order Psocoptera. Distributed in North America (Sokolova et al. 2010). rDNA sequences are available.

Enterocytozoonidae Cali & Owen, J. Protozool. 37(2): 145–155 (1990) emend. Y.S. Tokarev & Issi

Index Fungorum Identifier 90399

The parasite is apansporoblastic, polysporous and has characteristics not previously reported in *Microsporida*: an electron lucent inclusion not usually seen in *Microsporida* is prominent and always present; extremely elongated sausage-shaped nuclei occur in the proliferative phase of parasite development; the polar tube development uniquely involves production of electron dense discs, yet results in the formation of a typical spore; and polar tube development occurs prior to the final division of the multi-nucleate sporont (extracted from Cali & Owen 1990).

Family type – *Enterocytozoon* Desportes, Le Charpentier, Galian, Bernard, Cochand-Priollet, Lavergne, Ravisse & Modigliani, 1985

Ecology & life modes – obligate parasites of crustacean, fish, falcon, macaque, cattle, marsupials, humans. Cosmopolitan parasites.

Phylogeny – All genera are closely related. They constitute a monophyletic clade rooted within clade IV or class *Terresporidia* as defined by Vossbrinck & Debrunner-Vossbrinck (2005). The only unifying morphological characteristics are the precocious polar filament formation and how they develop; the polar filament complexes organized around the nuclei before the sporogonic plasmodium begins to divide into sporoblasts (Palenzuela et al. 2014). The genomes of *Enterocytozoon bieneusi* (3.86 Mb, 3,632 protein-coding genes; ABGB00000000.1; Corradi et al. 2007, Akiyoshi et al. 2009) and *E. hepatopenaei* (3.12 Mb, JAPMUG000000000.1; Wiredu Boakye et al. 2017) are sequenced.

Enterocytozoon Desportes, Le Charpentier, Galian, Bernard, Cochand-Priollet, Lavergne, Ravisse & Modigliani, J. Protozool. 32(2): 253 (1985)

Index Fungorum Identifier 30481

Description of the genus corresponds to the description of the family.

Type species – *Enterocytozoon bieneusi* Desportes, Le Charpentier, Galian, Bernard, Cochand-Priollet, Lavergne, Ravisse & Modigliani, 1985

Note – The genus comprises four species

Other genera in *Enterocytozoonidae*

Desmozoon M.A. Freeman & C. Sommerville, Parasites & Vectors 2: 58 (2009).
Index Fungorum Identifier 568905; one epithet is listed in Index Fungorum (2025)

Type species – *Desmozoon lepeophtherii* Freeman & Sommerville 2009.

Notes – Species are reported as an obligate intracellular parasite of Copepoda in the European Atlantic Ocean. rDNA sequences are available.

Enterospora Stentiford, K.S. Bateman, Longshaw & Feist, Dis. Aquat. Org. 75(1): 61–72 (2007).
Index Fungorum Identifier 580969; two epithets are listed in Index Fungorum (2025)

Type species – *Enterospora canceri* Stentiford, Bateman, Longshaw & Feist 2007.

Notes – Species are reported as obligate intracellular parasites of crabs and fish in the European Atlantic Ocean. rDNA sequences are available, as well as the genome assembly for *E. canceri* (3.1 Mb, 2169 protein-coding genes, LWDP00000000.1) is available in GenBank.

Hepatospora G.D. Stentiford, K.S. Bateman, A. Dubuffet, E. Chambers & D.M. Stone, J. Invert. Path. 108(3): 156–166 (2011).
Index Fungorum Identifier 569213; one epithet is listed in Index Fungorum (2025)

Type species – *Hepatospora eriocheir* (Wen Wang & Jain Xiu Chen) Stentiford, Bateman, Dubuffet, Chambers & Stone 2011.

Notes – Species are reported as obligate intracellular parasite of crabs in Europe. rDNA sequences as well as genome assembly for two strains of *H. eriocheir* (*H. eriocheir* ASM208788v1, 4.57 Mb in size, with 2691 protein-coding genes, LVKB00000000.1) are available in GenBank.

Nucleospora R.P. Hedrick, J.M. Groff & D.V. Baxa, (1991)
Index Fungorum Identifier 30539; five epithets are listed in Index Fungorum (2025)

Type species – *Nucleospora salmonis* Hedrick, Groff & Baxa 1991.

Notes – Species are reported as obligate intracellular parasites of fish in North America. rDNA sequences are available.

Obruspora A. Diamant, S.B.S. Rothman, M. Goren, B.S. Galil, M.B. Yokes, A. Szitenberg & D. Huchon, Dis. Aquat. Org. 109: 38 (2014).
Index Fungorum Identifier 92229; one epithet is listed in Index Fungorum (2025)

Type species – *Obruspora papernae* Diamant, Rothman, Goren, Galil, Yokes, Szitenberg & Huchon 2014.

Notes – Species are reported as obligate intracellular parasites of fish in Europe. rDNA sequences are available.

Heterovesiculidae Lange, Macvean, Henry & Streett 1995 Journal of Eukaryotic Microbiology. 42(5): 552–558 (1995)
Index Fungorum Identifier 90516

Meronts in the hyaloplasm of the host cell proliferate by binary fission until the formation of a plasmodium stage. Rounded merogonial plasmodium transform into a chain or ribbon-shaped stage with diplokaryotic nuclei and concurrent formation of a delicate interfacial envelope. During the disporoblastic sequence, tetranucleate diplokaryotic sporonts resulting from multiple fission of the same original plasmodium and inside delicate interfacial envelopes undergo binary fission to form diplokaryotic sporoblasts. During the octosporoblastic sequence, binucleate sporonts with isolated nuclei undergo karyokinesis until an octonucleate fusiform stage is reached. A uninucleate sporoblast develops from each nucleus, and the eight sporoblasts remain inside a robust interfacial

envelope. Two morphological types of spores are produced, uninucleate and binucleate. Eight uninucleate spores formed inside a persistent interfacial envelope. Variable numbers of binucleate spores formed inside nonpersistent interfacial envelopes.

Family type – *Heterovesicula* Lange, Macvean, Henry & Streett

Ecology & life modes – Obligate biotrophic parasites of orthopterans from North America (Lange et al. 1995).

Notes – Sprague et al. (1992) proposed *Heterovesiculidae* using interfacial characters (features that characterize the region of contact between parasite and host cell). Unlike *Heterovesicula*, members of established families were not known to develop two different morphological types of interfacial envelopes for disporoblastic and octosporoblastic developmental sequences. *Heterovesiculidae* was therefore proposed for dimorphic microsporidia that produce two different types of spores (uninucleate and binucleate) in two distinct kinds of interfacial envelopes (Lange et al. 1995).

A molecular phylogenetic study placed the type species *Heterovesicula*, *H. cowani,* as a sister taxon to the Nosema-Vairimorpha clade, forming a dichotomy with the Encephalitozoon specie branch (Sokolova et al. 2008).

Heterovesicula Lange, Macvean, Henry & Streett, Journal of Eukaryotic Microbiology. 42(5): 552–558 (1995)

Index Fungorum Identifier 30496

Description as for the family.

Note – Described one species of microsporidium *Heterovesicula cowani*, a pathogen of adipose tissue of Mormon crickets, *Anabrus simplex* (Sokolova et al. 2008).

Mrazekiidae Leger & Hesse, C. R. Acad. Sci. 174: 327–330 (1922)

Index Fungorum Registration Identifier IF 90588

Microsporidia with variable morphology, including forms with either diplo- or monokaryotic nuclear apparatus throughout the life cycle. Sporogony with a variable number of nuclear divisions. Spore shape varies from cylindrical to spherical. Polaroplast lamellar or vesicular (in *Globosporidium*). The polar tube is either manubrial or isofilar (Issi et al. 2010, Yakovleva et al. 2020).

Family type – *Mrazekia* Leger & Hesse (1916)

Ecology & lifestyle – obligate biotrophic pathogens of ciliates, oligochaetes, crustaceans and insects (Yakovleva et al. 2020).

Phylogeny – After the initial molecular phylogenetic reconstruction had been obtained for *Mrazekia macrocyclopis* (Issi et al. 2010), several related genera were included in the family of *Mrazekiidae*, which displayed rather variable morphology (Yakovleva et al. 2020). This made it impossible to unify morphological traits into a coherent family diagnosis.

Mrazekia Leger & Hesse, C. R. Soc. Biol. 78: 345–348 (1916) emend. Issi et al. Acta Protozool. 49: 75–84 (2010)

Index Fungorum Registration Identifier IF 30527

Merogony and sporogony are diplokaryotic. Disporoblastic. Spores diplokaryotic, cylindrical, without tail-like prolongations. Sporophorous vesicles are produced during late sporogony and contain individual young spores. Polar filament with a straight, wide anterior manubroid part, of which the posterior end is prominently enlarged, and a narrow, coiled posterior section. Polar filament bent anteriorly, forming an angle to the longitudinal axis of the spore; the filament is ejected at a more or less prominent angle to the spore. Only one sporogonial sequence observed.

Type species – *Mrazekia argoisi* Leger & Hesse

Notes – three species are described from aquatic Crustacea in Europe, for one of which the rDNA sequence is available (Issi et al. 2010).

Other genera included in *Mrazekiidae*

Agmasoma E.I. Hazard & Oldacre, Tech. Bull. U.S. Dep. Agric. 1530: 8 (1975)
Index Fungorum Identifier 30436; Index Fungorum (2025) lists three epithets, and Species Fungorum (2025) did not list any name.
Type species – *Agmasoma penaei* (V. Sprague) E.I. Hazard & Oldacre 1975

Anostracospora N.O. Rode, J. Landes, E.J.P. Lievens, E. Flaven, A. Segard, R. Jabbour-Zahab, Michalakis, P. Agnew, C.P. Vivarès & T. Lenormand, Parasitology 104(9): 1168–1185 (2013)
Index Fungorum Identifier 582987; Index Fungorum (2025) lists one epithet, and Species Fungorum (2025) did not list any names.

Type species – *Anostracospora rigaudi* N.O. Rode, J. Landes, E.J.P. Lievens, E. Flaven, A. Segard, R. Jabbour-Zahab, Y. Michalakis, P. Agnew, C.P. Vivarés & T. Lenormand 2013

Euplotespora Fokin, Di Giuseppe, Erra & Dini, J. Eukary. Microbiol. 55(3): 226 (2008)
Index Fungorum Identifier 30609; Index Fungorum (2025) lists one epithet, and Species Fungorum (2025) did not list any names.

Type species – *Euplotespora binucleata* Fokin, Di Giuseppe, Erra & Dini 2008

Globosporidium Y. Yakovleva, Nassonova, N.A. Lebedeva, O. Lanzoni, G. Petroni, A. Potekhin & E. Sabaneyeva, Parasitology 147(9): 969 (2020)
Index Fungorum Identifier 92224; Index Fungorum (2025) and Species Fungorum (2025) list one epithet.

Type species – *Globosporidium paramecii* Y. Yakovleva, E. Nassonova, N. Lebedeva, O. Lanzoni, G. Petroni, A. Potekhin, E. Sabaneyeva 2020

Helmichia J.I.R. Larss., Protistologica 18: 353–370 (1982)
Index Fungorum Identifier 30493; Index Fungorum (2025) lists five epithets and Species Fungorum (2025) did not list any names.

Type species – *Helmichia aggregata* J.I.R. Larss. 1982

Hrabyeia Lom & Dyková, Eur. J. Protist. 25(3): 243–248 (1990)
Index Fungorum Identifier 30499; Index Fungorum (2025) lists one epithet, and Species Fungorum (2025) did not list any names

Type species – *Hrabyeia xerkophora* Lom & Dyková 1990

Jirovecia J. Weiser (1977)
Index Fungorum Identifier 30507; Index Fungorum (2025) lists nine epithets, and Species Fungorum (2025) lists two names.

Type species – *Jirovecia caudata* (L. Léger & E. Hesse) J. Weiser 1977

Rectispora J.I.R. Larss., Eur. J. Protist. 26: 55–64 (1990)
Index Fungorum Identifier 30566; Index Fungorum (2025) lists one epithet, and Species Fungorum (2025) did not list any names.

Type species – *Rectispora reticulata* J.I.R. Larss. 1990

Nosematidae Y.S. Tokarev, Huang, Solter, Malysh, Becnel & Vossbrinck
Index Fungorum Identifier 904516

Developmental cycles are diverse. Xenomas are usually not formed. Spores are ovoid or elongated oval. The main sporulation sequence is disporoblastic and diplokaryotic (unikaryotic presporulation developmental stages may occur). Development is in direct contact with host cytoplasm. Binucleate mature spores with a thick spore wall and a polar tube with several coils in 1–2 rows which are infectious to new hosts are produced. An early sporulation sequence may occur

at the primary site of infection. An additional octosporous sporogony is possible within the same host to produce eight sporoblasts within a sporophorous vesicle. Alternatively, the developmental stages are monokaryotic throughout the life cycle. Infections are typically systemic, although tissue tropism occurs in some species, and transmission can be transovarial, per os or both (Y.S. Tokarev et al. 2020).

Family type – *Nosema* Nägeli

Ecology & life modes – obligate biotrophic pathogens of lepidopteran, hemipteran, hymenopteran and coleopteran insects, as well as crustaceans and mites (Y.S. Tokarev et al. 2020).

Notes – The family is the most remarkable example of a long-lasting confusion in *Microsporidia* systematics, where the presence of additional octosporous sporogony, though present in some representatives of both sister lineages corresponding to *Nosema* and *Vairimorpha*, was used to allocate all such taxa to *Vairimorpha.* Though mentioned for decades (Baker et al. 1994, Vossbrinck & Debrunner-Vossbrinck 2005), this confusion was not resolved until the formal redefinition based upon a molecular phylogenetic study was performed (Y.S. Tokarev et al. 2020). Genomes for *N. bombycis* (15.7 Mb, 4468 protein-coding genes; ACJZ00000000.1; Pan et al. 2013), *N. antheraeae* (6.6 Mb; Pan et al. 2013), *N. ceranae* (three strains are sequenced; reference genome: *N. ceranae* ASM98816v1, 5.69 Mb, 3264 protein-coding genes, GCA_000988165.1; Cornman et al. 2009, Pelin et al. 2015), *N. muscidifuracis* (14.4 Mb; JAIOKI000000000.1), *N. granulosis* (8.86 Mb, 3639 protein-coding genes, SBJO00000000.1; Cormier et al. 2021a), *Vairimorpha apis* (8.57 Mb, 2764 protein-coding genes, ANPH00000000.1; Chen et al. 2013) are sequenced.

Nosema Nägeli, Bot. Ztg. 15: 760 (1857)
Index Fungorum Identifier 30537

The genus description corresponds to that of the family.

Type species – *Nosema bombycis* Naegeli

Notes – The first microsporidium ever found, described from the silkworm *Bombyx mori* (Insecta, Lepidoptera), causes severe epizootics with excessive damage to sericulture worldwide. The *Nosema*-like developmental cycle is widespread among microsporidia, and numerous descriptions based on morphology tended to allocate species from various clades to this genus before molecular phylogenetics was widely applied (Issi et al. 2020). Small subunit ribosomal RNA gene sequence similarity to that of the type species, GenBank accession number D85503 is ≥94%. Ribosomal gene architecture is usually LSU-ITS-SSU" (Y.S. Tokarev et al. 2020).

Other genus in *Nosematidae*

Vairimorpha B.M. Pilley, (1976).
Index Fungorum Identifier 30598; 13 epithets are listed in Index Fungorum (2025), and no epithets are accepted in Species Fungorum (2025).

Type species – *Vairimorpha necatrix* (J.P. Kramer) B.M. Pilley 1976.

Notes – Species are reported as obligate intracellular parasites of insects. Distribution is cosmopolitan. Sequences are available, including complete genome sequences of *V. ceranae* (8.8 Mb) and *V. apis* (8.5 Mb).

Ordosporidae Larsson, Ebert & Vávra, Eur. J. Protist. 33(4): 432–443 (1997)
Index Fungorum Identifier 90600

All life cycle stages have isolated nuclei. Merogonial and sporogonial stages appear together in a parasitophorous vacuole of host cell origin. Sporogony tetra- or polysporoblastic in ribbon-like configurations (Larsson et al. 1997).

Family type – *Ordospora* Larsson, Ebert & Vávra

Ecology & lifestyle – obligate biotrophic pathogens of cladoceran crustaceans

Phylogeny – Members of this family are closely related to members of *Encephalitozoonidae* and share a high level of genome compaction. The genomes are sequenced for *Ordospora colligate.*

In *O. colligata* genome, horizontal transfer of a septin gene from the animal host is demonstrated, which might facilitate host cell entrance by endocytosis (Pombert et al. 2015).

Ordospora Larsson, Ebert & Vávra, Eur. J. Protist. 33(4): 432–443 (1997)
Index Fungorum Identifier 30544

Spores pyriform, exospore uniform, polaroplast uniform and lamellar, polar filament isofilar (Larsson et al. 1997).

Type species – *Ordospora colligata* Larsson, Ebert & Vávra

Notes – Two species are described from *Daphnia* species (*Cladocera*: *Crustacea*), in Europe.

Microsporidia families *incertae sedis*
Abelsporidae Azevedo J. Parasit. 49: 83–92 (1987)
Index Fungorum Identifier 90822

Merogony in the hyaloplasm of the host cell. Sporulation in a vacuole enveloped by a membrane from the host. Sporogony disporoblastic" (Sprague et al. 1992). "One uninucleate schizont giving rise to two sporonts, each giving rise to two sporoblasts within a sporophorous vacuole circumscribed by a persistent pansporoblastic membrane (Azevedo 1987).

Family type – *Abelspora* Azevedo 1987

Ecology & life modes – Obligate biotrophic pathogens of crustaceans.

Notes – The original description provided by Azevedo (1987) lacked a genus description, restricting it to the family and the type species diagnosis.

Abelspora Azevedo, J. Parasit. 49: 83–92 (1987)
Index Fungorum Identifier 30434

Merogony is similar to that of *Unikaryon*. Sporophorous vesicle contains two spores. The sporophorous vesicle envelope is not tightly adhered to the spore wall. Infected hepatopancreas cells are hypertrophied (Issi & Voronin 2007).

Type species – *Abelspora portucalensis* Azevedo 1987

Notes – The genus comprises one species. Obligate intracellular parasite of crabs from Europe. Sequence data are unavailable.

Areosporiidae Stentiford, Bateman, Feist, Oyarzún, Uribe, Palacios & Stone J. Invert. Path. 118: 1–11 (2014)
Index Fungorum Identifier 586901

Merogonic and sporogonic stages occur within the cytoplasm of phagocytes and connective tissue cells of marine crustacean hosts. Parasite life stages may be bound within a sporophorous vesicle. Early sporogony is defined by a distinctive rosette-like structure, bound within a sporophorous vesicle. Rosettes comprise 8 pre-sporonts. Transition of rosette-like sporonts to early sporoblasts marked by formation of spore-extrusion precursors and migration of tubular bristles to the surface of the pre-sporoblast exospore layer. Monokaryotic spores are ornamented with distinctive bristles. Distinction from other known genera within the phylum based upon partial sequence of the small subunit rRNA gene (Stentiford et al. 2014). (*Strict morphological definition of the family is not possible due to the potential for the discovery novel, morphological variants and the well documented potential for plasticity in closely related microporidium taxa)

Family type – *Areospora* Stentiford, Bateman, Feist, Oyarzún, Uribe, Palacios & Stone 2014

Ecology & life modes – obligate biotrophic pathogens of crabs

Notes – Erection of the family was proposed based upon distinction of the parasite described herein from all other known families within the phylum (using partial sequence data for the ssrRNA gene). The partial sequence of the small subunit rRNA gene has a maximum identity of less than 70% with homologous regions of its closest match in GenBank. Distinctions of rRNA gene sequence and morphology as compared to other known genera of *Microsporidia* provided evidence for the erection of a new genus and species (Stentiford et al. 2014).

Areospora Stentiford, Bateman, Feist, Oyarzún, Uribe, Palacios & Stone, J. Invert. Path. 118: 1–11 (2014)
Index Fungorum Identifier 586900

Similar to the family description

Type species – *A. rohanae* Stentiford, Bateman, Feist, Oyarzún, Uribe, Palacios & Stone 2014

Notes – The genus comprises one species that is an obligate intracellular parasite of crabs from South America. One s equence (PP852508) is available in GenBank (Stentiford et al. 2014).

Burenellidae Jouvenaz & J. Protozool. 25(1): 24–29 (1978)
Index Fungorum Identifier 90068

One sporulation sequence, "*Thelohania*-like", ending with 8 uninucleate spores in a vesicle. Other sporulation sequences "*Nosema*-like", ending with binucleate and isolated spores (Sprague et al. 1992). Spores of both types possess a lamellar polaroplast and a thin isofilar polar tube (Issi & Voronin 2007).

Family type – *Burenella* Jouvenaz & Hazard 1978

Ecology & life modes – obligate biotrophic pathogens of insects

Burenella Jouvenaz & Hazard, J. Protozool. 25(1): 28 (1978)
Index Fungorum Identifier 30454

Uninucleate, then diplokaryotic meronts divide by binary fission. Sporogony of the two types occur simultaneously in different host tissues (Issi & Voronin 2007). "Disporous sporonts sporulate in hypodermis producing binucleate, non-membrane bounded (NMB) spores; multinucleate sporonts produce 8 uninucleate, membrane bounded (MB) spores in fat cells; pansporoblastic membrane not persistent in the single known species: NMB spores coniform, MB spores broadly oval; polar filament of both spores nearly uniform in diameter and, in the single known species, longer in the MB spores; polaroplast structure indistinct, exospores thin, endospores thick; surfaces smooth in both spores (Jouvenaz & Hazard 1978).

Type species – *Burenella dimorpha* Jouvenaz & Hazard 1978

Notes – The genus comprises one species that was reported as an obligate intracellular parasite of ants from North America. No sequence information is available.

Other genera in *Burenellidae*

Pilosporella E.I. Hazard & Oldacre, Tech. Bull. U.S. Dep. Agric. 1530: 84 (1975).
Index Fungorum Identifier 30557; two epithets are listed in Index Fungorum (2025)

Type species – *Pilosporella fishi* Hazard & Oldacre 1975.

Notes – Species are reported as obligate intracellular parasites of mosquitoes in North America. Sequences are unavailable.

Tabanispora H.I. Bykova, Y.Y. Sokolova & I.V. Issi, (1987).
Index Fungorum Identifier 30582; two epithets are listed in Index Fungorum (2025), and no epithets are accepted in Species Fungorum (2025).

Type species – Tabanispora bacillifera Bykova, Sokolova & Issi 1987.

Notes – Species are reported as obligate intracellular parasites of flies in Europe. Sequences are unavailable.

Cougourdellidae Poisson, Traite de Zoologie, Paris 1(2): 798–906 (1954)
Index Fungorum Identifier 90219

Sporogony polysporoblastic with formation of 4 to 16, usually 8 spores. The sporophorous vesicle envelope has a variable structure. Spores are clavate or elongated-pyriform. Anterior polaroplast is made up of large chambers. Polar tube is isofilar or anisofilar (Issi & Voronin 2007).

Family type – *Cougourdella* Hesse 1935

Ecology & life modes – Obligate biotrophic pathogens of crustaceans.

Cougourdella Hesse, Archs Zool. Exp. Gen. 12: 655 (1935)
Index Fungorum Identifier 30466

Multinucleate merogonial plasmodia divide by binary fission. Sporogonial plasmodia with 2, 4, 8, or 16 nuclei. Spores are long, thin-walled, with a pestle-like widened posterior end, with a large helicoidal polaroplast filled with finely granulated material (Issi & Voronin 2007).

Notes – The type species is poorly described (Issi & Voronin 2007) and is based upon data obtained for *C. polycentropi* Weiser 1965.

Type species – *Cougourdella magna* Hesse 1935

Notes – Seven species are known as obligate intracellular parasites of crustaceans from Europe. Sequence data are unavailable.

Cylindrosporidae Issi & Voronin, Protozoologiya 10: 6–136 (1986)
Index Fungorum Identifier 90294

The polar tube is greatly widened at the base, short, and not coiled. Interfacial envelope present during sporulation, presumably elaborated by sporont, subpersistent as an octosporophorous vesicle" (Sprague et al. 1992). Sporogony results in 8 or multiples of 8 long and cylindrical spores. Polaroplast spongy, containing no or few lamellas. Polar tube straight, short, and notably widened at its base in a funnel-like manner. Parasitophrous vesicle is formed (Issi & Voronin 2007).

Family type – *Cylindrospora* Issi & Voronin 1986

Ecology & life modes – obligate biotrophic pathogens of dipterans (Issi & Voronin 2007).

Cylindrospora Issi & Voronin, J. Protozool. 10: 81 (1986)
Index Fungorum Identifier 27958

Sporogony is octosporous, Endospore underdeveloped, exospore smooth, two-layered. Polaroplast spongy or with a small number of lamellas. Spores covered with mucocalyx (Issi & Voronin 2007).

Type species – *Cylindrospora chironomi* Issi & Voronin 1986

Notes – Two species are known. Both were reported as an obligate intracellular parasite of dipterans from Europe. Sequence data is unavailable.

Duboscqiidae Sprague, Comparative Pathobiology (New York) 2: 1–510 (1977)
Index Fungorum Identifier 90342

Interfacial envelope is usually produced precociously (by a merogonial plasmodium before the final merogonic division), enclosing more than 1 sporont (each represented by a pair of nuclei in the final merogonial plasmodium). Sporophorous vesicle may contain 8 or, usually, multiples of 8 spores (Sprague et al. 1992).

Family type – *Duboscqia* Pérez, C. r. Séanc. Soc. Biol. 65: 632 (1908)

Ecology & life modes – Obligate biotrophic pathogens of insects

Duboscqia Pérez C. r. Séanc. Soc. Biol. 65: 632 (1908)
Index Fungorum Identifier 30477

Round 16-nucleate meront divides into uninucleate merosoites by rosette-like fission, and 16 spores are formed within sporophorous vesicle with a stable envelope (Issi & Voronin 2007). "Interfacial envelope present during sporulation. The parasite and host cell form a conspicuous xenoma. Spores uninucleate, ovoid to ellipsoidal (Sprague et al. 1992).

Type species – *Duboscqia legeri* Perez

Notes – The parasite was described from termites in Maryland, USA. Sprague created the family *Duboscqiidae* for genera which resemble *Thelohania* in sporogony but usually produce 8 spores within a sporophorous vesicle (Sprague et al. 1992). The genus description, summarized by

Sprague et al. (1992), is further supplemented by additional data by Issi & Voronin (2007). Sequence information is unavailable.

Other genera in *Duboscqiidae*

Mitoplistophora Codreanu, Proceedings of the First International Congress of Parasitology: 602 (1966).

Index Fungorum Identifier 304526; one epithet is listed in Index Fungorum (2025)

Type species – *Mitoplistophora angularis* Codreanu 1966.

Notes – Species are reported as obligate intracellular parasites of mayflies in Europe. Sequences are unavailable.

Pulicispora Vedmed, S.V. Krylova & I.V. Issi, (1991).

Index Fungorum Identifier 30564; one epithet is listed in Index Fungorum (2025)

Type species – *Pulicispora xenopsyllae* Vedmed, Krylova & Issi 1991

Notes – Species are reported as obligate intracellular parasites of fleas in Europe. Sequences are unavailable.

Tardivesicula J.I.R. Larss. & E.K.C. Bylén, Eur. J. Protist. 28: 25–36 (1992).

Index Fungorum Identifier 30583; one epithet is listed in Index Fungorum (2025)

Type species – *Tardivesicula duplicata* Larss. & Bylén 1992

Notes – Species are reported as obligate intracellular parasites of caddisflies in Europe. Sequences are unavailable.

Trichoduboscqia L. Léger, C. r. hebd. Séanc. Acad. Sci., Paris 182: 727 (1926).

Index Fungorum Identifier 30591; one epithet is listed in Index Fungorum (2025)

Type species – *Trichoduboscqia epeori* Léger 1926.

Notes – Species are reported as obligate intracellular parasites of mayflies in Europe. Sequences are unavailable.

Golbergiidae Issi, Protozoologiya 10: 6–136 (1986)

Index Fungorum Identifier 90443

Spores of two morphological types. Besides the *Nosema*-like sporogony, the polysporous one ends with a variable number (usually 8) of lanceolate or elongated pyriform uninucleate spores with thin walls. Some binucleate round (subspherical) and thin-walled spores (Issi & Voronin 2007).

Family type – *Golbergia* Weiser, Věstník Zoologii 41(4): 308–320 (1977)

Ecology & life modes – obligate biotrophic pathogens of insects.

Notes – The family was originally described by Issi (1986), and the translation of its original diagnosis was introduced by Sprague et al. (1992). Specified diagnosis by Issi & Voronin (2007) is given using the terminology and translation style of Sprague et al. (1992).

Golbergia Weiser, Věstník Zoologii 41(4): 308–320 (1977)

Index Fungorum Identifier 30489

Merogony by binary fission of diplokaryotic cells. Sporogony with two sequences, both involve sporogonial plasmodia; one ending with uninucleate sporoblasts in groups of 4–16; the other sequence ending with isolated binucleate sporoblasts. The binucleate spore is flattened on one side and on the anterior pole. Posterior end with a nail-like protrusion, ridged exospore and lamellate polaroplast. Uninucleate spore pyriform, with a thin wall and vesiculate polaroplast (Sprague et al. 1992). All developmental stages are in direct contact with the host cell cytoplasm. Uninucleate and binucleate spores are formed in summer and autumn, respectively (Issi & Voronin 2007).

Type species – *Golbergia spinosa* (Golberg) Weiser 1977

Notes – The type and only species was transferred from *Weiseria.* It is an obligate intracellular parasite of mosquitoes from Europe (Species Fungorum 2025).

Other genera in *Golbergiidae*

Krishtalia P.J. Kilochitskii, Věstník Zoologii 31: 15–23 (1997).
Index Fungorum Identifier 30465; one epithet is listed in Index Fungorum (2025)

Type species – *Krishtalia pipiens* P.J. Kilochitskii 1997.

Notes – Species are reported as obligate intracellular parasites of mosquitoes in Europe (Species Fungorum 2025).

Simuliospora Khodzhaeva, S.V. Krylova & I.V. Issi, (1990).
Index Fungorum Identifier 30574; two epithets are listed in Index Fungorum (2025)

Type species – *Simuliospora uzbekistanica* Khodzhaeva, Krylova & Issi 1990.

Notes – Species are reported as obligate intracellular parasites of blackflies in Asia (Species Fungorum 2025).

Microfilidae Sprague, Becnel & Hazard, Critical Reviews in Microbiology (Boca Raton) 18(5–6): 285–395 (1992)
Index Fungorum Identifier 90586

Interfacial envelope lacking. Distinguished from other families in the order by having tetrasporoblastic sporogony, manubroid polar filament, spore with a peculiar bilateral symmetry" (Sprague et al. 1992). All developmental stages are in direct contact with the host cell cytoplasm (Issi & Voronin 2007).

Family type – *Microfilum* Faye, Toguebaye & Bouix, J. Protozool. 38(1):30–40 (1991)

Microfilum Faye, Toguebaye & Bouix, J. Protozool. 38(1): 30–40 (1991)
Index Fungorum Identifier 30522

Direct contact with the cytoplasm of the host cell occurs in all stages of development. Unikaryotic (isolated nucleus) during the whole cycle. Merogony by binary division. Tetrasporoblastic sporogony. Spore with a manubrium terminating in a very short polar filament in the form of a curved appendix (Faye et al. 1991).

Type species – *Microfilum lutjani* Faye, Toguebaye & Bouix 1991

Notes – The genus comprises one species and is reported as a parasite of fish in Africa (Species Fungorum 2025).

Neonosemoidiidae Faye, Toguebaye & Bouix, Eur. J. Protistol. 32: 320–326 (1996)
Index Fungorum Identifier 90591

Sporophorous vesicle absent; two merogonial phases; the first one with diplokaryotic nuclei, the second one with unpaired nuclei; sporogony monokaryotic and polysporoblastic (Faye et al. 1996).

Family type – *Neonosemoides* Faye & Toguebaye 1996

Ecology & life modes – Obligate biotrophic pathogens of fish.

Neonosemoides Faye & Toguebaye, Eur. J. Protistol. 32: 320–326 (1996)
Index Fungorum Identifier 30533

Sporophorous vesicle absent; two merogonial phases and one sporogonial sequence; meronts of the first merogonial phase are diplokaryotic and divide by binary fission; those of the second merogonial phase are monokaryotic and divide by plasmotomy into uninucleate merozoites; the separation of the diplokaryon nuclei occurs at the transition from first merogony-second merogony; monokaryotic merozoites resulting from second merogony enter sporogonic phase; sporogony monokaryotic and polysporoblastic; sporogonial plasmodia divide by plasmotomy; spores with an anisofilar polar filament and a polaroplast exhibiting two lamellar parts (Faye et al. 1996).

Type species – *Neonosemoides tilapiae* (Sakiti & Bouix 1987)

Notes – The genus is known only from the type species, which is a parasite of fishes in Africa. Sequences are unavailable.

Pleistosporidiidae Codreanu-Balcescu & Codreanu, J. Protozool. 29: 515 (1982)
Index Fungorum Identifier 90607

Meronts bi- or tetranucleate in direct contact with the host cell. Sporogony occurs in two phases. Primary (maternal) sporont divides into 4 secondary (daughter) sporonts in a parasitophorous vacuole. Multinucleate secondary sporonts divide by rosette-like fission, forming 12–16 spores. Polaroplast vacuolar-lamellar (Issi & Voronin 2007).

Family type – *Pleistosporidium* Codreanu-Balcescu & Codreanu 1982

Ecology & life modes – obligate biotrophic pathogens of gregarines.

Pleistosporidium Codreanu-Balcescu & Codreanu, J. Protozool. 29: 515 (1982)
Index Fungorum Identifier 30559

Description is similar to the family description.

Type species – *Pleistosporidium hyperparasitica* Codr.-Balc. & Codreanu (1982)

Notes – The genus is monotypic. Hyperparasite of gregarines from mayflies and reported from Europe.

Pseudopleistophoridae Sprague, Comparative Pathobiology (New York) 2: 1–510 (1977)
Index Fungorum Identifier 90610

Sporogonial plasmodium is bounded by a membrane that interdigitates with the cytoplasm of the host cell. Sporogony is accompanied by the formation of a sporogony vacuole within the bounding membranes. Sporoblast binucleate. Polysporous. Spores structurally similar to those of *Nosema"* (Sprague 1977). "Sporogony di- or polysporoblastic within a sporophorous vesicle (Issi & Voronin 2007).

Family type – *Pseudopleistophora* Sprague 1977

Ecology & life modes – obligate biotrophic pathogens of cestodes, mussels.

Notes – Family was proposed by Sprague (1977), but reduced to the rank of subfamily under the family *Nosematidae* by Issi (1986). However, Sprague et al. (1992) reinstated the family, and this was accepted by Issi & Voronin (2007).

Pseudopleistophora Sprague 1977 in Bulla et al. (Eds), Comparative Pathobiology (New York): 67 (1977)
Index Fungorum Identifier 30563

Sporophorous vesicle envelope is integrated with the host cell cytoplasm by finger-like protrusions. Each sporont gives rise to a large number of spores. Plasmodium division into sporoblasts is performed by fusion of small vacuoles (Issi & Voronin 2007).

Type species – *Pseudopleistophora szollozi* Sprague

Notes – The genus comprises one species that is a parasite of cestodes in North America. Sequence data are unavailable.

Other genus in *Pseudopleistophoridae*

Steinhausia R. Sprague, Ormières & Manier, J. Invert. Path. 20: 231 (1972).
Index Fungorum Identifier 30578; four epithets are listed in Index Fungorum (2025), and no epithets are accepted in Species Fungorum (2025).

Type species – *Steinhausia mytilovum* (I.A. Field) Sprague, Ormières & Manier 1972.

Notes – Species are reported as obligate intracellular parasites of mussels. Sequences are unavailable.

Striatosporidae Issi & Voronin, Protozoologiya 10: 6–136 (1986)

Index Fungorum Identifier 90614

Sporogony is octosporoblastic. An interfacial envelope may be present during sporulation. Spore short-cylindrical or elongated-cylindrical, uninucleate. The length of a thin polar tube usually does not exceed 2/3 of the spore length. Polaroplast spongy, lamellar or chambered (Issi & Voronin 2007).

Family type – *Striatospora* Issi & Voronin 1986

Ecology & life modes – Obligate biotrophic pathogens of aquatic insects.

Striatospora Issi & Voronin, Protozoologiya 10: 6–136 (1986)
Index Fungorum Identifier 30580

Octosporous sporulation is said to occur within pansporoblastic membranes, and several sporulating forms in different stages of development occur together in a parasitophorous vacuole. Sporont is a diplokaryotic cell. Sporogony is octosporoblastic, presumed to be accompanied by meiosis. Spore uninucleate, short cylindrical. Exospore ornamented with longitudinal rows of electron-dense material. Several sporophorous vesicles, each containing a certain stage of parasite development, are contained within one parasitophorous vacuole. Eight short, cylindrical spores are formed in the vesicle. Endospore is underdeveloped, its outer membrane ornamented with longitudinal rows of electron-dense material (Issi & Voronin 2007). Spore uninucleate, polar filament isofilar, short, straight (Sprague et al. 1992).

Type species – *Striatospora chironomi* Issi & Voronin 1986

Notes – The genus comprises one species that is an obligate intracellular parasite of mosquitoes from Europe. Sequence data are unavailable.

Other genera in *Striatosporidae*

Toxospora Voronin 1993
Index Fungorum Identifier 30588; two epithets are listed in Index Fungorum (2025)

Type species – *T. volgae* Voronin.

Notes – Obligate intracellular parasites of dipterans in Europe. Sequences are unavailable.

Telomyxidae Léger & Hesse, Zool. Anz. 206: 137–153 (1910)
Index Fungorum Identifier 90615

Sporogony is disporoblastic; the sporophorous vesicle envelope is either tightly adhered to the spore surface or is detached, leaving a lumen. Spores lay freely or joined into pairs with a cementing matter (Issi & Voronin 2007).

Family type – *Telomyxa* Léger & Hesse 1910

Ecology & life modes – Obligate biotrophic pathogens of insects

Notes – Leger & Hesse (1910) proposed *Telomyxidae* to accommodate *Telomyxa*. Issi (1986), however, abandoned this family and assigned *Telomyxa* to *Thelohaniidae*. This assignment was found untenable by Sprague et al. (1992), as *Telomyxa* is not octosporous and doubtfully possesses a diplokaryotic stage, and *Telomyxidae* was reinstated. Ultrastructure was described by Codreanu & Vavra (1970) and Larsson (1981).

Telomyxa Léger & Hesse, C. r. hebd. Séanc. Acad. Sci., Paris 150: 413 (1910)
Index Fungorum Identifier 30584

The sporonts in the fat body cells of *Ephemera danica* develop a double membrane. Electron-opaque material (which is the polar ring of the future diplospore) is deposited at the opposite poles of the sporont in the space between the 2 membranes. The cell division which follows leads to the formation of 2 sporoblasts and later of 2 spores inside a membrane. The permanent assemblage of 2 spores embedded in electron-dense material and enveloped by a common membrane is the diplospore, which is thus a special type of pansporoblast (Codreanu & Vavra 1970).

Type species – *T. glugeiformis* Léger & Hesse 1910

Notes – The genus comprises four species that are obligate intracellular parasites of mosquitoes from Europe. Sequences are unavailable.

Toxoglugeidae Larsson
Index Fungorum Identifier 90618
Family description is similar to the generic description.

Family type – *Toxoglugea* Léger & Hesse 1924

Ecology & life modes – obligate biotrophic pathogens of insects

Toxoglugea Léger & Hesse Trav. Lab. Hydrobiol. Piscic. Univ. Grenoble 14: 54 (1924)
Meiosis results in the transformation of an octonucleate sporogonial plasmodium into 8 bow-like spores within a thin sporophorous vesicle envelope" (Issi & Voronin 2007).

Type species – *T. vibrio* Léger & Hesse 1924

Notes – Currently, 15 species are described as obligate intracellular parasites of dipterans from Europe (Species Fungorum 2025).

Other genera in *Toxoglugeidae*
Toxospora Voronin 1993,

Type species – *Toxospora volgae* Voronin, Parazitologiya 27: 148–154 (1993).

Tuzetiidae Sprague, Tuzet & Maurand, in Sprague, Comparative Pathobiology (New York) 2: 1–510 (1977)
Index Fungorum Identifier 90620

Merogony in hyaloplasm. An interfacial envelope is present during sporulation, produced by the sporont, dividing during sporogony, leaving 1 (usually) or 2 spores within a vesicle (Sprague et al. 1992). Sporont divides by rosette-like fission into 4–16 sporoblasts alongside the sporoforous vesicle envelope, so that each spore is surrounded by an individual vesicle (Issi & Voronin 2007).

Family type – *Tuzetia* Maurand, Fize, Vernick & Michel 1971.

Ecology & life modes – Obligate biotrophic pathogens of insects, copepods, cestodes.

Notes – Sprague (1977) introduced the family and redefined it by Sprague et al. (1992).

Tuzetia Maurand, Fize, Vernick & Michel, Protistologica 7: 231 (1971)
Index Fungorum Identifier 30596

Late meronts develop into sporonts, forming sporogonial plasmodium, enclosed by the sporophorous vesicle envelope. One sporont produces up to 8 spores. After fission, each sporophorous vesicle envelope includes a separate sporoblast and then spores. The sporophorous vesicle lumen contains a tubular secretion (Issi & Voronin 2007).

Type species – *T. infirma* (Kudo) Maurand, Fize, Fenwick & Michel 1971

Notes – The genus comprises seven species that are reported as obligate intracellular parasites of copepods in Europe. Sequences are unavailable.

Other genera in *Tuzetiidae*
Nelliemelba J.I.R. Larss., Protistologica 19: 323–355 (1983).
Index Fungorum Identifier 30532; one epithet is listed in Index Fungorum (2025)

Type species – *Nelliemelba boeckella* (Milner & J.A. Mayer) Larsson 1983.

Notes – Species are reported as obligate intracellular parasites of mosquitoes in Europe. Sequences are unavailable.

Pankovaia A.V. Simakova, Y.S. Y.S. Tokarev & I.V. Issi, Eur. J. Protist. 45: 19 (2009).
Index Fungorum Identifier 537568; one epithet is listed in Index Fungorum (2025)

Type species – *Pankovaia semitubulata* Simakova, Y.S. Tokarev & Issi 2009.

Notes – Species are reported as obligate intracellular parasites of mayflies in Eurasia. Sequences are unavailable.

Paratuzetia L.G. Poddubnaya, Y.S. Y.S. Tokarev & I.V. Issi, Protistology (Stuttgart) 4(3): 276 (2006).
Index Fungorum Identifier 30084; one epithet is listed in Index Fungorum (2025)

Type species – *Paratuzetia kupermani* Poddubnaya, Y.S. Tokarev & Issi 2006.

Notes – Species are reported as hyperparasites of cestodes in Europe. Sequences are unavailable.

Rozellomycota orders *incertae sedis*
Paramicrosporidiales Corsaro
Paramicrosporidiaceae D. Corsaro in: Microsporidia. Current Advances in Biology. Weiss L.M., Reinke A.W. (Eds.) Springer, pp. 71–90 (2022)
Index Fungorum Identifier IF 92528

The diagnosis of the monotypic family was not provided by the author. Consider the diagnosis for the family type.

Family type – *Paramicrosporidium* Corsaro, Walochnik, Venditti, Steinmann, Müller & Michel 2014

Ecology & life modes – obligate intranuclear parasites (parasitoids) of lobose amoebae. Described from the hosts collected in Europe.

Notes – rRNA gene sequence is available for two species of *Paramicrosporidium* and for several unclassified *Paramicrosporidium* sp. (Corsaro et al. 2014a). Genome assembly is available for *P. saccamoebae* (7.17 Mb; 3750 protein-coding genes, GCA_002794465.1; mitochondrial circular contig – Quandt et al. 2017). The parasite has a canonical mitochondrial genome, similar to the mitochondrial genomes of fungi, which encodes the genes necessary for oxidative phosphorylation, including cytochrome oxidase genes. The nuclear genome shows many typically "fungal" features.

Paramicrosporidium D. Corsaro, J. Walochnik, D. Venditti, J. Steinmann, K.D. Müller & R. Michel, Parasitol. Res. 113 (5): 1909–1919 (2014); Fig. 97
Index Fungorum Identifier 807391

The diagnosis provided by Corsaro et al. (2014) is following: "Unicellular fungi, with aflagellated infective spores with a chitinous wall and an inactive polar filament. Intranuclear parasites of amoebae multiply as unwalled cells by merogony".

Note – It is unknown whether the polar filament is active or inactive, i.e. whether it can be discharged under certain stimuli and may serve as a device for extruding sporoplasm into a host cell. In *Paramicrosporidium*, there is only one round of proliferative division in the life cycle, so it should be considered as sporogonial division, thus the merogony is apparently missing.

Type species – *Paramicrosporidium saccamoebae* Corsaro, Walochnik, Venditti, Steinmann, Müller & Michel 2014

Notes – The genus comprises two species, identified based on SSU rDNA sequence data, and named based on their respective amoeba hosts (*P. vannellae* ex *Vannella* sp. isolated from a keratitis patient (Michel et al. 2000) and *P. saccamoebae* ex *Saccamoeba* sp. (Fig. 97) isolated from a pond (Michel et al. 2009a), formed a clade within the 'cryptomycotan' clade III *sensu* Lazarus & James (2015). Other possible representatives are not yet characterised, including uncultured environmental SSU rDNA clones (e.g., Joinv23).

Morellosporales Corsaro 2022
Morellosporaceae D. Corsaro, in Microsporidia. Current Advances in Biology. Weiss L.M., Reinke A.W. (Eds.) Springer, pp. 71–90 (2022)
Index Fungorum Identifier IF 92532

The diagnosis of the monotypic family was not provided by the author. Consider the diagnosis for the family type.

Family type – *Morellospora* Corsaro, Walochnik, Venditti, Hauröder & Michel 2020

Ecology & life modes – obligate intracytoplasmic parasites (parasitoids) of lobose amoebae. Described from the host collected in Europe.

Notes – rRNA gene sequence available for the only described species, *Morellospora saccamoebae.* In the phylogenetic tree, it branches within the clade LKM15 *sensu* Corsaro et al. 2019 (the clade X *sensu* Lazarus & James 2015), which also includes *Mitosporidium daphniae* (Haag et al. 2014) and a parasite of plasmodial slime molds *Lamproderma* sp. (Yajima et al. 2013).

Morellospora D. Corsaro, J. Walochnik, D. Venditti, B. Hauröder & R. Michel, Parasitol. Res. 119 (3): 925–934 (2020); Fig. 98

Index Fungorum Identifier 92258

Unicellular organisms, forming morula-like inclusions in the cytoplasm of the host cell (Fig. 98). With infective nonflagellated walled spores; naked trophic cells free in the host cytoplasm, developing into multinucleated plasmodia in which spore formation occurs by vacuolation (endogenous sporogony).

Type species – *Morellospora saccamoebae* D. Corsaro, J. Walochnik, D. Venditti, B. Hauröder & R. Michel, Parasitol. Res. 119: 925–934 (2020)

Notes – The genus comprises one species, which is a cytoplasmic parasite of *Saccamoeba lacustris* (*Amoebozoa*). The sequence is 96.5% similar to an unknown organism whose cysts were found in the plasmodial slime molds *Lamproderma* (Yajima et al. 2013).

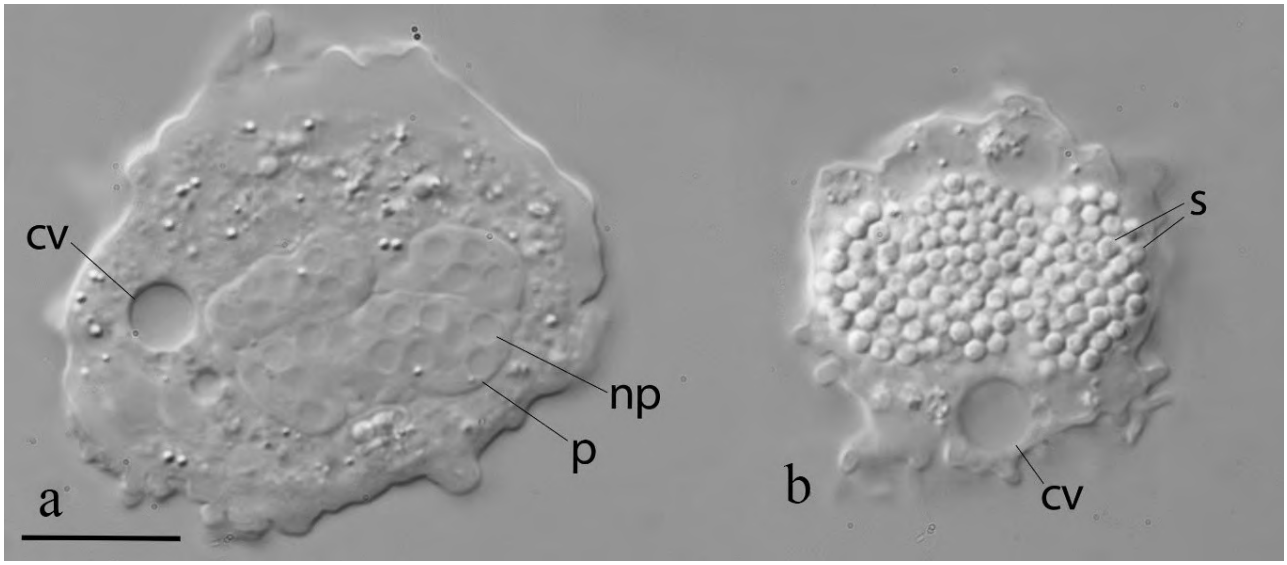


Figure 97 – *Paramicrosporidium vannellae* KAUN, an intranuclear parasite of *Vannella* sp. isolated from a keratitis patient. a Multinucleate plasmodia developing within amoeba nucleus. b Mature spores. Abbreviations: cv = contractile vacuole; np = nucleus of parasite; p = plasmodium; s = spore. Scale bar: 10 µm. Micrographs courtesy of Yelisei S. Mesentsev, St. Petersburg University. The cultures of parasites and amoebae were kindly provided by Rolf Michel (Germany). Reproduced with permission of the publisher from: Glotova & Nassonova 2022.

Mitosporidiaceae Corsaro, in: Microsporidia. Current Advances in Biology. Weiss L.M., Reinke A.W. (Eds.) Springer, pp. 71–90 (2022)

Index Fungorum Identifier 904000

The diagnosis of the monotypic family was not provided by the author. Consider the diagnosis for the family type.

Family type – ***Mitosporidium*** Haag, James, Pombert, Larsson, Schaer, Refardt & Ebert 2014

Ecology & life modes – obligate parasites (parasitoids) of cladocerans (Crustacea, Cladocera). Described from the hosts collected in Europe.

Notes – rRNA gene sequence and genome assembly are available for the only described species. The phylogenomic analysis, which includes six species of *Microsporidia* and *Rozella allomycis* showed that *M. daphniae* branches at the base of the clade corresponding to *Microsporidia* (Haag et al. 2014). Unlike amitochondriate microsporidia, *Mitosporidium daphniae* retained the mitochondrial genome, which contains genes involved in the process of oxidative phosphorylation (however, it lacks the complex I of the oxidative phosphorylation pathway), and its nuclear genome (5.6 Mb, 3322 protein-coding genes, GCA_000760515.2) is less reduced than the genomes of typical microsporidia. In the phylogenetic tree based on analysis of the SSU rRNA gene, *M. daphniae* branches together with *Morellospora saccamoebae* (Corsaro et al. 2020), with an unknown endoparasite of plasmodial slime molds *Lamproderma* sp. (Yajima et al. 2013) and with the environmental sequences from the clade LKM15 (Corsaro et al. 2016, 2019, Bass et al. 2018).

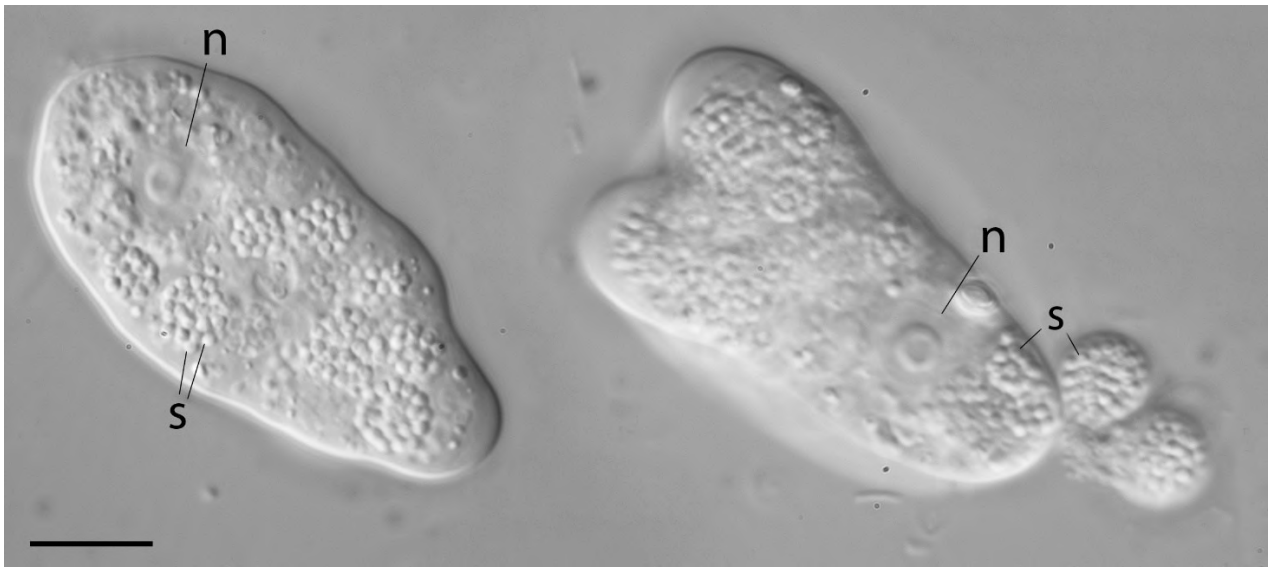


Figure 98 – *Morellospora* sp. KSL8, intracytoplasmic parasite of *Saccamoebae* sp. Abbreviations: n = nucleus of amoeba; s = spores of parasite. Scale bar: 10 µm. Micrographs courtesy of Yelisei S. Mesentsev, St. Petersburg University. The cultures of parasites and amoebae were kindly provided by Rolf Michel (Germany). Reproduced with permission of the publisher from: Glotova & Nassonova 2022.

Mitosporidium K.L. Haag, T.Y. James, Pombert, R. Larsson, T.M.M. Schaer, D. Refardt & D. Ebert, Proc. Natl. Acad. Sci. USA 111(43): 15480–15485 (2014)
Index Fungorum Identifier 588770

All stages of the life cycle have isolated nuclei (monokaryotic). Meiotic division has not been observed. Successive mitoses yield a multinucleate plasmodium, and simultaneously, the plasma membrane is covered by an electron-dense material. Two-layered tubular aggregates similar to mitosomes appear in the proximity of the nuclei. The growing vacuoles split the plasmodium successively into smaller parts. A multinucleate sporogonial plasmodium generates a great and irregular number (>20) of ovoid or slightly bent, uninucleate spores in a sporophorus vesicle lacking prominent inclusions of the episporontal space. Spores have a thin, electron-opaque exospore and a wide, electron-lucent endospore, a uniform, weakly developed polaroplast of concentrically arranged lamellae, and an anisofilar polar filament, which connects anteriorly to a curved polar sac. The polar sac of the mature spore is cup-shaped, following the profile of the front end of the spore, and filled with granular material. The polar filament is widest anteriorly, and the width is successively reduced in the posterior direction. A wide manubrium-like anterior end of the

filament, followed by one wide and one narrow coil. The polar filament approaches and connects to the polar sac, but there are no visible coupling devices, and no part of the filament enters the polar sac. The rounded nucleus is located in a lateral position to the polar filament in the equatorial area of the spore. The posterior vacuole is present close to the posterior pole of the spore.

Type species – *Mitosporidium daphniae* Haag, James, Pombert, Larsson, Schaer, Refardt et Ebert 2014; Fig. 99

Notes – The genus is monotypic and represented by an obligate endoparasite known only from the lower midgut epithelium of the water flea *Daphnia magna* in North-Western Europe.

Nucleophagales Corsaro
Nucleophagaceae D. Corsaro, in Microsporidia. Current Advances in Biology. Weiss L.M., Reinke A.W. (Eds.) Springer, pp. 71–90 (2022)
Index Fungorum Identifier 904001
The diagnosis of the monotypic family was not provided by the author. Consider diagnosis for the family type.

Family type – *Nucleophaga* Dangeard 1895, emend. Corsaro, Walochnik, Venditti, Müller, Hauröder & Michel 2014

Ecology & life modes – obligate intranuclear parasites (parasitoids) of lobose amoebae. Described from the hosts collected in Europe.

Notes – rRNA gene sequence available for three species of *Nucleophaga*. The highly derived sequences of *Nucleophaga* spp. formed a long branch that grouped closely to canonical microsporidia with low support (Corsaro et al. 2014b, 2016).

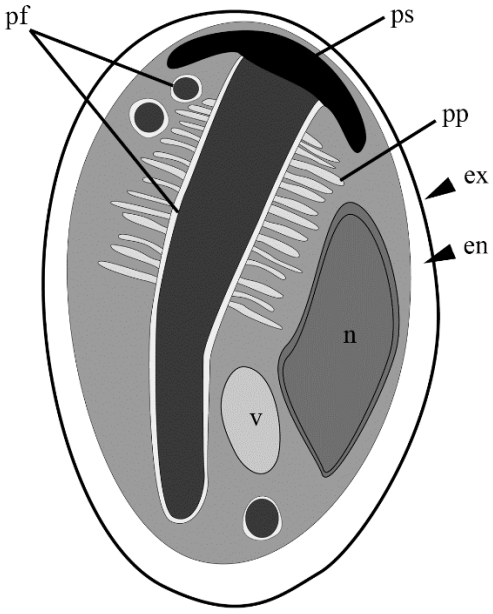


Figure 99 – Schematic drawing of the mature spore of *Mitosporidium daphniae*, an obligate endoparasite of the water flea *Daphnia magna*. Abbreviations: ex = exospore; en = endospore; n = nucleus; pf = polar filament; pp = polaroplast; ps = polar sac; v = posterior vacuole. A complex of organelles similar to the microsporidian invasion apparatus with polar sac (ps), polar filament (pf), and polaroplast (pp) is clearly visible. Drawing is based on the micrographs published in Haag et al. (2014).

Nucleophaga P.A. Dangeard, Le Botaniste. 4: 199-248 (1895) (Fig. 100)
Index Fungorum Identifier 20374

According to Corsaro et al. (2016), the representatives are “unicellular, with aflagellated infective spores with chitinous wall; anchoring disc and atypical polar filament present. Intranuclear parasites of amoebae as unwalled cells, fingerlike projections at cell surface”. The spores of *Nucleophaga* are engulfed by the amoeba during phagocytosis, and then the endoparasites reach the nucleus of the amoeba, where one of the first detectable changes is the enlargement of the circularly arranged pieces of the nucleolar substance. Subsequently, the parasites grow and develop into multinucleate plasmodia, causing a 2-3-fold enlargement of the host amoeba's nucleus. As a result of multiple nuclear divisions within the plasmodia (endogenous sporogony), sporoblasts are forming, which contain a network of endoplasmic reticulum and mitochondria. The sporoblasts, which more and more resemble spheres, form a wall and mature by becoming spores (Michel et al. 2022).

Note – The statement about the presence of an anchoring disk in the spore of *Nucleophaga* is apparently erroneous (Kamyshatskaya et al. unpublished).

Type species – *Nucleophaga amoebae* Dangeard 1895; Fig. 100

Notes – Eight species have been described, and four of them were (re)isolated recently and studied by morphological and molecular means (Michel et al. 2009b, 2012, Corsaro et al. 2014b, 2016, Michel et al. 2021, 2022, Shklyar et al. in press). There are many reports of *Nucleophaga*-like parasites in early literature, summarized by Gordetskaya et al. (2019) and Blackwell et al. (2019). All of them are intranuclear parasites of *Amoebozoa*, one case of intranuclear infection in the euglenoid organism *Peranema trichophorum* was also mentioned (*N. peranemae fide* Hollande & Balsac 1941). A recent revision of the genus was provided by Blackwell et al. (2019).

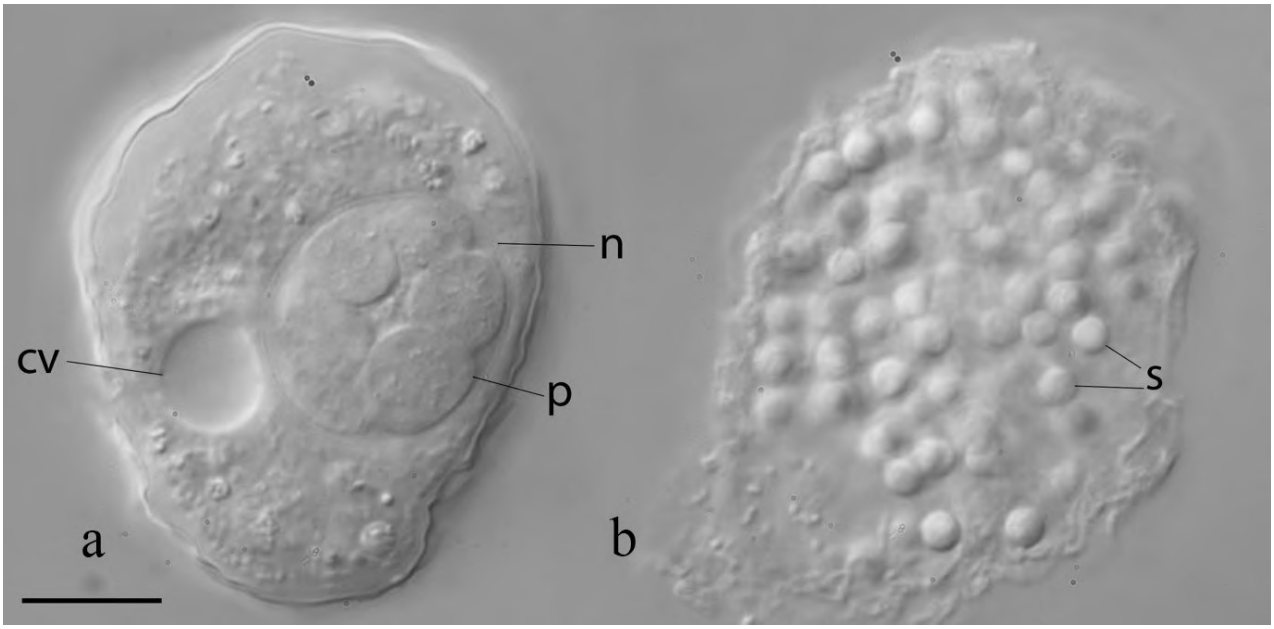


Figure 100 – *Nucleophaga amoebae* KTq-2, an intranuclear parasite of *Thecamoeba quadrilineata* isolated from moss meshwork. a Multinucleate plasmodia (p) developing within the nucleus of amoebae (n). b Young spores (s) in the dead amoebae cell. Scale bar: 10 µm. Micrographs courtesy of Yelisei S. Mesentsev, St. Petersburg University. The cultures of parasites and amoebae were kindly provided by Rolf Michel (Germany). Reproduced with permission of the publisher from: Glotova & Nassonova (2022).

SANCHYTRIOMYCOTA Galindo, López-García, Torruella, Karpov & Moreira
Sanchytriomycetes Tedersoo, Sanchez-Ramirez, Kõljalg, Bahram, M. Döring, Schigel, T.W. May, M. Ryberg & Abarenkov
Sanchytriales Tedersoo, Sanchez-Ramirez, Kõljalg, Bahram, M. Döring, Schigel, T.W. May, M. Ryberg & Abarenkov

Sanchytriaceae Karpov & Aleoshin, Fungal Biology 121(8): 735 (2017)

Amoeboid zoospores with anterior lamellipodium producing subfilopodia, and lateral and posterior filopodia; with (rarely without) posterior pseudocilium; kinetosome composed of nine microtubule singlets or singlets/doublets, 1–1.5 μm in length. Zoospores attach to the algal cell wall, encyst and penetrate the host wall with a short branching rhizoid. Interphase nuclei in sporangia have a centrosome of two centrioles composed of nine microtubular singlets. Predominantly parasites of freshwater algae.

Family type – *Sanchytrium* Karpov & Aleoshin, Fungal Biology 121(8): 735 (2017)

Notes – Sanchytrids are obligate parasitoids of freshwater algae superficially similar to *Chytridiomycetes*. They have rounded to elongated anatropous sporangium and unusual amoeboid zoospores with filopodia and posterior pseudocilium (reduced immotile flagellum). The first sanchytrid was studied by B.V. Gromov with co-authors as a parasite of yellow-green alga *Tribonema gayanum* at the end of the 20th century (unpublished material), which was later described as *Amoeboradix gromovi* Karpov, López-García, Mamkaeva & Moreira (Karpov et al. 2018). A year earlier, a new genus and species *Sanchytrium tribonematis* was described on the basis of molecular phylogenetic and light microscopic studies and placed in *Monoblepharidomycetes* with an unstable position among them (Karpov et al. 2017c). Both species are closely related to each other and unexpectedly gave a long branch among higher fungi on the 18S phylogenetic tree (Karpov et al. 2018). Their sister position to the *Glomeromycota* looked suspicious because of moderate support and probable long-branch attraction artifact, therefore, the genomes and transcriptomes of both species have been assembled, and a multigene phylogeny has shown that *Amoeboradix* and *Sanchytrium* form a separate lineage sister to *Blastocladiomycota* (Galindo et al. 2021). Ultrastructural studies of their zoospores and sporangia revealed extreme peculiarities in both species: highly reduced flagellar apparatus having a very long kinetosome (up to 1.5 μm) composed of 9 singlets of microtubules and the axoneme of just four microtubules supporting a thin immobile pseudocilium; the centrioles in sporangia were also composed of nine singlets (Karpov et al. 2017c, 2018, 2019). Based on phylogenetic position and morphological peculiarities, the genera *Amoeboradix* and *Sanchytrium* were placed in the new phylum *Sanchytriomycota* (Galindo et al. 2021).

Sanchytrium Karpov & Aleoshin, Fungal Biology 121(8): 735 (2017)
Index Fungorum Identifier 818909

Parasite of algae. Sporangia epibiotic, spherical to ovate, with one or more discharge papillae. Zoospores attach to the algal cell wall, encyst, and penetrate the host wall with a short, branched rhizoid (Karpov et al. 2017c).

Type species – *Sanchytrium tribonematis* Karpov & Aleoshin 2017; Fig. 101 (d-f)

Other genus included

Amoeboradix Karpov, López-García, Mamkaeva & Moreira, Protist 169: 137 (2017) [2018]
Index Fungorum Identifier 55642; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Amoeboradix gromovi* Karpov, López-García, Mamkaeva & Moreira; Fig. 101 (a-c)

ZOOPAGOMYCOTA Gryganskyi, M.E. Sm., Spatafora & Stajich
Zoopagomycetes Doweld
Zoopagales Bessey ex R.K. Benj.
Cochlonemataceae in Ainsworth, Sparrow & Susmann, The Fungi (London) 4B: 233 (1974)
Index Fungorum Identifier 80618

Develop conidia that germinate when attached to the pellicle of the rhizopods, or are swallowed by nematodes. Produce either a vegetative endozoic *thallus* (in *Cochlonema* and *Aplectostoma*) or a haustorium (in *Amoebophilus* and *Bdellospora*) that germinates in the host or

fertile hyphae forming single conidia). The germination tube usually disappears when a young thallus is liberated from the distal end of the germination tube, although the germination tube can persist between conidium and thallus during *thallus* development in some species of *Cochlonema*. In most species of *Cochlonema* and *Endocochlus*, the young thallus grows into a coiled structure accompanied by dichotomous branching. Conidiiferous hyphae form aerially and produce chained conidia, cylindrical to fusiform, often multinucleated. Produces zygophoric hyphae with a septum to delimit the gametangium before fusion. After fusion, the zygosporangium develops as a bud-like outgrowth from one of two fused gametangia (Saikawa & Katsurashima 1993, Hirotani-Akabane & Saikawa 2010, Saikawa 2011, Benny et al. 2016b).

Family type – *Cochlonema* Drechsler, Mycologia 27(1): 18 (1935)

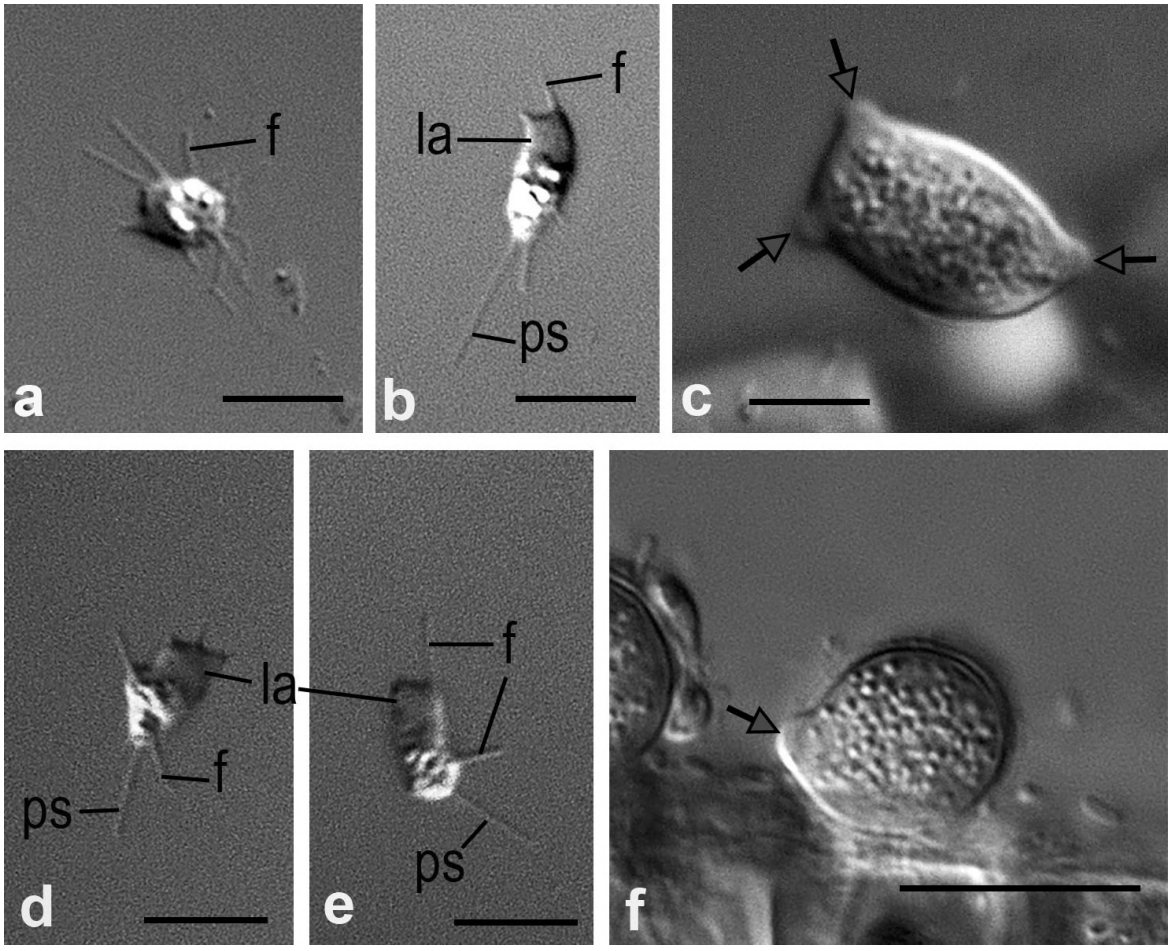


Figure 101 – Main life-cycle stages of *Amoeboradix gromovi* (a-c) and *Sanchytrium tribonematis* (d-f). a Immotile amoeboid zoospore with several filopodia (f). b, d, e Moving zoospores with anterior lamellipodium (la), filopodia (f) and posterior pseudocilium (ps). c, f Mature sporangia with papillae (arrows). Scale bars: a-e = 5 µm; f = 10 µm.

Ecology and life modes – saprobes, most species are endoparasites of testaceous or non-testaceous rhizopods of protozoa, except for species in *Euryancale*, which parasitize nematodes. Require engulfment by phagocytosis or ingestion by their host to germinate (Benny et al. 2014). The host spectrum is variable (Michel et al. 2014).

Notes – Drechsler (1935) introduced this family, which comprises six genera, 33 species, and two varieties (Saikawa 2011) provided a comprehensive ultrastructural comparison of *Zoopagaceae* and *Cochlonemataceae*.

Cochlonema Drechsler, Mycologia 27(1): 18 (1935); Fig. 102
Index Fungorum Identifier 20135

Endoparasites of amoebae and rhizopods. Form a coiled thallus, rarely digitate, usually three or more times wider than the asexual hyphae. Haustoria not formed. Thalli are usually inconspicuous, simple or branched, conidiogenous hyphae with a few branches, each producing a chain of multispored conidia. Spores cylindrical to fusiform, smooth-walled or irregular in outline. Zygospores with a depressed, warted, or peg-like ornament; suspensors hyphoid or somewhat enlarged or more or less parallel or entwined.

Notes – *Cochlonema* comprises 20 species and two varieties and all species are parasites of rhizopods and amoebae Koehsler et al. 2007). Cultures and sequences are available in GenBank.

Type species – *C. verrucosum* Drechsler 1935

Other genera in *Cochlonemataceae*

Amoebophilus P.A. Dang., Botaniste 11: 57 (1910)
Index Fungorum Identifier 20024; Index Fungorum (2025) and Species Fungorum (2025) accepted six species.

Type species – *Amoebophilus penardii* P.A. Dang. 1910,

Notes – Species are ectoparasites of amoebae. Sequence data are unavailable.

Aplectosoma Drechsler, Mycologia 43(2): 173 (1951)
Index Fungorum Identifier 20041; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Aplectosoma microsporum* Drechsler 1951

Notes – Members of the genus are parasites of amoebae, distribution unknown. Sequences are unavailable

Bdellospora Drechsler, Mycologia 27(1): 25 (1935)
Index Fungorum Identifier 20070; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Bdellospora helicoides* Drechsler 1935

Notes – Species are reported as ectoparasites of amoebae and distribution is unknown. Sequences are unavailable

Endocochlus Drechsler, Mycologia 27(1): 14 (1935)
Index Fungorum Identifier 20205; Index Fungorum (2025) and Species Fungorum (2025) accepted four species.

Type species – *Endocochlus asteroides* Drechsler 1935

Notes – Species are endoparasites of amoebae, distribution unknown. Sequences are unavailable.

Euryancale Drechsler, Mycologia 31(4): 410 (1939)
Index Fungorum Identifier 20226; Index Fungorum (2025) and Species Fungorum (2025) accepted five species.

Type species – *Euryancale sacciospora* Drechsler 1939

Notes – Parasite of nematodes, isolated in Europe and Japan. Sequences are unavailable.

Helicocephalidaceae Boedijn, 1958 [1959] (Sydowia 12: 355).
Index Fungorum Identifier 80840

Produces branched haustoria arising from appressoria that can adhere to and hold the living host. Sporangiosphores arise from basal rhizoids, form spores blastosporically on pedicels directly from the sporophores or pedicellate sporangiola on fertile vesicles or arthrospores resulting from disarticulation of the sporophore apex (Benny et al. 2016b). The spores are relatively large and pigmented. Zygospores not described.

Family type – *Helicocephalum* Thaxt. 1891

Ecology and life modes – haustorial parasites of nematodes and nematode eggs.

Notes – Members of the *Helicocephalidaceae* are very rarely reported in the literature, except *Rhopalomyces* (Benny et al. 2016b)

Helicocephalum Thaxt., Bot. Gaz. 16: 201 (1891); Fig. 103
Index Fungorum Identifier 20262

Nematophagous. Produces dark brown arthrospores from the terminal portion of the conidiophore, which is anchored to the substratum by a mass of rhizoidal hyphae. The conidiophores are tall, erect, unbranched, tapering at the distal end and coiled abruptly two or three times. Cultures and sequences are not available.

Type species – *Helicocephalum sarcophilum* Thaxt., Bot. Gaz. 16: 201 (1891)

Notes – *Histocephalum* has six species described from nematodes and nematode eggs; see Kirk et al. (2013; genus accepted), Benny et al. (2016b; classification), cultures and sequences are unavailable.

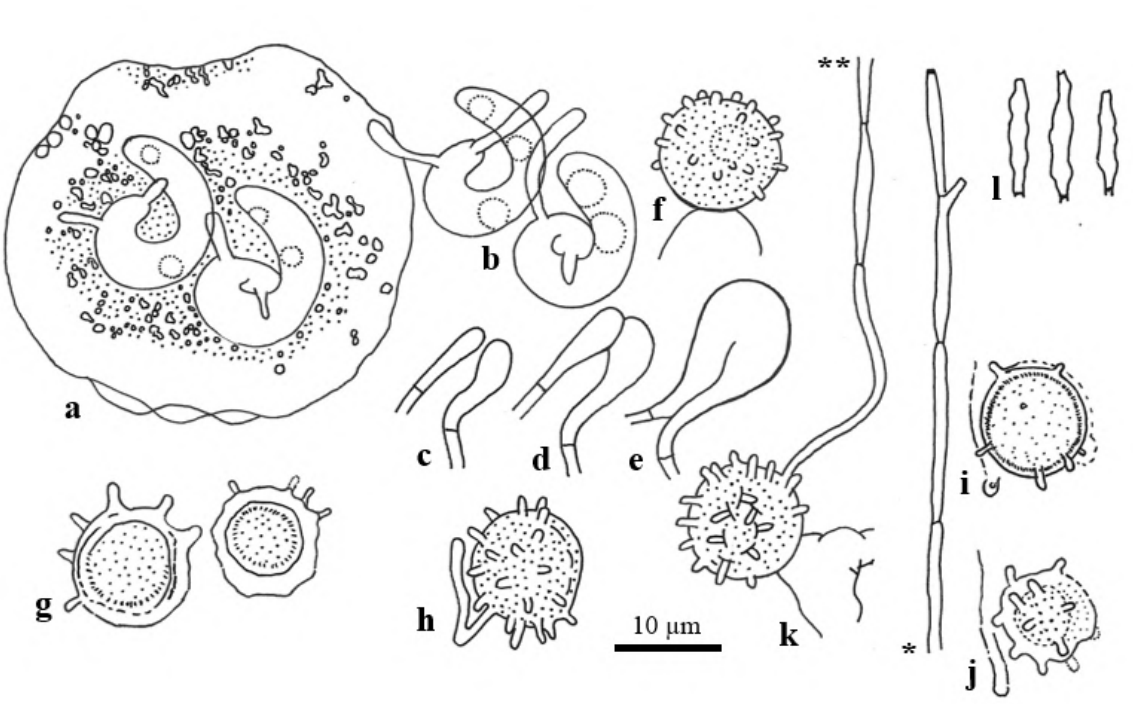


Figure 102 – *Cochlonema cerasphorum*. a-e Successive stages of a pair of gametangia, developed from separate thalli in an amoeba (intervals, ca. 20 min; the two thalli, omitted in c–e). The horn-like projection is seen on the right side of one of the two thalli (a, b). f An immature zygosporangium. g Two mature, thick-walled zygospores in an optical section. h-j A zygospore immediately after the germination shown by a line drawing (h) and two optical sections (i, j). k An empty zygospore after the development of chains of conidia. l Three conidia. Scale bar: a–l = 10 µm (redrawn from Hirotani-Akabane & Saikawa 2010).

Other genera in *Helicocephalidaceae*

Brachymyces G.L. Barron, Canadian Journal of Botany 58(23): 2450 (1980)
Index Fungorum Identifier 20088; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Brachymyces megasporus* G.L. Barron 1980

Rhopalomyces Corda, Pracht-Fl. Eur. Schimmelbild.: 3 (1839)

Index Fungorum Identifier 20489; Index Fungorum (2025) lists 22 epithets, but Species Fungorum (2025) accepted twelve species.

Type species – *Rhopalomyces elegans* Corda

Verrucocephalum Degawa, Mycoscience 55(2): 10.1016/j.myc.2013.07.002 [145] (2013) [2014]
Index Fungorum Identifier 519623; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Verrucocephalum latericorvinisporum* Degawa 2014

Notes – The nematophagous type species was reported from dung and distributed in Asia. Sequences are unavailable.

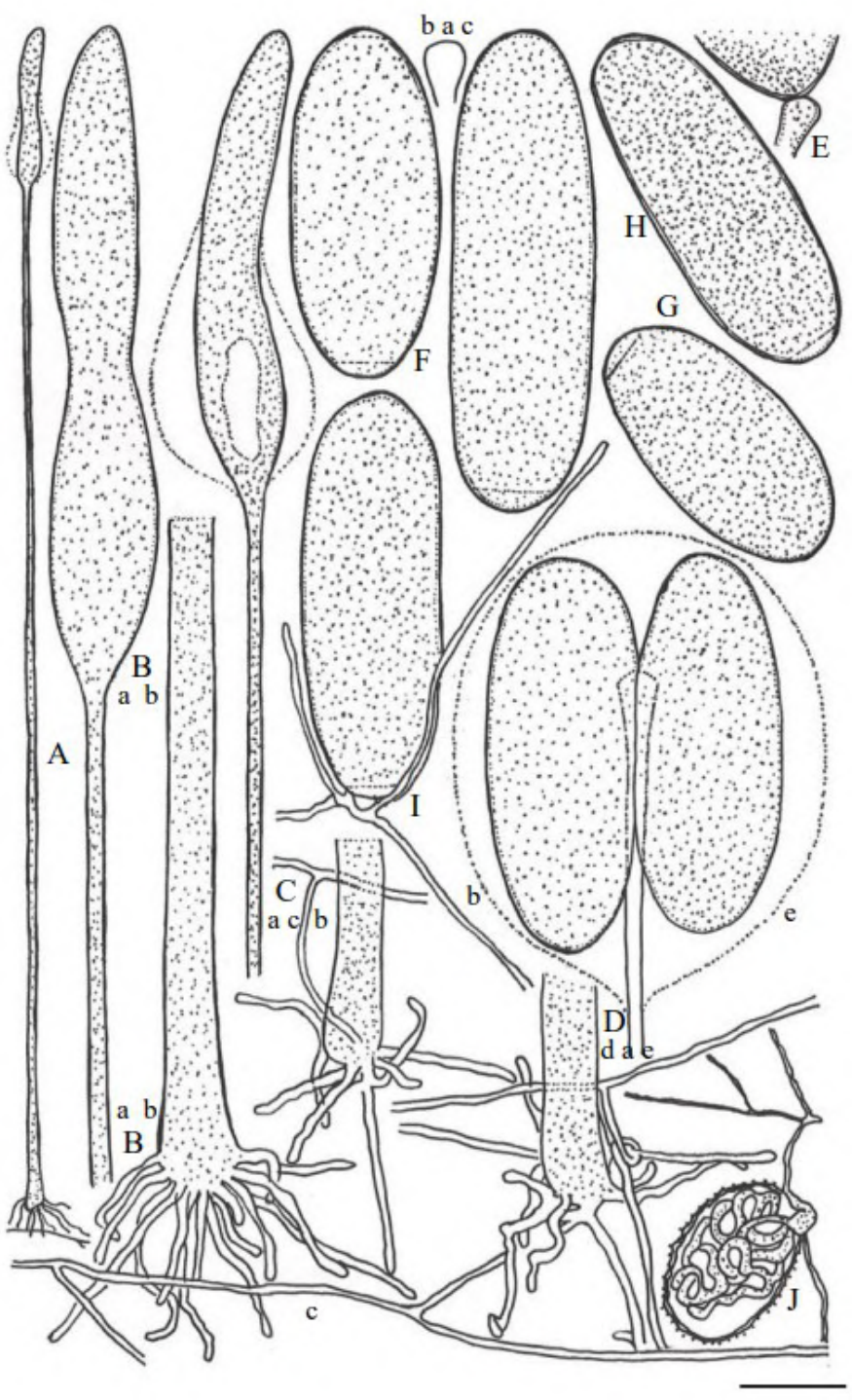


Figure 103 – *Helicocephalum diplosporum* drawn with the aid of a camera lucida; all parts except A shown at a magnification of 500 diameters. A full-grown, immature sporophore with lower portion of terminal head surrounded by a droplet of watery liquid; X125. B Portions of the same sporophore shown at a magnification four times greater: a upper portion showing the slender proximal attachment and median constriction of the terminal head, the outline of the adhering droplet being omitted; b lower portion, showing distribution of the rhizoidal branches about the slightly bulbous base, and connection of the basal part with the mycelial filament c. C Portions of a sporophore almost fully grown: a, upper portion, showing slender attachment and slight median constriction of terminal head, as well as envelopment of the wider proximal part of the head in a droplet of water liquid; b, lower portion, showing distribution of rhizoidal branches about the slightly expanded base; c, mycelial branch connecting sporophore with the mycelium. D Portions of a fully mature sporophore: a terminal portion to which are adhering the inverted proximal spore b and the distal spore **c** with its apex directed upward; both spores being surrounded by a droplet of watery liquid; d, expanded basal portion of sporophore, showing it's supporting rhizoidal branches as well as the hypha connecting it to the mycelial filament e. E Basal portion of proximal spore and tip of mature sporophore, showing manner of disarticulation. F Expanded tip of mature sporophore: **a** flanked by the two spores, b and c, in usual arrangement, the proximal spore b inverted, the exceptionally long terminal spore c in normal posture, with apex directed upward. G An exceptionally short spore of proximal origin. H Spore of average dimensions formed terminally in the same head as G. I Spore of proximal origin germinating from its distal end. J Slender exploratory branch with an appressorium from which a haustorium has grown into a nematode egg (from Drechsler 1943).

Piptocephalidaceae Schroter, 1893 (In Engler and Prantl, Pflanzenfam. 1(1): 132)
Index Fungorum Identifier 816505

The sporangiospores are borne in rod-like merosporangia on branched (*Kukuhaea* and *Piptocephalis*) or unbranched (*Syncephalis*) aerial sporangiophores. The zygospores are warty and are borne on tongs-like suspensors, which are often spirally wound, and with globose outgrowths (especially in *Syncephalis*) (Benjamin 1959, Gräfenhan 1998).

Family type – *Piptocephalis* de Bary, 1865 (Abh. Senckenerg. Naturf. Ges. 5: 356)

Ecology and life modes – Haustorial parasites of fungi, especially *Mucorales*. Members of *Piptocephalidaceae* can be isolated from almost any substrate, especially dung and soil that support the growth of a suitable host.

Notes – Benjamin (1959) was the first to demonstrate that the only true members of *Piptocephalidaceae* are *Piptocephalis* and *Syncephalis*, and this concept has been followed by most subsequent studies (Zycha et al. 1969, Hesseltine & Ellis 1973, Kirk et al. 2013).

Piptocephalis de Bary, 1865 (Abh. Senckenerg. Naturf. Ges. 5: 356)
Index Fungorum Identifier 20422

Mycoparasite. Most species are haustorial parasites of Mucorales, but one can use ascomycete anamorphs as the host. Sporangiophores are dichotomously branched several times; head cells, if formed, and merosporangia are produced on the ultimate branches. Merosporangia uni- or multispored, usually cylindrical. Spores are variously shaped, and when mature, are released dry or in a spore droplet. Zygospores, when formed, are more or less globose; suspensors are opposed. Merosporangia not moniliform, simple or branched; chains of spores straight.

Notes – *Piptocephalis* has c. 40 described species (Reynolds et al. 2019) from fungi, soil and dung (Reynolds et al. 2019, classification).

Type species – *Piptocephalis freseniana* De Bary, 1865 (Abh. Senckenb. Natf. Ges. 5:356)

Other genera in *Piptocephalidaceae*
Kuzuhaea R.K. Benj., Bot. J. Linn. Soc. 91(1-2): 122 (1985)

Index Fungorum Identifier 23077; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Kuzuhaea moniliformis*

Notes – Species is known from soil and shows cosmopolitan distribution. Cultures and sequences available.

Syncephalis Tiegh. & G. Le Monn., Annls Sci. Nat., Bot., sér. 5 17: 372 (1873)
Index Fungorum Identifier 20558; Index Fungorum (2025) lists 73 epithets, but Species Fungorum (2025) accepted 65 species.

Type species – *Syncephalis cordata* Tiegh. & G. Le Monn.

Notes – The species shows worldwide distribution (Benny et al. 2016a, Benny & Smith 2018).

Sigmoideomycetaceae Benny, R.K. Benjamin & P.M. Kirk, 1992 (Mycologia 84: 620)
Index Fungorum Identifier 158553

Fertile head sessile or stalked, composed of regularly septate, coiled fertile hyphae that are dichotomously branched and terminate in sterile spines. Cells at the base of each branch, except the final 1 or 2, produce pairs of stalked fertile vesicles covered with pedicellate, unispored sporangiola. Probably parasitic and heterothallic. Zygospores and chlamydospores are unknown.

Family type – *Sigmoideomyces* Thaxt. Bot. Gaz. (Crawfordsville) 16: 22 (1891).

Ecology and life modes – All members of *Sigmoideomycetaceae* are haustorial parasites of other fungi.

Notes – The family comprises four genera and six species. Genera are *Sigmoideomyces* (type), *Reticulocephalis*, *Sphondylocephalum*, and *Thamnocephalis* (all accepted in Kirk et al. 2013). Classification of the genera is included in Benny et al. (2016a).

Sigmoideomyces Thaxt. Bot. Gaz. (Crawfordsville) 16: 22 (1891); Fig. 104a-c
Index Fungorum Identifier 158553

Sporulating heads more or less globose, sessile; fertile hyphae coenocytic initially, septate when mature, composed of coiled hyphae that bifurcate, one branch becoming a sterile spine, all sterile spine apices free, and the other continuing to grow; at each branching point, except the last 1 or 2, two stalks are produced each bearing a globose fertile vesicle covered with spores. Merosporangia globose to obovoid, unispored, ornamented, pedicellate. Zygospores unknown. Possibly a haustorial parasite.

Notes – *Sigmoideomyces* has two species, *S. divaricatus* McLean, 1923 (Trans. Brit. Mycol. Soc. 8:246) emend. Benny, R.K. Benjamin & P.M. Kirk, 1992 (Mycologia 84:629) (Benny et al. 1992, McLean 1923) and *S. dispiroides* Thaxter, 1891 [Botanical Gazette (Crawfordsville) 16:22] (Benny et al. 1992, Thaxter 1891). Saprobe, cosmopolitan, see Kirk et al. (2013; genus accepted), Benny et al. (2016a; 5492 classification), cultures and sequences are unavailable.

Type species – *Sigmoideomyces dispiroides* Thaxt. 1981

Other genera in *Sigmoideomycetaceae*

Reticulocephalis Benny, R.K. Benj. & P.M. Kirk, Mycologia 84(5): 633 (1992)
Index Fungorum Identifier 11232; Index Fungorum (2025) and Species Fungorum (2025) accepted two species.

Type species – *Reticulocephalis gyrosus* Benny, R.K. Benjamin & P.M. Kirk, 1992 (Mycologia 84:635) (Benny et al. 1992)

Sphondylocephalum Stalpers, Proc. K. Ned. Akad. Wet., Ser. C, Biol. Med. Sci. 77(4): 400 (1974)
Index Fungorum Identifier 9996; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Sphondylocephalum verticillatum* (Thaxt.) Stalpers, 1974 (Proc. K. Ned. Akad. Wet., Ser. C, Biol. Med. Sci. 77(4): 400)

Thamnocephalis Blakeslee, Bot. Gaz. 40: 165 (1905); Fig. 104d-j
Index Fungorum Identifier 20570; Index Fungorum (2025) and Species Fungorum (2025) accepted three species.

Type species – *Thamnocephalis quadrupedata* Blakeslee, 1905 [Botanical Gazette (Crawfordsville) 40:165]

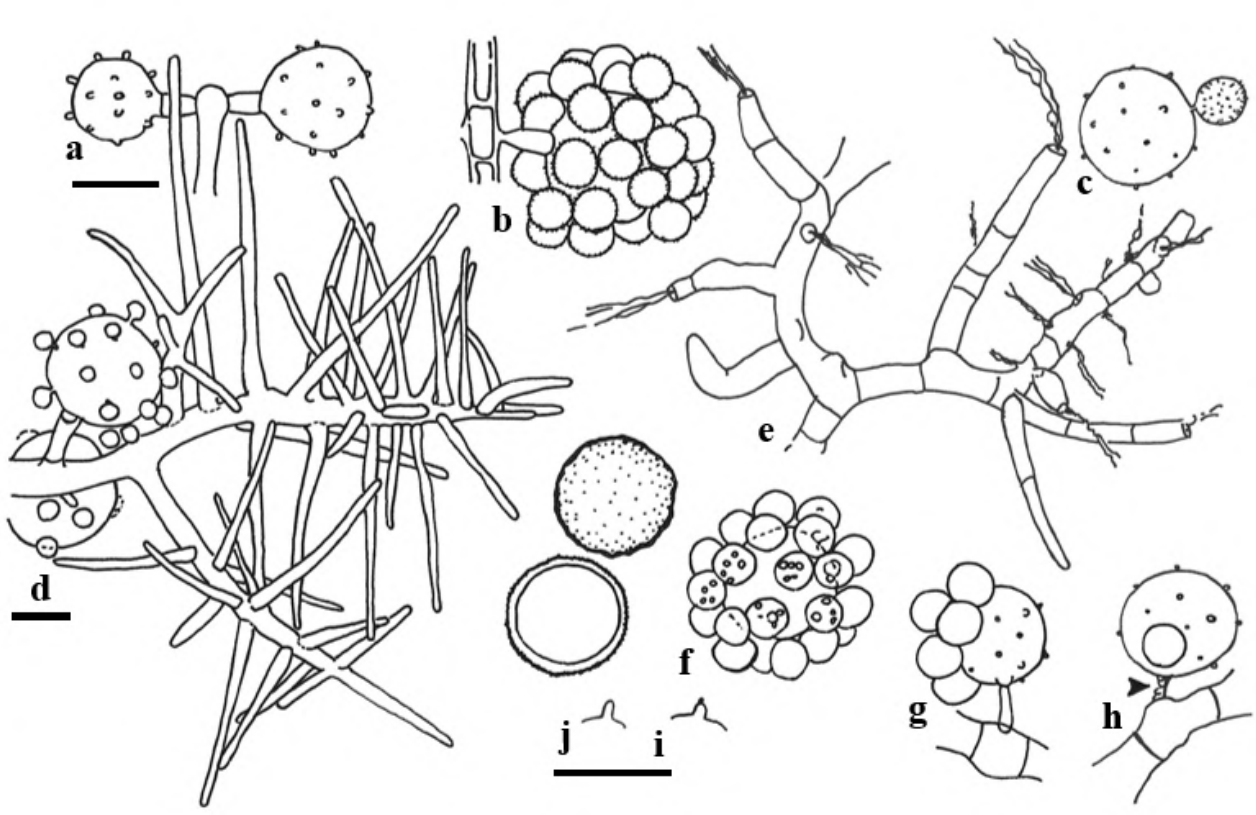


Figure 104 – *Sigmoideomyces* and *Thamnocephalis*. a–c *T. quadrupedata* (FH). a A typical pair of stalked fertile vesicles. b A single, stalked, fertile vesicle covered with sporangiola. c A single fertile vesicle with a sporangiolum still attached. Note relative length of pedicel. d–j *S. divaricatus* (Thaxter 1891). d Apical portion of a young branch showing the large number of small spines produced at more or less right angles to the main branches. **e** Apical portion of a mature branch showing that some cells and lateral spines have lysed leaving the outer wall layer as a membranous remnant. f A fertile vesicle covered with sporangiola. **g** A stalked fertile vesicle still attached to a fertile hypha. h A fertile vesicle after evanescence of the subtending stalk (arrowhead). i Two typical pedicels. j Two sporangio1a, the one below in optical section and the other showing the spinose surface. Scale bars: a - j= 10 µm (Redrawn from Benny et al. 1992).

Zoopagaceae Drechsler ex Drechsler, 1938 (Mycologia 30: 154) emend. Duddington, 1973 (Ainsworth et al., *The Fungi* IVB, p. 233).

Index Fungorum Identifier 81537

Producing extensive, fine, highly branched, external hyphae which give rise to haustoria upon contact with a host. Spores are produced singly or in chains. Zygospores are hyaline, with an ornamented zygosporangial wall; suspensors are apposed, hyphoid.

Family type – *Zoopage* Drechsler, Mycologia 27(1): 30 (1935)

Ecology and life modes – Fungi predacious on amoebae, nematodes, or rotifers. Members of the *Zoopagaceae* can be observed where a suitable host animal can be found including soil, dung, humus, rotting vegetation Saikawa 2011).

Notes – The family comprises seven genera and 71 species. Genera are *Zoopage* Drechsler (type), *Acaulopage* Drechsler, *Cystopage* Drechsler, *Lecophagus* M.W. Dick, *Stylopage* Drechsler, *Tentaculophagus* Doweld, *Zoophagus* Sommerst. All genera were accepted in Kirk et al. (2013) and Benny et al. (2016a).

Zoopage Drechsler, Mycologia 27(1): 30 (1935)
Index Fungorum Identifier 501283

Predaceous on amoebae and, less frequently, rhizopods. Capture the host by secretion of a sticky substance. Haustoria are produced within the host, and vegetative and reproductive hyphae are produced externally. Propagules are produced on relatively short sporangiophores. Merosporangia multispored, simple or branched. Spores fusiform, long-fusiform or falcate, wall smooth or rough; spore appendages not formed, one species with empty cells. Zygospores are more or less globose, with a cupulate zygosporangium; suspensors are hyphoid, more or less equal.

Type species – *Zoopage phanera* Drechsler [as 'planera'], Mycologia 27(1): 30 (1935)

Notes – *Zoopage* is a haustorial parasite of amoebae and testaceous rhizopods that trap hosts with an adhesive. Cultures and sequences are unavailable.

Other genera in *Zoopagaceae*

Acaulopage Drechsler, Mycologia 27(2): 185 (1935)
Index Fungorum Identifier 20002; Index Fungorum (2025) lists 34 epithets, but Species Fungorum (2025) accepted 31 species.

Type species – *Acaulopage rhaphidospora* Drechsler, 1935 (Mycologia 27:188)

Notes – All species were reported as parasites of amoebae.

Cystopage Drechsler, Mycologia 33(3): 251 (1941)
Index Fungorum Identifier 20156; Index Fungorum (2025) and Species Fungorum (2025) accepted nine species.

Type species – *Cystopage lateralis* Drechsler, Mycologia 33(3): 251 (1941)

Notes – All species were reported as haustorial parasites of amoebae and nematodes.

Lecophagus M.W. Dick, Mycol. Res. 94(3): 351 (1990)
Index Fungorum Identifier 25454; Index Fungorum (2025) lists nine epithets, but Species Fungorum (2025) accepted eight species.

Type species – *Lecophagus fasciculatus* M.W. Dick, Mycol. Res. 94(3): 351 (1990)

Stylopage Drechsler, Mycologia 27(2): 197 (1935)
Index Fungorum Identifier 20555; Index Fungorum (2025) lists 19 epithets, but Species Fungorum (2025) accepted 18 species.

Type species – *Stylopage lepte* Drechsler, Mycologia 27(2): 202 (1935)

Tentaculophagus Doweld, Index Fungorum 78: 1 (2014)
Index Fungorum Identifier 550381; Index Fungorum (2025) and Species Fungorum (2025) accepted one species.

Type species – *Tentaculophagus karlingii* Doweld 2014

Zoophagus Sommerst., Öst. bot. Z. 61: 372 (1911)
Index Fungorum Identifier 20600; Index Fungorum (2025) lists five epithets, but Species Fungorum (2025) accepted four species.

Type species – *Zoophagus insidians* Sommerst., Öst. bot. Z. 61: 372 (1911)

Notes – Species are reported as ectoparasites of loricate rotifers and nematodes.

Fossil non-*Dikarya* fungi

Selected genera and species of non-*Dikarya* fungi, along with their location, horizon, age, and relevant references, are presented in Table 3.

Table 3 Fossil non-*Dikarya* fungi

Phylum	Genus	Species	Location and Horizon/ age	Reference
Chytridiomycota	*Brijax*	*B. amictus*	UK, on archaeosporalean acaulospores from Rhynie Chert, Early Devonian	Krings & Harper (2020)
	Cultoraquaticus	*C. trewinii*	Great Britain, from eggs of *Lepidocaris rhyniensis* from Rhynie Chert, Early Devonian	Strullu-Derrien et al. (2016)
	Globicultrix	*G. nugax*	Great Britain, in glomeromycotan spore from Rhynie Chert, Early Devonian	Krings et al. (2009)
	Grilletia	*G. sphaerospermi*	France, on seeds of *Sphaerospermum oblongum*, Late Carboniferous	Renault & Bertrand (1885)
	Guizhounema	*G. endosporicum*	Guizhou, China, Late Permian	Mu (1977)
	Illmanomyces	*I. corniger*	Great Britain, within a loose accumulation of land plants and fungal spores and tissues, Early Devonian	Krings & Taylor (2013)
	Krispiromyces	*K. discoides*	Great Britain, Early Devonian	Taylor et al. (1992)
	Lyonomyces	*L. pyriformis*	Great Britain, Early Devonian	Taylor et al. (1992)
	Milleromyces	*M. rhyniensis*	Great Britain, Early Devonian	Taylor et al. (1992)
	Nimbosphaera	*N. rothwellii*	Great Britain, Windyfield Chert, Early Devonian	Harper & Krings (2019)
	Oochytrium	*O. lepidodendri*	France, Late Carboniferous	Renault (1894)
	Palaeozoosporites	*P. renaultii*	Great Britain, on roots of *Asteroxylon mackei*, Rhynie Chert, Early Devonian	Strullu-Derrien in Strullu-Derrien et al. (2015)
	Perexiflasca	*P. tayloriana*	Great Britain, on silicified chert, Early Devonian	Krings et al. (2017)
		P. ventricosa	Great Britain, in silicified chert, Early Devonian	Krings & Harper (2019)
	Rhizophydites	*R. matryoshkae*	Great Britain, Rhynie Chert, Early Devonian	Krings & Harper in Krings et al. (2021)
		R. shutei	Great Britain, in silicified fossil in chert matrix on glomeromycotan acaulospores of *Archaeosporites rhyniensis* type from Rhynie Block of Dryden Flags Formation, Early Devonian, early (but not earliest) Pragian to earliest Emsian	Krings (2024)
	Trewinomyces	*T. annulifer*	Great Britain, occurs as tufts on decaying land plant axes from the Rhynie Chert, Early Devonian	Krings et al. (2016)
Glomeromycota	*Archaeosporites*	*A. rhyniensis*	Great Britain, Early Devonian	Walker et al. in Harper et al. (2020)
	Gigasporites	*G. myriamyces*	Antarctica, in root cortex of *Antarcticycas*	Phipps & Taylor (1996)
	Glomites	*G. cycestris*	Fremouw Peak, near the Beardmore Glacier, Antarctica, Early-Middle Triassic	Phipps & Taylor (1996)

Table 3 Continued

Phylum	Genus	Species	Location and Horizon/ age	Reference
		G. rhyniensis	Rhynie, Aberdeenshire, Scotland, Early Devonian	Taylor et al. (1995)
		G. sporocarpoides	Rhynie, Aberdeenshire, Scotland, Early Devonian	Karatygin et al. (2006)
		G. vertebrariae	Associated with rootlets of *Vertebraria*, in permineralized peat, Antarctica, Late Permian	Harper et al. (2013)
	Glomorphites	*G. intercalaris*	Antarctica, Permian	Garcia Massini (2007)
	Palaeoglomus	*P. boullardii*	Great Britain, in aerial stems of *Horneophyton lignieri*, Early Devonian	Strullu-Derrien & Strullu in Strullu-Derrien et al. (2014)
		P. grayi	Wisconsin, USA, in dolomitic rocks, Mid-Ordovician	Redecker et al. (2002)
	Palaeomyces	*P. agglomeratus*	Muir of Rhynie, Aberdeenshire, Scotland, Early Devonian	Kidston & Lang (1921)
		P. asteroxyli	Muir of Rhynie, Aberdeenshire, Scotland, Early Devonian	Kidston & Lang (1921)
		P. gordonii	Muir of Rhynie, Aberdeenshire, Scotland, Early Devonian	Kidston & Lang (1921)
		P. horneae	Muir of Rhynie, Aberdeenshire, Scotland, Early Devonian	Kidston & Lang (1921)
		P. simpsonii	Muir of Rhynie, Aberdeenshire, Scotland, Early Devonian	Kidston & Lang (1921)
	Udaria	*U. saxenae*	Sirmaur District, Himachal Pradesh, India, Subathu Formation, Early Tertiary	Gupta (1996)
		U. singhii	Sirmaur District, Himachal Pradesh, India, Subathu Formation, Early Tertiary	Gupta (1996)
	Zwergimyces	*Z. vestitus*	Muir of Rhynie, Aberdeenshire, Scotland, Early Devonian	Krings & Taylor (2013)
Mucoromycota	*Lithomucorites*	*L. miocenicus*	Tlangsam, Mizoram, India, Miocene	Kar et al. (2010)
		L. tripuraensis	South Tripura District, Tripura, India, Bhuban Formation, Early Miocene	Mandaokar & Saxena (2014)
	Palaeomycites	*P. acinus*	Cypress Hills locality, Alberta, Canada, Maastrichtian	Srivastava (1968), Kalgutkar & Jansonius (2000)
		P. bharwainensis	Una District, Himachal Pradesh, India, Miocene-Pliocene	Singh & Saxena (1981), Kalgutkar & Jansonius (2000)
		P. butleri	Bronson, southeastern Kittson County, Minnesota, USA, Late Pleistocene.	Rosendahl (1943), Kalgutkar & Jansonius (2000)
		P. carbonarius	Near South Bend, Nebraska, USA, Upper part of Missouri Series, Late Pennsylvanian	Elias (1966), Kalgutkar & Jansonius (2000)
		P. cerasiformis	Mackenzie Delta Region, Mackenzie District, N.W. Territory, Canada, Pliocene to possibly Palaeogene	Norris (1986), Kalgutkar & Jansonius (2000)
		P. disodylis	Italy, Miocene	Baccarini (1900), Kalgutkar & Jansonius (2000)

Table 3 Continued

Phylum	Genus	Species	Location and Horizon/ age	Reference
		P. frodinghamii	Great Britain, Jurassic	Ellis (1915), Kalgutkar & Jansonius (2000)
		P. minnesotensis	Springfield, Minnesota, USA, Early Pleistocene	Rosendahl (1943), Kalgutkar & Jansonius (2000)
		P. robustus	Kutch, India, Oligocene	Kar (1979), Kalgutkar & Jansonius (2000)
Oomycota (Kingdom: *Chromista*)	*Apodachlya*	*A. pyrifera*	Great Britain, Rhynie Chert, Early Devonian	Harvey et al. (1969
	Combresomyces	*C. caespitosus*	Antarctica, silicified peat associated with plant debris around leaf deposits of *Glossopteris*, *Noeggerathiopsis* and *Vertebraria*, Middle Permian	Slater et al. (2013)
		C. cornifer	France, periderm of *Lepidodendron rhodumnense*, Late Visean/ Mississippian	Dotzler et al. (2008
		C. rarus	Antarctica, silicified peat associated with *Australoxylon* and *Vertebraria*, Middle Permian	Slater et al. (2013)
		C. williamsonii	Great Britain, stem of *Lyginopteris oldhamia*, Bashkirin Stage, Pennsylvanian	Strullu-Derrien et al. (2010)
	Palaeodikaryomyces	*P. baueri*	Bavaria, Germany, in miniscule fragments of amber occurring in coal-bearing sandstone, Early Triassic	Dörfelt & Schäfer (1998)

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DECLARATION OF COMPETING INTEREST

The authors have declared that no competing interests exist.

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