Title: Parasitic zoosporic eufungi: taxonomic and phylogenetic diversity, ecology, and impacts

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Abstract: Zoosporic eufungi (i.e., chytrids, *sensu lato*) comprise a phylogenetically and ecologically diverse guild of early diverging fungal phyla (Chytridiomycota, Monoblepharomycota, Neocallimastigomycota, Blastocladiomycota, Sanchytriomycota, Aphelidiomycota, Cryptomycota/Rozellomycota, and Olpidiomycota). While most circumscribed zoosporic eufungi function as decomposers of recalcitrant materials, such as pollen, chitin, and keratin, many taxa are parasites of algae and other microorganisms, land plants, and animals in terrestrial and aquatic ecosystems. The effects of parasitic chytrids on their hosts—and the downstream ecological consequences—are generally poorly understood, particularly when compared to better characterized host-parasite systems in the Dikarya. The most infamous chytrid fungus is the amphibian pathogen *Batrachochytrium dendrobatidis*, and its discovery and effect on global amphibian populations spurred a renewed interest in the diversity of zoosporic eufungi. Increasingly, research in freshwater and marine habitats has demonstrated that zoosporic eufungi regulate algal communities and serve as an important link between trophic levels in aquatic food webs. As pathogens of land plants, zoosporic eufungi can result in yield losses directly both as a pathogen or by serving as a vector for plant viruses. This chapter explores the diversity of chytrid fungi *sensu lato* in light of recent reclassifications with an emphasis on species that are parasites and pathogens of a variety of hosts ranging from autotrophs (algae and land plants), unicellular microorganisms (e.g., amoebae, flagellated heterotrophs), and invertebrate and vertebrate animals. The ecosystem dynamics of zoosporic eufungi parasites and pathogens are discussed, highlighting their impact on agriculture and industry.

Introduction

The zoosporic eufungi are a diverse, paraphyletic group (Figure 1) that inhabit a variety of terrestrial, freshwater, and marine habitats. Historically, zoosporic eufungi with a single, smooth, posteriorly-oriented flagellum were classified in a single order, the Chytridiales, colloquially referred to as chytrid fungi. Phylogenetic analyses using zoospore ultrastructure and molecular sequences resulted in the reclassification of chytrid fungi into several phyla, these being Chytridiomycota (containing a plethora of orders), Monoblepharomycota, Neocallimastigomycota, Blastocladiomycota, Cryptomycota/Rozellomycota and Olpidiomycota. Zoosporic eufungi function as decomposers of recalcitrant materials, such as chitin, cellulose, keratin, and pollen, and as parasites of algae & other microorganisms, land plants, and animals in terrestrial and aquatic ecosystems. The most infamous zoosporic eufungus is *Batrachochytrium dendrobatidis*, and its devastating impact on global amphibian populations spurred a renewed interest in the diversity of zoosporic eufungi. As parasites, zoosporic eufungi regulate communities of algae, microcrustaceans, aquatic dipterans, rotifers, etc., and serve as an important link between trophic levels in aquatic food webs. As parasites of land plants, zoosporic eufungi and the viruses they vector can result in substantial yield losses. This chapter explores the diversity of zoosporic eufungi in light of recent reclassifications with an emphasis on species that are parasites and how they affect ecosystem dynamics, agriculture, and industry. Finally, the chapter closes with open questions and suggestions for the areas most in need of research at this time.

Diversity of zoosporic eufungi

Historically, the description and classification of zoosporic eufungi were based on morphological traits that we now know are highly convergent and plastic and, thus, unreliable. The advent of zoospore ultrastructural and molecular phylogenetic analyses has provided a more robust hypothesis of evolutionary relationships (Figure 1) and therefore significant changes in taxonomy. However, many taxa described on the basis of morphology have not been re-evaluated using zoospore ultrastructure or molecular phylogenetics, and their placement within the contemporary classification is uncertain. In such cases, we treat these taxa as belonging to the contemporary counterpart of their original placement. For example, all described species of *Phlyctochytrium* (Figure 2j) are discussed as members of that genus within the order Chytridiales, though future ultrastructural or molecular phylogenetic analyses may place them elsewhere. Additionally, all species of *Polyphagus* are included as members of Polyphagales, though this order is represented by only two species in contemporary analyses. Thus, the classification scheme used below is simply for ease of discussion and is not meant as a definitive treatment of the groups. The phyla Aphelidiomycota, Blastocladiomycota, Chytridiomycota, Cryptomycota/Rozellomycota, Monoblepharomycota, Olpidiomycota, Sanchytriomycota are presented herein.

Aphelidiomycota

Aphelids are intracellular parasites of various algal lineages (Karpov *et al*., 2014b). Hosts of aphelids include chlorophycean green algae (Gromov and Mamkaeva, 1970; Karpov *et al*., 2013; Letcher *et al*., 2013, 2015b), trebouxiophycean green algae (Gromov and Mamkaeva, 1968; Seto *et al*. 2020a), yellow green algae (Karpov *et al*., 2016b, 2017b, c), and diatoms (Scherffel, 1925; Schweikert and Schnepf, 1996). Some taxa have been found in mass culture of algae for commercial use such as *Scenedesmus* and have caused crashes of farmed algal cultures (Gromov and Mamkaeva, 1970; Letcher *et al*., 2013, 2015b; Ding *et al*., 2017; Seto *et al*., 2020a).

Aphelid life cycles resemble those of chytrid fungi in producing posteriorly uniflagellate zoospores (although some produce amoeboid cells without a flagellum). Unlike most chytrid fungi, which grow as a zoosporangium with a chitinous cell wall and acquire nutrients by osmotrophy, aphelids penetrate the host cell as a naked cell and consume host cytoplasm by phagocytosis. Molecular phylogenetic analyses revealed that aphelids formed a clade along with rozellids (Cryptomycota/Rozellomycota) and Microsporidia, which are related to Fungi (Karpov *et al*., 2013). Although the so-called ARM clade (Aphelid-Rozellid-Microsporidia clade, Karpov *et al*., 2013) were not supported strongly, Karpov *et al*. (2014b) proposed it as a new superphylum Opisthosporidia, including the three phyla: Cryptomycota/Rozellomycota, Microsporidia, and newly established Aphelida. However, phylogenomic analysis (Torruella *et al*., 2018) revealed that Opisthosporidia was paraphyletic and an aphelid, *Paraphelidium tribonemae* was sister to core fungi (Dikarya, Chytridiomycota *sensu lato*, and paraphyletic Zygomycota). The affiliation of aphelids is still controversial; Karpov *et al*. (2014b) regarded aphelids as not true fungi and included them into a protistan phylum Aphelida. By contrast, in the recently proposed taxonomic system of Fungi (Tedersoo *et al*., 2018), aphelids were included into Fungi as a new fungal phylum Aphelidiomycota.

Currently, Aphelidiomycota includes 1 class, 1 order, 1 family, and 5 genera (Letcher and Powell, 2019; Hyde *et al*., 2024). Three genera inhabit freshwater environments and are distinguished based on characteristics of asexual spores. *Aphelidium* produces posteriorly uniflagellate zoospores with pseudopodia. In contrast, *Amoeboaphelidium* (Figure 2n) produces amoeboid cells with or without pseudocilium (Karpov *et al*., 2013). The recently described genus *Paraphelidium* resembles *Aphelidium* but is distinguished based on pseudopodia (Karpov *et al*., 2017b,c). The monotypic genera *Pseudaphelidium* and *Protaphelidium* are from marine environments, the latter parasitizing a *Rhizoclonium* sp. green alga (Seliuk and Karpov, 2024).

Blastocladiomycota

Blastocladiomycota, or blastoclad fungi, are a morphologically and ecologically diverse lineage of zoosporic eufungi sister to Dikarya, Mucoromycota, Zoopagomycota, and *Olpidium bornovanus* (James *et al*., 2014; Spatafora *et al*., 2016; Chang *et al*., 2021; Ames *et al*., 2022). Traditionally, blastoclad fungi were placed with chytrid fungi in Chytridiomycota. Four features that separate Blastocladiomycota from other phyla are the alternation of generations, sporic meiosis, anisogamy, closed nuclear poles during mitosis, and the presence of a nuclear cap in the zoospore, which James *et al*. (2006), in combination with molecular phylogenetic analyses, used to describe the phylum (James *et al*., 2014). Taxonomy within the phylum is in flux as several taxa were found to be para/polyphyletic in molecular phylogenetic analyses (Porter *et al*., 2011), while others have yet to be included in molecular studies (James *et al*., 2014). According to Wijayawardene *et al*. (2018), Blastocladiomycota contains 1 class, 3 orders, 8 families, and 14 genera. However, Wijaywardene *et al*. (2018) did not include the genera *Urophlyctis*, *Blastocladiella*, *Catenaria*, *Polycarpum*, or *Myrmicinosporidium*, which would bring the number of genera to 19. These 19 genera contain species that are either saprobes or parasites of invertebrates and photosynthetic organisms (James *et al*., 2014; Gorczak and Trigos-Peral, 2021); the exception being *Catenaria allomycis*, which is a parasite of the saprobic blastoclad genus *Allomyces* (James *et al*., 2014). Taxonomy remains open for interpretation, however, as Hyde *et al*. (2024) recommend the phylum contains 2 classes, 4 orders, 8 families, and 12 genera, with *Microallomyces* and *Retesporangicus* as *incertae sedis*.

Blastocladian parasites of invertebrates include species in the genera *Catenaria* (some of which Doweld (2014a) segregated into *Nematoceromyces*), *Sorochytrium*, *Callimastix*, *Coelomomyces* (Figure 3w), *Coelomycidium*, *Polycarpum*, *Endoblastidium*, and *Myricinosporidium*. Gleason *et al*. (2010b) provided a detailed review of these parasites and their importance in aquatic food webs. Briefly, *Callimastix* is a parasite of copepods; some *Catenaria* species are parasites of nematodes; *Coelomomyces*, *Coelomycidium*, *Endoblastidium, Nematoceromyces*, and *Myrmicinosporidium* are insect parasites; *Polycarpum* is a parasite of *Daphnia*; *Sorochytrium* is a parasite of tardigrades (Gleason *et al*., 2010b; James *et al*., 2014). Very little is known about *Callimastix* and *Endoblastidium*. Species of *Nematoceromyces* and *Catenaria* that infect midge eggs (Diptera, Chironomidae) can cause mortality rates of 7-39% (Martin, 1981, 1984, 1991). Species of *Coelomomyces* have been well studied due to their potential use as a biocontrol agent of mosquitoes (Couch and Bland, 1985; Scholte *et al*., 2004), and *Polycarpum* has received some attention due to its effect on *Daphnia* populations, which are key invertebrates in many aquatic food webs (Gleason *et al*., 2010; James *et al*., 2014). *Myrmicinosporidium* are widespread in several temperate and sub-tropical ant species, but very little is known about their impact on the host (Goncalves *et al*., 2012; Espadaler and Santamaria, 2012; Trigos-Peral *et al*., 2017; Quevillon and Hughes, 2018; Gorczak and Trigos-Peral, 2021).

Most blastocladian parasites of photosynthetic organisms can be found in the ecologically and agriculturally relevant genera *Paraphysoderma*, *Physoderma* (Figure 2a,b), and *Urophlyctis*, though the generic boundaries between *Physoderma* and *Urophlyctis* are not clear (Porter *et al*., 2011; Letcher *et al*., 2016). The one exception is *Blastocladiella anabaenae* (also known as *Clavochytridium anabaenae*), which parasitizes cyanobacteria in the genus *Anabaena* (Canter and Willoughby, 1964). The monotypic species of *Paraphysoderma*, *P. sederbokerensis*, is a threat to the industrial production of astaxanthin through culturing the green alga *Haematococcus* (James *et al*., 2011). Most species of *Physoderma* parasitize plants that grow in moist/swampy/marshy areas, though a couple, such as *P. maydis* (Figure 2a,b) are important crop parasites (Karling, 1950).

Chytridiomycota

Caulochytriales

Caulochytrium was erected to accommodate a parasite of *Gloeosporium* with unusual morphology (Voos, 1969). *Caulochytrium gloeosporii* and other members of the genus parasitize hyphal fungi growing on above-ground plant tissues (Voos, 1969; Olive, 1980; Powell, 1993). The genus is unique in its formation of aerial sporangia and the production of a secondary zoospore if the primary zoospore fails to encyst on a host (Voos, 1969; Powell, 1993). These characteristics converge upon evolutionary trends seen in the oomycetes, particularly the Peronosporales, and other organisms that grow on the above-ground structures of plants (Powell, 1993). A second instance of convergent evolution in the genus is in the parasite-host interface; just like plant parasites in Dikarya and mycorrhizas, the haustoria of *Caulochytrium* do not penetrate the host plasma membrane (Powell, 1993). Because species of *Caulochytrium* are readily culturable with their host, they make an ideal system to study the selective pressures leading to the convergent evolution of these traits.

Doweld (2014b) erected Caulochytriomycota and Caulochytriales due to the morphological and ecological distinctiveness of the genus compared to other species in Chytridiomycota. However, whole genome phylogenetic analyses place *Caulochytrium protostelioides* within Chytridiomycota (Ahrendt *et al*., 2018), and thus, accepting Caulochytriomycota would render Chytridiomycota needlessly paraphyletic. Therefore, at this time, we reject Caulochytriomycota with the caveat that inclusion of the other species in molecular phylogenetics may validate its description.

Chytridiales

The first chytrid fungi were described by botanists as minute microorganisms parasitizing algae and aquatic plants (e.g., Braun, 1851; Zopf, 1884; Dangeard, 1886). Thus, the initial history of zoosporic eufungi is directly linked to the observation and description of multiple parasitic species, such as *Chytridium olla* (Braun, 1851), *Rhizidium mycophilum* (Braun, 1856), *R. algaecolum* (Zopf, 1884), *Phlyctochytrium hydrodictyi* (Schroeter, 1893), *Rhizophydium cornutum* (Rabenhorst, 1868), and *Rhizidium euglenae* (Dangeard, 1886). Two important modifications in the systematics of Chytridiales correspond to the sequencing of the type species, *Chytridium olla* and its inclusion in a phylogenetic reconstruction (Vélez *et al*., 2011). The results make possible the establishment of a limit of the order Chytridiales, where this genus is included. Additionally, Letcher and Powell (2014) suggested that during the evolutionary process there was a reduction in the ultrastructural complexity of the zoospores produced by representatives of this order. However, the major impact in Chytridiales systematics was the transferring of *Rhizophydium* representatives to the new order Rhizophydiales, as this genus had the largest number of species among all genera of the phylum, among which several are parasites of algae, plants, animals, and other fungi (Letcher *et al*., 2006). Some of these parasitic species were then transferred to other genera (Letcher and Powell, 2012; Letcher *et al*., 2008b, 2015a) and will be discussed below.

Chytridiales *sensu* Letcher and Powell (2014) still encompasses a wide variety of parasites that infect green algae, brown algae, diatoms, dinoflagellates, plants, and other fungi. For example, Vélez *et al.* (2011), isolated and sequenced the obligate parasite *Chytridium olla*, infecting *Oedogonium capilliforme*, while Leshem *et al.* (2016) observed a new species, *Dinochytrium kinnereticum,* parasitizing dinoflagellates in Lake Kinneret, Israel. Seto *et al*. (2017) revealed that "*Rhizophydium*" *planktonicum* is positioned in Chytridiales, so this species needs to be transferred to a distinct genus. Seto and Degawa (2018b) described *Pendulichytrium sphaericum* parasitizing the diatom *Aulacoseira granulata.* Kagami *et al*. (2021) reported additional lineages of diatom parasites in Chytridiales by single-cell sequencing. These taxa are distributed among two families–Chytridiaceae and Chytriomycetaceae–and an *incertae sedis* group. However, several old genera in Chytridiales, such as *Chytridium*, *Chytriomyces* (Figure 2f–h), *Phlyctochytrium* (Figure 2j), and *Rhizidium* include a number of parasitic species (Sparrow, 1960). As well, there are still numerous parasites described before the advent of molecular techniques that were not cultured or sequenced and remain *incertae sedis* in the taxonomic scheme developed from molecular phylogenetic analyses. Accurately placing them will require the utilization of PCR and single-cell techniques (e.g., Ishida *et al*., 2015; Ahrendt *et al*., 2018).

Although the phylogenetic affiliations of several Chytridialian genera remain uncertain, it is likely that they play important roles in aquatic ecosystems and food webs, where they parasitize a variety of microalgal and microfungal hosts. For example, *Phlyctochytrium hidrodictyi*, *Rhizidium algaecolum*, *R. euglenae* and *Rhizidium mycophilum* are parasites on a variety of algae (Braun, 1851, 1856; Zopf, 1884; Dangeard, 1886). *Septosperma rhizophydii* (Figure 3r,s) is a hyperparasite of chytrid fungi *Rhizophydium spp., Rhizidium spp.* and *Rhizophlyctis spp.*, intensively growing over the host zoosporangium and causing significant mortality (Whiffen, 1942; Sparrow, 1952; Willoughby, 1956). *Entophlyctis apiculata* was described as a parasite of *Chlamydomonas* sp. (Braun, 1856; Fisher 1892) and was cited by Shin *et al*. (2001) as a species able to control algal blooms in an agricultural pond in Korea. *Blyttiomyces spinulosus* and *B. laevis* can infect filamentous green algae *Spirogyra* spp., *Sirogonium* sp. and *Zygnema* sp. (Sparrow, 1952; Blackwell *et al*., 2011), while *B. rhizophlyctis* is a parasite of the ubiquitous saprophytic chytrid *Rhizophlyctis rosea* (Sparrow, 1960).

Significant progress has been made in our understanding of the systematics and ecology of the parasites in Chytridiales; however, there are still several species that need to be included in phylogenetic analysis. The description of multiple parasites in the last decade is an indication of the potential of these taxa in influencing host dynamics, but few researchers have examined the implications of these interactions.

Gromochytriales and Mesochytriales

Gromochytriales and Mesochytriales are orders recently established to include a few algal-parasitic chytrids (Karpov *et al*., 2014a, 2018b). Karpov *et al*. (2010, 2014a) investigated the molecular phylogenetic positions and zoospore ultrastructures of *Mesochytrium penetrans* infecting a green alga *Chlorococcum minutum* (Gromov *et al*., 2000) and *Gromochytrium mamkaevae* infecting a yellow-green alga *Tribonema gayanum* (Karpov *et al*., 2014a). In the phylogenetic analysis by Karpov *et al*. (2014a), *M. penetrans* was placed in the order-level novel clade composed of environmental sequences, which were collectively recognized as “Novel Clade I” (Lefèvre *et al*., 2008) or “Snow Clade 1” (Naff *et al*., 2013); *G. mamkaevae*, along with a few environmental sequences, was sister to the clade including *M. penetrans*. Based on the unique characteristics of zoospore ultrastructure, Karpov *et al*. (2014a) proposed Mesochytriales and Gromochytriales for these novel lineages. Recently, an additional parasitic species on *T. gayanum*, *Apiochytrium granulosporum*, was described (Karpov *et al*., 2018b).

Currently, Gromochytriales and Mesochytriales are small orders including two and one species, respectively. However, many environmental sequences were related to these orders, especially Mesochytriales (Karpov *et al*., 2014a, 2018b, Hyde *et al.*, 2024). These sequences are from diverse environments such as freshwater lakes, high-elevation soil, and snow. It is likely that continued sampling from these habitats will reveal additional algal parasites within these orders.

Lobulomycetales

Upon the discovery that the Chytridiales was polyphyletic (James *et al*., 2000), zoospore ultrastructural characters were reevaluated, and it was concluded that there was additional morphological variation to enhance the description of the molecularly-delineated lineages. Thus, the Lobulomycetales was described to accommodate taxa affiliated with the species *Lobulomyces angularis* (≡*Chytriomyces angularis*). The order includes 7 genera (Simmons *et al*., 2009, 2012; Doweld, 2014h; Seto and Degawa, 2015; Van den Wyngaert *et al*., 2018), and most taxa are regarded to be saprobes. Environmental sequences and isolation efforts have indicated that representatives of the order can be found in diverse habitats, including temperate soils (Küpper *et al*., 2006; Simmons *et al*., 2009; Seto and Degawa, 2015), alpine soils (Freeman *et al*., 2009), equine fecal samples (Simmons *et al*., 2012), freshwater samples (Jobard *et al*., 2012; Seto and Degawa, 2015; Van den Wyngaert *et al*., 2018), and marine samples of arctic habitats (Majaneva *et al*., 2012; Hassett and Gradinger, 2016; Hassett *et al*., 2017) and deep-sea thermal vents (Le Calvez *et al*., 2009).

At the time of its description, the Lobulomycetales contained mostly saprobic species from soil or aquatic samples, with the noted exception of *Algochytrops polysiphoniae* (≡*Chytridium polysiphoniae*), a parasite of red and brown algae, which was previously associated with *L. angularis* (Küpper *et al*., 2006). Later, *Algomyces stechlinensis* was described as a pathogen of colonial volvocine algae *Eudorina elegans* and *Yamagishiella unicocca* and the desmid *Staurastrum* in freshwater samples from Germany (Van den Wyngaert *et al*., 2018). “*Zygorhizidium*” *affluens* (see below) parasitic on a diatom *Asterionella formosa* was placed in Lobulomycetales (Rad-Menéndez *et al*., 2018). Furthermore, Kagami *et al*. (2021) showed that unidentified parasites on diatoms *Aulacoseira* spp. belong to Lobulomycetales based on single-cell analyses. The correlation of Lobulomycetales sequence data to marine samples composed of chytrid-infected diatoms (Hassett *et al*., 2017) indicates that additional parasitic species likely remain to be described.

Nephridiophagales

Members of Nephridiophagales lack motile spores and do not have a flagellum. Based on these characters, the genus *Nephridiophaga* was previously placed in Haplosporidia and Microsporidia (Radek *et al*., 2017). However, molecular phylogenetic analyses place *Nephridiophaga* within Chytridiomycota (Strassert *et al*., 2021). The genus was erected in 1937 by Ivanic for an organism infecting the Malpighian tubules of the honey bee *Apis mellifera* (Voigt *et al*., 2021), but the order was only recently erected by Doweld (2014c). There are 14 species within *Nephridiophaga* (Voigt *et al*., 2021) with all known members infecting the Malpighian tubules of insects. Spores are small, flattened ovals that resemble a red blood cell with one nucleus (Woolever, 1966). Some hypothesized members of the order have more elongated spores with two nuclei or lateral protrusions and polar openings (Voigt *et al*., 2021). Although much is known about the life cycle (Woolever, 1966; Lange, 1993; Radek and Herth, 1999; Radek *et al*., 2017), the ecology and evolution of these fungi remains poorly understood. In a pioneering study, Strassert *et al*. (2022) showed that cockroaches infected with *Nephridiophaga* had reduced fat reserves, reduced mobility, increased susceptibility to pesticides, lower fecundity, and shorter life spans. These effects were exacerbated when the cockroaches were co-infected with *Nephridiophaga* and a nematode gut parasite (Strassert *et al*., 2022).

Polyphagales

Polyphagus was erected by Nowakowski to accommodate *Chytridium euglenae* (Sparrow, 1960). An additional 11 species were added to the genus by subsequent authors (Index Fungorum) with the unifying features of the genus being the ability to infect multiple host cells at the same time, the formation of a prosporangium, and zoospore release through an inoperculate, apical pore (Sparrow, 1960; Karpov *et al*., 2016a). Doweld (2014g) added an additional three species that were formerly invalidly published; however, two of those species (*Arnaudovia hyponeustonica* and *Sporophlyctis chinensis*) were placed in other genera by the original authors, and it is unclear why Doweld (2014g) transferred them into *Polyphagus*.

Polyphagales was established by Doweld (2014d) based on the zoospore ultrastructure of the type species *Polyphagus euglenae* described in Powell (1981). In Karpov *et al*.’s (2016a) molecular phylogeny, *Polyphagus parasiticus* placed as a lineage sister to the Gromochytriales and Mesochytriales, which they interpreted as validating the elevation of the genus to an order. However, while zoospore ultrastructural characters are used to define orders in Chytridiomycota and Karpov *et al*.’s (2016a) molecular phylogeny does place *P. parasiticus* in its own lineage, neither Doweld (2014d) nor Karpov *et al*. (2016a) examined multiple species within the genus *Polyphagus*. Since the genus is still defined based on unreliable morphological characters, the inclusion or exclusion of the other 14 *Polyphagus* species in this order is uncertain; thus, the erection of the order was perhaps premature. Recently, Van den Wyngaert *et al*. (2018) revealed that *Endocoenobium eudorinae* (also called *Volvorax ingoldii*), parasitic on colonial volvocalean green algae, was sister to *P. parasiticus*, indicating it is an additional member of the order.

Polyphagus species tend to be parasites on species of *Euglena*, *Chlamydomonas*, *Tribonema*, *Sphaerocystis* (Sparrow, 1960), a variety of species in Volvocales (Johns, 1964), and *Spondylosium* (Canter, 1963). Inclusion of Doweld's (2014g) species expands the host range to include *Botrydiopsis*, which is a biofuel candidate, and *Draparnaldia*. If the circumscribed species do indeed form a monophyletic genus and order, their broad host range, sexual life cycle, and culturability make them a tractable system in which to study Red Queen dynamics and the molecular underpinnings of host-parasite interactions.

Rhizophlyctidales

Rhizophlyctidales was established using the molecular monophyly and zoospore ultrastructure of *Rhizophlyctis rosea*-like isolates. Currently, this order is composed of four monophyletic families, which are differentiated by their respective zoospore ultrastructures (Arizonaphlyctidaceae, Borealophlyctidaceae, Rhizophlyctidaceae and Sonoraphlyctidaceae), and by four genera (*Arizonaphlyctis*, *Borealophlyctis*, *Rhizophlyctis* and *Sonoraphlyctis*) (Powell and Letcher, 2014b; Davis *et al*., 2016a; Hyde *et al*., 2024).

Species in Rhizophlyctidales are commonly found in the soil as saprobes of cellulosic substrates, with the globally distributed species *Rhizophlyctis rosea* most often found in agricultural soils (Letcher *et al*., 2008a; Marano *et al*., 2011; Powell and Letcher, 2014b). However, there are reports of this species in aquatic ecosystems detected through the baiting technique and environmental sequencing (Milanez *et al*., 2007; De Almeida Nascimento *et al*., 2011; Kagami *et al*., 2012; Steciow *et al*., 2012). References to parasitic species of this order are scarce. Sparrow (1960) and Karling (1977) mentioned *R. mastigotrichis*, *R. tolytpotrichis*, *R. palmellacearum* and *R. borneensis* as parasites of the cyanobacteria genera *Mastigothrix* and *Tolypothrix*, an unnamed palmellaceous green algae, and diatoms, respectively. Years later, Canter and Ingold (1984) observed a chytrid they identified as *Rhizophlyctis* sp. parasitizing arthroconidia of the basidiomycete *Dacrymyces stillatus*. Although most species have been isolated as saprobes, our attention must be drawn to the parasitic potential of taxa within this group.

Rhizophydiales

Proposed by Letcher *et al*. (2006), Rhizophydiales was initially established to include representatives of *Rhizophydium*, formerly classified in Chytridiales, based on distinct zoospore ultrastructure and because it formed a clade outside of Chytridiales in the phylogenetic analysis of ribosomal genes. In subsequent years, *Rhizophydium* was divided into several genera based on molecular analyses and subtle differences in zoospore ultrastructure. Presently, the order comprises 19 valid families and 24 legitimate genera (Hyde *et al*., 2024).

Rhizophydiales contains a number of facultative and obligate parasitic species with a wide variety of hosts, such as algae, plants, animals, dinoflagellates, oomycetes, and other fungi (Sparrow, 1960; Letcher *et al*., 2006; Letcher and Powell, 2012). The importance of parasitism in the genus was evidenced by Sparrow (1960), who circumscribed the species of *Rhizophydium* based on the type of hosts they could infect. However, several of these species were considered dubious because most of them were never observed again after their original description. Consequently, the phylogenetic positions of a significant number of species, especially those classified in *Phlyctidium* (an invalid genus), remain uncertain. As well, the genus *Rhizophydium* is known to be non-monophyletic (e.g., Ding *et al*., 2018; Seto *et al*., 2017).

The molecular analysis of ribosomal genes revealed that several parasites described since Sparrow (1960) belong to Rhizophydiales. The best-studied–and arguably most devastating–are *Batrachochytrium dendrobatidis* (or *Bd*) and *B. salamandrivorans* (or *Bsal*) that are responsible for the decline and extinction of many amphibian species around the world (Longcore *et al*., 1999; Martel *et al*., 2013). Although both species form long branches in phylogenetic analyses of ribosomal genes, zoospore ultrastructure confirms their affiliation to Rhizophydiales. In recent years, other important parasites within this order have been described. Lepellitier *et al*. (2014) described the new species *Dinomyces arenyensis* parasitizing marine dinoflagellates. Van der Wyngaert *et al*. (2017) described *Staurastromyces oculus* infecting the freshwater desmid *Staurastrum* sp. Seto and Degawa (2018a) described the new species *Collimyces mutans* (Figure 3a–c) parasitizing *Microglena coccifera*. Garvetto *et al*. (2019) reported an unknown chytrid associated with the marine diatom *Skeletonema* sp., and it was positioned in Rhizophydiales based on a single-cell sequencing and molecular phylogenetic analysis. More recently, McKindles *et al*. (2021) isolated seven strains of *Rhizophydium* infecting the cyanobacteria *Planktothrix agardhii* and *P. rubescens*. Karpov *et al*. (2021) newly described *Ericiomyces syringoforeus* parasitizing dinoflagellates in brackish habitats.

Among orders in Chytridiomycota, Rhizophydiales represents a particularly rich clade for exploring the phylogenetic and ecological diversity of parasitic species, as most of the putatively parasitic species described in the mid-19th century have yet to be included in any molecular analysis. Moreover, the number of parasites described in recent years reinforces the idea that more attention should be given to Rhizophydiales for a better understanding of the diversity of the parasites across Chytridiomycota.

Spizellomycetales

Spizellomycetales was established by Barr based on zoospore ultrastructure, segregating it from the Chytridiales (Barr, 1980). At present, this order is composed of two monophyletic families, Powellomycetaceae and Spizellomycetaceae. These two families are distinguished by different modes of thallus development, which is exogenous and endobiotic in Powellomycetaceae and endogenous and epibiotic in Spizellomycetaceae (Simmons, 2011; Simmons and Longcore, 2012; Powell and Letcher, 2014b). Powellomycetaceae contains four genera and eight species: *Fimicolochytrium* (2), *Geranomyces* (4), *Powellomyces* (1) and *Thoreauomyces* (1). Spizellomycetaceae contains eight genera, and twenty-one species: *Barromyces* (1), *Brevicalcar* (1), *Bulbosomyces* (1), *Gaertneriomyces* (5), *Gallinipes* (3), *Kochiomyces* (1), *Spizellomyces* (7), and *Triparticalcar* (2) (Longcore *et al*., 1995; Simmons, 2011; Simmons and Longcore, 2012; Davis *et al*., 2016b; Letcher and Powell, 2018a, Powell *et al*., 2018; Hyde *et al*., 2024), with *Gaertneriomyces* and *Spizellomyces* as polyphyletic genera (Wakefield *et al*., 2010). The genera *Caulochytrium*, *Olpidium* (Figure 3v), *Rhizophlyctis* and *Rozella* (Figure 3m–o) placed in Spizellomycetales previously by Barr (1980) were excluded due the phylogenetic placement in molecular analyses (James *et al*., 2006; James and Berbee, 2011; Karpov *et al*., 2010; Wakefield *et al*., 2010; Letcher and Powell 2018a).

Baiting techniques as well as environmental sequencing demonstrated that Spizellomycetales members are commonly found as saprobes from native and disturbed soil, including those at high elevations, dung, and lakes (Lozupone and Klein, 2002; Freeman *et al*., 2009; Wakefield *et al*., 2010; Simmons, 2011; Simmons and Longcore, 2012; Kuramae *et al*., 2013; Powell and Letcher, 2014b; Letcher and Powell, 2018a). They have also been found in nematodes, arbuscular mycorrhizae, and oospores of downy mildews, though it is not clear from these observations if they are acting as saprobes or parasites (Person *et al*., 1955; Kenneth *et al*., 1975; Ross and Ruttencutter, 1977; Daniels and Menge, 1980; Paulitz and Menge, 1984). These last authors observed that in natural environments *Spizellomyces punctatus* can be a saprobe or a weak facultative parasite of the spores of the mycorrhizal fungus *Gigaspora margarita*. More recently, *Gaertneriomyces semiglobifer* was isolated as a parasite of azygospores of *Entomophaga maimaiga* (Figure 3p,q). This entomophthoralean fungus is an important pathogen of the moth *Lymantria dispar* (Hajek *et al*., 2013) and a prospective biocontrol agent; it is unclear how parasitism by *G. semiglobifer* might influence its host’s ability to control invasive insect populations.

Synchytriales

The name Synchytriales has been in use since 1948 (Schussnig, 1948, as in Longcore *et al*., 2016), though it was only formally described much later using zoospore ultrastructural characters (Doweld, 2014e). It contains one family *Synchytriaceae* that has four genera: *Synchytrium* (Figure 2c,d; 3g), *Carpenterophlyctis*, *Endodesmidium*, *Johnkarlingia*, *Micromyces* (Figure 2k), and *Micromycopsis* (Hyde *et al*., 2024). The order may also contain a second family, Chrysophlyctaceae, with the sole species *Chrysophlyctis desmodii*, which Doweld (2014f) transferred out of *Synchytrium* without explanation. However, while the genera in Synchytriales are in need of taxonomic revision, this should not be done without the guidance of molecular phylogenetics and the inclusion of aquatic species, such as those in *Micromyces* (Canter, 1949; Blackwell *et al*., 2018; Longcore *et al*., 2016) and the undescribed species observed by Davis *et al*. (2019).

The largest genus and the one with the most direct effect on human affairs is *Synchytrium* with over 200 species (Karling, 1964; Longcore *et al*., 2016). With the exception of *Synchytrium microbalum* (Longcore *et al*., 2016) and a potentially undescribed species (Davis *et al*., 2019), the genus is composed of plant parasites that are often mistaken as rusts (Karling, 1964). Species are distributed world-wide and occur in tropical, temperate, and arctic habitats from sea level to 3000-meter elevations (Karling, 1964). The most infamous species is *Synchytrium endobioticum,* which causes black wart disease of potatoes. However, there are several other species that infect plant hosts important to agriculture and industry, which will be discussed later in this chapter.

Synchytrium species inhabit plant cells and cause the formation of galls or warts. Species are either short-cycled or long-cycled. Short-cycled species develop only sori, sporangia, and zoospores, or, resting spores, sori, and zoospores. Long-cycled species develop prosori, sori, sporangia, zoospores, and resting spores that germinate into sori, sporangia, and zoospores. In both cases, the resting spores serve as resistant structures and remain viable for long periods of time in the soil (Karling, 1964).

Zygophlyctidales and Zygorhizidiales

Zygorhizidiales and Zygophlyctidales are recently established orders to accommodate species of the genus *Zygorhizidium s. l.* (Seto *et al*., 2020b). *Zygorhizidium* is a small genus described by Löwenthal (1905) and characterized by an operculate zoosporangium and sexual reproduction in which male and female thalli fuse via a conjugation tube. All the species of the genus are parasites of algae including green, chrysophycean, and diatom algae (Karling, 1977). *Zygorhizidium* was formerly included in Chytridiales, but its phylogenetic position was unknown. Recently, molecular phylogenetic analyses and/or zoospore ultrastructural observations of select species (Seto *et al*., 2017, 2020b; Rad-Menéndez *et al*., 2018) revealed that *Zygorhizidium* is polyphyletic. The type species, *Z. willei* (Figure 3d,e) on zygnematophycean green algae was phylogenetically distinct from any known orders (Seto *et al*., 2020b). Three species of diatom parasites, *Z. asterionellae* (Figure 3j–l), *Z. melosirae* (Figure 3i), and *Z. planktonicum,* were placed in the so-called Novel Clade II (Jobard *et al*., 2012), an order-level novel clade composed of environmental sequences (Seto *et al*., 2017, 2020b). Based on zoospore ultrastructural characteristics, Seto *et al*. (2020b) established the new order Zygorhizidiales to accommodate *Z. willei* and Zygophlyctidales including the three diatom parasites which were transferred to a distinct genus, *Zygophlyctis*. Another diatom parasite, *Zygorhizidium affluens,* was positioned in the order Lobulomycetales (Rad-Menéndez *et al*. 2018) and needs to be moved to a distinct genus. Other likely *Zygorhizidium* species that are known to parasitize green or chrysophycean algae have yet to be characterized using molecular phylogenetic methods.

In Zygorhizidiales and Zygophlyctidales, the ecological and evolutionary dynamics between *Zygophlyctis asterionellae* (better known by its former name, *Zygorhizidium planktonicum*) and its diatom host *Asterionella formosa* have been studied extensively. The effect on the succession of host diatoms in lakes (Van Donk and Ringelberg, 1983), host specificity (Canter and Jaworski, 1986), co-evolution between chytrid and host diatom (De Bruin *et al*., 2008), and trophic link between inedible diatom and zooplankton via chytrid (Kagami *et al*., 2007b) have been investigated.

Cryptomycota/Rozellomycota

The phylum Cryptomycota/Rozellomycota (= Rozellida = Rozellosporidia) is a group of endoparasitic organisms and one of the sister lineages of core fungi (Chytridiomycota *s. l.*, zygomycetes, and Dikarya). It was originally recognized as an unknown fungal clade composed of environmental sequences (Van Hannen *et al*., 1999; Berney *et al*., 2004; Luo *et al*., 2005). Subsequent analyses revealed that these environmental sequences and the endoparasitic genus *Rozella* (Figure 3m–o) formed a clade sister to core fungi. New names Rozellida (Lara *et al*., 2010) and Cryptomycota (Jones *et al*., 2011a, 2011b) were suggested for the clade. Other names, Rozellomycota (James and Berbee, 2011; Doweld, 2013; Corsaro *et al*., 2014a) and Rozellosporidia (Karpov *et al*., 2017c) were also proposed. Here, we use the fungal phyla names Cryptomycota/Rozellomycota.

The most well-known member of Cryptomycota/Rozellomycota is the genus *Rozella*, an endoparasite of mainly chytrid fungi or oomycetes (Letcher and Powell, 2018b), but with one potential algal parasite (Sparrow *et al*., 1965). Like aphelids, *Rozella* develops as a naked cell in the host cell, phagocytizes host cytoplasm (Powell, 1984; Powell *et al*., 2017), and produces chytrid-like posteriorly uniflagellate zoospores. Other members of the phylum are Microsporidia-like endoparasites. These recently recognized lineages resemble Microsporidia in producing spores with polar filament-like structure, but their rDNA sequences are much less divergent than typical Microsporidia. Currently, four genera are known for the so-called short-branched Microsporidia (Bass *et al*., 2018): *Paramicrosporidium* and *Nucleophaga*, endonuclear parasites of amoeba (Corsaro *et al*., 2014a, 2014b), *Morellospora*, a cytoplasmic parasite of amoeba (Corsaro *et al*., 2020), and *Mitosporidium*, a gut parasite of *Daphnia* (Haag *et al*., 2014). Phylogenomic and comparative genomic analyses of *Mitosporidium* and *Paramicrosporidium* (Haag *et al*., 2014; Quandt *et al*., 2017) indicated that short-branched Microsporidia are intermediates between *Rozella* and canonical Microsporidia. Currently, Cryptomycota/Rozellomycota still includes uncharacterized clades of environmental sequences (Bass *et al*., 2018). These lineages are possibly endoparasitic organisms as with *Rozella* and short-branched Microsporidia. Based on network analyses of metabarcoding data (Doliwa *et al*., 2021), Apicomplexa, Cercozoa, Fungi, and Metazoa are suspected as potential hosts of short-branched Microsporidia. Further investigation into the endoparasites of these organisms is likely to expand the known diversity of Cryptomycota/Rozellomycota.

Monoblepharomycota

The monoblephs are a monophyletic group of the zoosporic eufungi in the phylum Monoblepharomycota (Doweld, 2001; Tedersoo *et al*., 2018; Grossart *et al*., 2019; Calabon *et al*., 2020; Wijayawardene *et al*., 2020; Voigt *et al*., 2021; Hyde *et al.*, 2024; erroneously reported as Monoblepharidiomycota by Powell and Letcher 2014a and Simmons et al., 2020). This phylum is composed of the classes Hyaloraphidiomycetes and Monoblepharidomycetes, with the orders Hyaloraphidiales and Monoblepharidales, respectively. Hyaloraphidiales comprises a single family, Hyaloraphidiaceae, whereas Monoblepharidales contains five: Harpochytriaceae, Gonapodyaceae, Monoblepharidaceae, Oedogoniomycetaceae and Telasphaerulaceae (Wijayawardene *et al*., 2020). Sanchytriaceae was excluded from the order Monoblepharidales, since *Sanchytrium tribonematis* (Figure 2l), the type species, was considered a new divergent taxon, together with *Amoeboradix gromovi* (Figure 2m), which were inserted as *incertae sedis* within the kingdom Fungi (Karpov *et al*., 2017a, 2018a). More recently, these two species were placed in the new phylum

Sanchytriomycota, sister to the Blastocladiomycota, discussed elsewhere (Galindo *et al*., 2021).

Hyaloraphidiomycetes is comprised of a monocentric genus (*Hyaloraphidium*), and Monoblepharidomycetes by two monocentric (*Harpochytrium* (Figure 2i), *Oedogoniomyces*), one polycentric (*Telasphaerula*) and three mycelial (*Gonapodya*, *Monoblepharella, Monoblepharis*) genera, totaling approximately 38 species (Mycobank 2021). The monocentric genera, *Harpochytrium* and *Oedogoniomyces*, have uniaxial, filamentous thalli, commonly rod-shaped, with an extracellular basal holdfast, while *Hyaloraphidium*, with a single species, *H. curvatum*, is unicellular, crescent-shaped and pelagic (Ustinova *et al*., 2000; Powell and Letcher, 2014a; Dee *et al*., 2015). The single genus with a polycentric thallus, *Telasphaerula*, was recently described by Karpov *et al*. (2017a), increasing the thallus types in the class. The mycelial genera, *Gonapodya*, *Monoblepharella* and *Monoblepharis*, 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*., 2017a). Oogamous sexual reproduction and the vacuolated cytoplasm that gives a characteristic foamy appearance to the thallus are important features of this group of fungi (Powell and Letcher, 2014a, 2014b). These genera all produce uniflagellate zoospores, with the exception of *H. curvatum*, once considered a colorless green alga, that produces autospores (Powell and Lechter, 2014a, 2014b). The Monoblepharidomycetes *s. l.* phylogeny based on SSU and LSU rDNA regions performed by Dee *et al*. (2015) show that the mycelial genera formed a monophlyletic group sister to the monocentric *Harpochytrium* and *Oedogoniomyces,* with *Hyaloraphidium* as basal genus. *Telasphaerula*, the more recently described polycentric genus, with the single species, *T. gracilis*, appears to be sister to mycelial genera (Karpov *et al*., 2017a).

Monoblephs are commonly found in freshwater ecosystems as saprotrophs of plant material, such as submerged fruits and twigs, and algae (Jane, 1946; Kobayashi and Ôkubo, 1954; Emerson and Whisler, 1968; Karling, 1977; Powell and Letcher, 2014a, 2014b; Karpov *et al*., 2017a), but Emerson and Whisler (1968) mentioned the relationship of some monocentric genera, especially *Harpochytrium* (Figure 2i), with several species of algae, leading to some speculation that they were parasites. Monoblephs have also been observed on the surface of shells of living snails from Japanese ponds (Kobayashi and Ôkubo, 1954), in submerged soil samples near the edge of a sugar cane field in Costa Rica (Emerson and Whisler, 1968), and in sediment samples from Brazilian freshwater bodies (Jesus, 2019). Environmental sequencing has also revealed their presence in a variety of marine systems, including a sea cucumber farm in northern China (Guo *et al*., 2015), deep-sea sediments of the Magellan seamount in the northwest Pacific (Luo *et al*., 2020), and coastal sediments in the eastern United States (Picard, 2017), though their functional roles in these habitats remain unclear. Culture-independent techniques have also found these fungi in decaying oak leaves in tree holes, with or without the presence of mosquito larvae of *Ochlerotatus triseriatus* (Kaufman *et al*., 2008), though direct parasitization of insects has yet to be confirmed.

Olpidiomycota and *Olpidium*

The genus *Olpidium* (Figure 3v) is characterized by a holocarpic thallus: it produces a simple zoosporangium without any rhizoidal systems. Many members of the genus are endoparasites of algae, fungi, moss protonema, plants, and aquatic microfauna (Sparrow, 1960). *Olpidium* belongs to the family Olpidiaceae along with some other holocarpic genera and traditionally have been included in Chytridiales *s. l.* (Sparrow, 1960). Based on the zoospore ultrastructure of some plant pathogenic *Olpidium* (Barr and Hadland-Hartmann, 1977; Lange and Olson 1978), Barr (1980) included Olpidiaceae in the order Spizellomycetales. Subsequently, molecular phylogenetic analyses of plant pathogenic lineages (James *et al*., 2006; Sekimoto *et al*., 2011) revealed that *Olpidium* was separated from major zoosporic lineages (e.g., Blastocladiomycota, Chytridiomycota). Instead, plant pathogenic *Olpidium* species were clustered with paraphyletic Zygomycota, but their exact position could not be determined. Recently, phylogenomic analysis of the cucumber parasite *O. bornovanus* (Chang *et al*., 2021) showed that it was sister to Dikarya and a paraphyletic Zygomycota. In the recently proposed taxonomic systems of Fungi (Tedersoo *et al*., 2018; Hyde *et al.*, 2024), *Olpidium* was placed in an independent phylum Olpidiomycota. However, the treatment by Tedersoo *et al*. (2018) was based only on plant pathogenic species, despite *Olpidium* species also parasitizing various lineages of algae and microscopic animals. Doweld (2014i, 2014j, 2014k, 2014l) placed some species of *Olpidium* in distinct genera: 5 species including *O*. *bornovanus* in *Leiolpidium*, *O*. *majus* infecting cucumber root in *Schizolpidium*, *O*. *brassicae* and *O*. *virulentus* in *Olpidiaster*, and *O*. *saccatum* and *O*. *utriculiforme* infecting desmid algae in *Perolpidium*. However, these taxonomic revisions were not based on molecular phylogeny. Recently, Amses *et al*. (2022) sequenced a single-cell genome of an *Olpidium*-like chytrid in a green alga *Micrasterias* cf. *truncata* and revealed that it was not related to *O. bornovanus* but positioned in Rhizophydiales based on phylogenomic analysis. This result indicates that *Olpidium* is a polyphyletic genus comprising multiple phylum-level lineages. It will be necessary to examine other described species, especially the type species *O. endogenum*, an endoparasite of zygnematophycean green algae, to clarify the taxonomy of *Olpidium*.

The most well-known species of the genus is *O. brassicae s. l.*, a plant root parasite. It is known as a vector of some viruses causing plant diseases (Rochon, 2016). One of the viruses transmitted by *O. brassicae* is Mirafiori lettuce big-vein virus, a causal agent of lettuce big-vein disease (Sasaya *et al*., 2008) which occurs worldwide in commercial lettuce producing areas (Maccarone, 2013). Despite its importance, the species concept of *O. brassicae* has been controversial (Rochon, 2016; Lay *et al*., 2018). According to the review by Lay *et al*. (2018), *O. brassicae s. l.* includes at least two separate species that cannot be distinguished based on morphology: *O. brassicae,* which infects mainly Brassicaceae plants and does not transmit viruses, and *O. virulentus*, which infects plant lineages other than Brassicaceae and acts as a vector of plant viruses. Another virus-transmitting species, *O. bornovanus*, is distinguished from *O. brassicae*/*virulentus* based on the morphology of zoospore and resting spore. *Olpidium bornovanus* infects various plant lineages (Sahtiyanci, 1962) and acts as a vector of viruses such as melon necrotic spot virus, cucumber necrosis virus, and squash necrosis virus (Dias, 1970; Campbell *et al*., 1991, 1995). As observed through next-generation sequencing (e.g., Leff *et al*., 2017; Tedersoo *et al*., 2017), microscopy (e.g., Bzdyk *et al*., 2016; Duran, 2017), and population genetic studies (Zelyüt and Ertunç, 2021), it is evident that additional root parasitic species awaiting description exist.

Sanchytriomycota

Sanchytriaceae (Sanchytriales, Sanchytriomycetes), the only family of Sanchytriomycota (Wijayawardene *et al*., 2020; Galindo *et al*., 2021), is comprised of two species, *Sanchytrium tribonematis* and *Amoeboradix gromovi. Sanchytrium tribonematis* was found as a parasite of the yellow-green alga *Tribonema gayanum*, causing total destruction of algal cells (Figure 2l), and *Amoeboradix gromovi* was isolated as a parasite of *T*. *gayanum* (Figure 2m), *T. vulgare* and *Ulothrix tenerrima* (Karpov *et al*., 2017a, 2018a). Both sanchytrid species have monocentric, epibiotic thalli, usually amoeboid zoospores with a highly reduced posterior flagellum (also called a pseudocilium) without locomotion, and long kinetosomes involved in the retraction of this flagellum. The amoeboid zoospores were found gliding on solid surfaces via thin filopodia growing in all directions and a broad hyaline pseudopodium at the anterior end (Karpov *et al*., 2018a; Galindo *et al*., 2021).

These chytrid-like species were previously *incertae sedis* within the kingdom Fungi (Karpov *et al*., 2018a). More recently, single-cell genome sequencing of both species revealed that they belong to a fast-evolving lineage sister to the Blastocladiomycota, circumscribed as Sanchytriomycota (Galindo *et al.*, 2021). Comparative genomic analyses also suggest the Sanchytriomycota are more derived parasites when compared to the blastocladiomycetes and chytrids.

Evolution of the zoosporic eufungi

The Rhynie chert (Aberdeenshire, Scotland) is an important sedimentary rock deposit that has been revealing information about the evolution of fungi, algae, vascular plants, and marine and terrestrial invertebrates during the Early Devonian, approximately 408-360 million years ago (Taylor *et al*., 1992; Krings *et al*., 2018; Strullu-Derrien *et al*., 2019; Berbee *et al*., 2020). The communities preserved in the Rhynie chert grew in a sub-tropical to tropical environment with CO_2 levels an order of magnitude or higher than present day. These communities were then entombed in silica precipitates that crystallized over time to microcrystalline quartz, which allowed for exquisite preservation of microscopic features (Strullu-Derrien *et al*., 2019).

The Devonian was an exceptional time for the evolution of fungi, especially those associated with algae and land plants. The fungal fossils described to date from the Rhynie chert constitute the largest body of structurally preserved fungi and fungal interactions from any rock deposit, and strongly suggest that fungi played important roles in the functioning of the Early Devonian Rhynie ecosystem (Krings *et al*., 2017; Strullu-Derrien *et al*., 2019). The record of fungi documented in the Rhynie chert currently comprises fungi belonging to all major lineages except Basidiomycota. An important characteristic of Rhynie Chert fossils is the fact that several were preserved together with their host, demonstrating the existence of different types of fungal associations, including several parasites of algae, land plants and even other fungi (Taylor *et al*., 1992; Hass *et al*., 1994; Krings *et al*., 2016; Strullu-Derrien *et al*., 2014). Fossils attributed to Chytridiomycota and Blastocladiomycota are relatively abundant in Rhynie Chert (Taylor *et al*., 1992; Hass *et al*., 1994; Krings *et al*., 2016; Strullu-Derrien *et al*., 2014, 2019; Krings and Harper, 2020) and have been recorded from other geological times as well.

It is remarkable how these fossils are morphologically similar to the modern representatives of the chytrids. *Rhizophidites triassicus* is a parasite on certain Triassic spores that resembles *Globomyces pollinis-pini*, a parasite of pine pollen (Daugherty, 1941). *Entophlyctis willoughbyi* from the Eocene has been compared to *E. lobata* (Bradley, 1967)*. Nimbosphaera rothwellii*, a microfossil composed of a vesicle containing spheroidal bodies enveloped in a prominent sheath resembles the zoosporangia of *Rhizophydium coronum* (Harper and Krings, 2019). A *Synchytrium*-like fossil from the Permian was found associated with plant tissues and probably represents an endoparasite (García-Massini, 2007). Other fossils attributed to chytrids were found parasitizing spores, pollen grains, and seeds from the Carboniferous (Millay and Taylor, 1978), while others resemble marine endolithic chytrids (Wisshak *et al*., 2018). *Brijax amictus* develops within the spore walls of archaeosporalean acaulospores from the Rhynie chert. Thallus morphology of this species is similar to certain present-day species of *Rhizophydium* (Rhizophydiales) and *Phlyctochytrium* (Figure 2j; Chytridiales); however, the systematic affinities and nutritional mode of *B. amictus* remain unresolved (Krings and Harper, 2020). *Striadiporites*, found in much later Eocene sediments, may or may not be a zoosporic eufungus; it bears resemblance to resting spores of *Coelomomyces* (Saxena *et al*., 2021).

The morphological similarity of fossils and present-day species is an indication that these organisms originated and evolved earlier in geological time. Recently, a fossil from a billion years ago (Precambrian) set back evolution of earliest fungi lineages for at least 500 million years (Krings and Harper, 2019; Berbee *et al*., 2020). However, molecular analyses have suggested that these fungi were simple (single-celled), probably similar to the modern amoeboid protists such as nucleariids and aphelids (Berbee *et al*., 2020). The earliest zoosporic eufungi were likely obligate parasites such as *Rozella* (Figure 3m–o), which phagocytizes host cytoplasm (e.g., Powell, 1984), and Microsporidia, which lost the capacity for phagotrophy and adapted as intracellular parasites (Berbee *et al*., 2020). Later, multiple saprophytic and parasitic lineages emerged and diversified; however, the majority of species representing zoosporic eufungi in molecular phylogenetic analyses are saprobes (Picard *et al*., 2009; Davis *et al*., 2013; Letcher *et al*., 2015a; Jesus *et al*., 2020). Sequencing of parasitic taxa would greatly improve our understanding of how these lineages diversified and the evolution of trophic mode across the zoosporic eufungi.

Sequencing and comparative analyses of several zoosporic eufungal, green algal, and plant genomes has revealed additional evidence of the long, shared history of the two lineages. Comparative genomic analyses of several plant-saprotrophic zoosporic eufungi indicated that multiple gene copies of diverse pectinases are retained (Krings *et al*., 2017; Berbee *et al*., 2020). In addition, the presence of the genes that code enzymes degrading xyloglucans, pectin, and lignin strongly suggests a potential action in the degradation of components of cell walls of algae or plants (Krings *et al*., 2017; Krings and Harper, 2019; Berbee *et al*., 2020). As well, comparative analyses of transcriptomes from several green algae species and terrestrial plant species indicate that the genes involved in mycorrhizal interactions are present and conserved in green algal lineages. Likely, these genes are involved in detecting fungal infection in green algal lineages and were later co-opted for regulating mycorrhizal interactions (Delaux *et al*., 2015). Thus, the evolution of zoosporic eufungi, green algal lineages, and plant lineages are intertwined.

Of course, zoosporic eufungi have shared evolutionary history and dynamics with more than the green algal and plant lineages. Zoosporic eufungi also parasitize dinoflagellates, diatoms, animals, various protists, and cyanobacteria. The effect of parasites on their hosts has frequently been described as an example of the Red Queen Hypothesis, which states that species involved in antagonistic interactions will continuously coevolve in a winnerless manner (Van, 1973, reviewed by Brockhurst *et al*., 2014). When applied to host-parasite interactions in a time-dependent manner, this race predicts that the dominant host genotype/phenotype will be targeted by the parasite, which increases the fitness of less dominant host types, which then become the target of other parasites, and so on (Capaul and Evert, 2003, Ebert, 2008, Rabajante *et al*., 2015).

The Red Queen hypothesis has been used to describe the relationship between chytrid parasites and their cyanobacterial hosts within the context of diverse secondary metabolite production. Chytrids related to *Rhizophidium megarrhizum* as isolated by Sønstebø and Rohrlack (2011) were found to exert strong selective pressure on certain chemotypes of their cyanobacteria hosts, *Planktothrix agardhii* and *Planktothrix rubescens*. Indeed, further work confirmed this strong selective pressure of chytrids on monoclonal hosts and additionally established that chytrids are capable of rapid adaptation to novel monoclonal hosts (Agha *et al*., 2018). Unfortunately, the story seems to be confounded in the environment, as sediment DNA analysis of a Norwegian lake showed that a single chemotype of *Planktothrix* was able to maintain dominance even in the presence of chytrid parasites (Kyle *et al*., 2015), and qPCR quantification of a US Laurentian Great Lakes embayment shows that chytrid presence during a *Planktothrix agardhii*-dominated bloom remains quite low (McKindles *et al*., 2021). Part of this may be that host population genetic diversity already confers chytrid resistance and hinders parasite adaptations, as shown by Agha *et al*. (2018) in *Planktothrix* and De Bruin *et al*. (2008) in diatom hosts. More recently, a 12-year study of the German eutrophic lake Muggelsee found that chytrid prevalence could reach almost 50% of the phytoplankton host population and that multiple phytoplankton taxa carried chytrid infections at any given time of the year; while commonly occurring cyanobacteria only rarely carried infections, diatoms were regularly infected (Gsell *et al*., 2022). These interactions combined hint that we are missing key components of host defense mechanisms which may explain how cyanobacterial hosts continue to evade their parasites under bloom conditions.

Ecosystem dynamics

Roles of zoosporic eufungi in aquatic ecosystems

Zoosporic eufungi play essential roles in aquatic ecosystems, both as parasites and decomposers. They substantially affect food web dynamics and material cycling. Among zoosporic eufungi, chytrids (Chytridiomycota) are well studied as important parasites of phytoplankton. Parasitic chytrids infect diverse groups of phytoplankton, such as diatoms, green algae, dinoflagellates, and cyanobacteria (Kagami *et al*., 2007a), actively consuming and killing the host phytoplankton. When parasitic chytrids infect and kill dominant phytoplankton species, the consumption by chytrids can account for 25% of primary production, as seen in Lake Biwa, Japan (Kagami *et al*., 2006).

Chytrids are also important decomposers in aquatic ecosystems. Dead plankton, such as planktonic aggregates, and crustacean exoskeletons were observed to be heavily colonized by chytrids (Wurzbacher *et al*., 2010). Pollen grains, which are deposited from terrestrial ecosystems, are efficiently utilized by chytrids. Pollen grains are rich in phosphorus, and pollen deposition can contribute between 2 to 22% of total phosphorus loading. Although pollen grains are hardly ingested by zooplankton nor degraded by bacteria due to their extracellular wall (exine), chytrids are able to utilize pollen with 30-60% P utilization efficiency (Kagami *et al*., 2017).

Chytrid zoospores (both parasitic and saprotrophic), which are released from zoosporangia infecting organic matter into the water, are a premier food source for zooplankton both in terms of size (2-3 μm in diameter) and quality (rich in polyunsaturated fatty acids PUFAs and cholesterols) (Kagami *et al*., 2007a). When chytrids infect large, inedible organic matter, such as large phytoplankton or pollens, the chytrids render them vulnerable to zooplankton grazing. Chytrids can also fragment large colonial cyanobacteria, making them more susceptible to grazing by zooplankton. In this way, chytrids create a trophic bridge between inedible organic matters and zooplankton. This pathway is termed “mycoloop”, and plays important roles in aquatic food webs, especially in eutrophic systems where large inedible algae/toxic cyanobacteria dominate or in seasons where pollen deposition is high (Kagami *et al*., 2007b, 2014, 2017).

Chytrids change the quality and quantity of accessible organic matter, which feeds back not only to higher trophic levels but also to the microbial loop. Chytrids use enzymes exuded from their rhizoids to degrade particulate organic matter (POM), which often increases the leakage of dissolved organic matter (DOM) and stimulates the growth of heterotrophic bacteria (Kagami *et al*., 2007a, 2017). As a result, the composition of DOM in an aquatic system where saprobic and parasitic chytrid activity is high is changed (Senga *et al*., 2018). Negative feedback should also happen due to the competition between fungi and bacteria for substrates. In fact, a substantial part of photosynthetic carbon is diverted from the microbial loop to the mycoloop when parasitic chytrids utilize host cell materials in advance, which is called the “fungal shunt” (Klawonn *et al*., 2021).

There are still many knowledge gaps of organic matter transformation pathways mediated by chytrids. One of the potential pathways is termed “mycoflux”, where fungi mediate flux through aggregation or disintegration of organic matter (Grossart *et al*., 2019). Fungi actively colonize organic aggregates, including marine/lake snow, which may lead to the release of DOM and nutrients into the water and affect aquatic carbon pump and sinking fluxes.

Most of the evidence undergirding both the mycoloop and mycoflux come from studies of freshwater chytrids, but mounting evidence suggests that parasitic zoosporic eufungi occupy similar important roles in the marine realm. Compared to their terrestrial counterparts, marine fungi are understudied, with zoosporic marine fungi particularly poorly characterized. The relative dearth of zoosporic taxa among described marine fungi has long been interpreted as an absence of these fungi from marine systems.

However, growing interest in marine fungal diversity and advances in environmental sequencing using both metabarcoding and metatranscriptomic techniques have revealed previously unknown lineages of marine zoosporic eufungi from benthic marine sediments (Picard, 2017), polar sea ice (Hassett and Gradinger, 2016; Hassett *et al.*, 2017), and coastal and pelagic waters (Comeau *et al.*, 2016; Jeffries *et al.*, 2016). Newly detected marine fungal phylotypes are found across nearly all zoosporic phyla, but phylotypes closely related to lineages that are obligately or frequently parasitic, including the Cryptomycota/Rozellomycota (Stern *et al.*, 2015) and Rhizophydiales in Chytridiomycota (Jeffries *et al.*, 2016; Taylor and Cunliffe, 2016), are especially common, often dominating the fungal communities sampled.

As in freshwater systems, marine zoosporic eufungi exhibit seasonality correlated to periods of high primary productivity and/or phytoplankton diversity (Banos *et al.*, 2020; Kilias *et al.*, 2020; Priest *et al.*, 2021; Vass *et al.*, 2022; Wang *et al.*, 2023). The abundance of putative zoosporic eufungal parasites has also been shown to be negatively correlated to booms in zooplankton populations (Banos *et al.*, 2020). Together, these co-occurrence patterns between marine zoosporic eufungi and diverse zoo- and phytoplankton taxa suggest that the marine mycoloop exists, with parasitic zoosporic eufungi playing a critical role in trophic bridging across aquatic habitats.

Roles of zoosporic eufungi in terrestrial ecosystems

Zoosporic eufungi are commonly found in terrestrial ecosystems, occupying several niches (Bills *et al*., 2004), and acting as opportunistic organisms. They are reported in moist and dry soils, acidic and alkaline soils, saline soils, oligotrophic and periglacial soils, rainforest tree-canopy detritus, herbivore dung, vegetated and crop soils (Longcore, 2005; Wakefield *et al*., 2010; Digby *et al*., 2010; Simmons *et al*., 2012; Powell and Letcher, 2014a), and under extreme or stressful environmental conditions (Gleason *et al*., 2010a). Specific adaptations and strategies of zoosporic eufungi that are thought to give them advantages over other microorganisms in soil ecosystems include chemotactic zoospores, mechanisms for adhesion to substrates, rhizoids which can penetrate substrates, resistant structures, fast growth rates and simple nutritional requirements (Gleason *et al*., 2010a, 2012).

In terrestrial ecosystems, zoosporic eufungi are commonly found as saprobes, and their importance in the decomposition of refractory materials is well established (Powell, 1993; Lozupone and Klein, 2002; Gleason *et al*., 2010a; Wakefield *et al*., 2010; Gleason *et al*., 2012; Powell and Letcher, 2014a; James *et al*., 2014). However, much less is known about the role of parasitic species in terrestrial ecosystems, especially as compared to aquatic ecosystems (Gleason *et al*., 2012). Some species play important roles as parasites of plants, such as the species of *Olpidium*, *Physoderma* (Figure 2a,b), *Rhizophydium*, *Synchytrium* (Figure 2c,d) and *Urophlyctis*, with some *Olpidium* species being vectors of viruses. Other species are important mycoparasites, such as *Phlyctochytrium lipsii* occurring in the ascospores of various species of ascomycetes (Sparrow, 1960), and species of *Catenaria*, *Caulochytrium*, *Chytridium*, *Gaertneriomyces* (Figure 3p,q), *Septosperma* (Figure 3r,s) and *Spizellomyces*, as parasites of fungi and fungi-like organisms. Several species, such as *Phlyctochytrium nematodeae* (Karling, 1946) and many blastoclads (James *et al*., 2014) are parasites of microscopic animals, with some being potential biological control agents of agriculturally destructive invertebrates.

Parasitic zoosporic eufungi in the Anthropocene

As an artifact of increased demands on agriculture, pesticide use and subsequent run-off into local water bodies have increased (reviewed by Chen *et al*., 2019). Fungicide use makes up about 17.5% of total pesticide use worldwide, equating to more than 350,000 tonnes each year (De *et al*., 2014). Recent work using environmentally relevant concentrations of the fungicides tebuconazole and azoxystrobin in culture showed that the fungicides could inhibit fungal parasites on cyanobacteria, consequently promoting the growth of the potentially toxin-producing host (Ortiz-Cañavate *et al*., 2019). This confirms a relationship found in a mesocosm study in Lake Taihu in China, where the fungicide azoxystrobin had a positive effect on *Microcystis* growth while inhibiting competing green alga species and decreasing fungal and viral transcript signals (Lu *et al*., 2019). Both studies show that cyanobacteria are resistant to run-off levels of some pesticides and benefit from the reduction of top-down regulation, e.g., a reduction of zoosporic eufungal parasites.

Cyanobacteria-dominated harmful algal blooms (cHABs) are expected to increase in severity and duration as climate change affects surface water temperature and increases extreme weather events (Jöhnk *et al*., 2008; Paerl and Huisman, 2008, 2009; Paerl and Otten, 2013). Many water bodies worldwide have started to test methodologies for the management of cHABs, including methods for nutrient management (Berg *et al*., 2004; Lürling and Faassen, 2012; Copetti *et al*., 2016), changing hydrodynamics (Mitrovic *et al*., 2011; Visser *et al*., 2016), chemical control (Matthijs *et al*., 2012; Barrington *et al*., 2013), and biological control (Kagami *et al*., 2007a; Gerphagnon *et al*., 2015; Van Wichelen *et al*., 2016). Cyanobacteria are host to several biological antagonists, many of which are being tested as possible biological control agents (Demeke, 2016; Ndlela *et al*., 2018).

In some regions, chytrids are thought to already play a significant role in the control of their phytoplankton hosts and could delay or even suppress bloom formation. In a eutrophic lake, where late summer cyanobacteria blooms are dominated by *Aphanizomenon flos-aquae*, monospecific chytrid prevalence increased rapidly, subsequently followed by a decrease in the presence of both the parasite and its host (Rasconi *et al*., 2012). This suppression is largely temperature-dependent and may not be indicative of the host-parasite relationship in every lake, particularly when we consider the effects of climate change. Chytrids tend to have a narrower temperature growth range than their cyanobacterial hosts, leading to the formation of thermal refuges where the host can grow but their parasite cannot. The lower thermal refuge for *Planktothrix* sp. when infected by *Rhizophydium megarrhizum* tends to be less than 11 °C (Rohrlack *et al*., 2015; Wierenga *et al*., 2022) while the upper thermal refuge tends to be above 27 °C (McKindles *et al*., 2021). The warming of cooler lakes may make it harder for cyanobacteria to evade their parasites, while the warming of already warm lakes may promote further bloom biomass accumulation as well as the inhibition of chytrid infectivity.

These thermal refuges are not unique to cyanobacteria and have also been found in diatom-chytrid systems. Field observations of the spring-bloom diatom *Asterionella formosa* and its two chytrid parasites *Zygorhizidium planktonicum* and *Rhizophydium planktonicum* noted that *Asterionella* already reproduces at temperatures below 3 °C, while the chytrids do not (Van Donk and Ringelberg, 1983). Later work confirmed that these chytrids will form resting spores at low temperatures, which keeps infection prevalence low, and added that at higher temperatures (above 21 °C), infection prevalence was kept low due to chytrid death (Gsell *et al*., 2013). These lower thermal refuges are important for establishing the host population prior to the establishment of the parasite, and climate change may be limiting the host's ability to establish itself. Interestingly, this can prevent the host population from reaching bloom densities while also denying the chytrid its chance to form an epidemic (Ibelings *et al*., 2011). Further, because diatoms tend to dominate in cooler waters than cyanobacteria, increases in water temperature driven by climate change are expected to increase infection prevalence, accelerating the termination of diatom-dominated spring blooms (Frenken *et al*., 2016). Unlike cyanobacteria blooms, which have human health and environmental concerns associated with them, diatom-dominated blooms are important for the ecological health of a waterbody, as they serve as an abundant food for herbivorous zooplankton and thus fuel the planktonic food web.

While climate change may promote cyanobacterial bloom growth due to better growth conditions and inhibition of chytrid infection, warming waters may benefit other populations, such as frog populations infected with *Batrachochytrium dendrobatidis*. It is known that ambient temperature can influence the severity of infection in ectothermic hosts (Woodhams *et al*., 2008), and despite optimal growth temperature of *B. dendrobatidis* in culture being between 17 – 25 °C, it has been shown to grow sufficiently at lower temperatures where the host may become stressed and immunocompromised (Woodhams and Alford, 2005; Bakar *et al*., 2016). Recent work looking at the relationship between sublethal infections of *B. dendrobatidis* and the effect of high and low temperatures showed that infection loads decreased at 24 °C, despite being within the temperature range for optimal growth in laboratory culture (Campbell *et al*., 2019). The authors note that this relationship will be dependent on the thermal tolerance of individual species and populations and hypothesize that reduced parasite loads at warmer temperatures are due to the frogs' immune response performing near optimal.

Due to the diversity of the zoosporic eufungi, it is hard to give broad generalizations about how they will react to climate change. For some species, warming temperatures means better growth conditions. For others, warming temperatures means they are out of sync with their hosts or they must infect under suboptimal conditions, forcing them to adapt or perish. Given the concern in science for climate change and the increased awareness of the importance of many overlooked fungal groups, more research will be forthcoming in the next few years to address many of these unknown interactions.

Impacts on agriculture and the industry

Several zoosporic eufungal taxa affect crops grown by humans. Some, such as *Synchytrium endobioticum*, *Physoderma maydis* and members of *Olpidium*, can cause substantial losses of major global crops. Others, such as *Synchytrium pogostemonis* and *S. psophocarpi*, cause serious problems for those who grow their plant hosts (Karling, 1964) but since they are not on crops of global economic importance, they are understudied. In addition to traditional crops, zoosporic eufungi are also a problem for businesses and individuals cultivating algae for the production of biofuel or chemicals. Not all impacts of zoosporic eufungi are negative, however; some species, such as *Coelomomyces* spp. (Figure 3w) and *Synchytrium solstitiale*, may prove useful as biocontrol agents.

Traditional agriculture

Prior to the emergence of *Batrachochytrium dendrobatidis* and *B. salamandrivorans*, the most well-known zoosporic eufungus was the causal agent of potato black wart, *Synchytrium endobioticum*, which results in devastating crop losses of 50-100% (Baayen *et al*., 2006). It was first encountered after the Irish Potato Famine as plant breeders brought potato cultivars from the Andes of South America to Europe to breed resistance against *Phytophthora infestans* (Hampson and Proudfoot, 1974; Baayen *et al*., 2006; Van de Vossenberg *et al*., 2019). *Synchytrium endobioticum* has spread to every region where potatoes are grown (CABI, 2021b) with over 40 known pathotypes (Prodhomme *et al*., 2020). In addition to human movement, *S. endobioticum* resting spores are dispersed by the wind (Hampson, 1996) and earthworms (CABI, 2021b). Due to the longevity of resting spores and resistance to chemical control measures, the most effective means of control are strict quarantine measures (Powell, 1993; Quintero and Rodriguez, 2020; CABI, 2021b). Additional research on resting spore viability, potential means of biological control, genomic mechanisms of virulence, and means of chemical control are needed.

Physoderma maydis (Figure 2a, b) was first observed in India in 1910 and then in the United States of America (USA) in 1911 (Robertson *et al*., 2018). It has since spread to all regions where maize is grown (CABI, 2021a). Early in its observation, it caused losses of 1-10% in the USA, and generally has not been seen as a disease of major economic importance (Robertson *et al*., 2018). However, that is changing in the USA and in other parts of the world. In the USA and Ontario, Canada, the prevalence of *P. maydis* and the yield loss due to infection increased substantially between 2012 and 2016 (Mueller *et al*., 2016; Robertson *et al*., 2018; Mueller *et al*., 2020). As portions of the Corn Belt in the USA become wetter due to climate change, it seems likely *P. maydis* will increasingly become a problem (Robertson *et al*., 2018). Climate change is also driving the increase of *P. maydis* in Cameroon where it is the second most common maize pathogen (Patrice *et al*., 2021). However, little is known about the life cycle of *P. maydis* or effective means of prevention and treatment (Robertson *et al*., 2018; Dooh *et al*., 2021; Patrice *et al*., 2021).

Synchytrium pogostemonis is an emerging threat that causes budok disease of patchouli (*Pogostemon cablin*) (Wahyuno, 2010a, 2010b; Wahyuno and Sukamto, 2010). Patchouli is cultivated in India, China, Malaysia, Singapore, and Indonesia for essential oil production (Swamy and Sinniah, 2016). In Indonesia, there have been outbreaks of *S. pogostemonis* that have disrupted the country's production of patchouli (Wahyuno, 2010a, 2010b; Wahyuno and Sukamto, 2010), with up to 90% loss of yield (Sriwati *et al*., 2021). As such, research into the life cycle of *S. pogostemonis* (Wahyuno, 2010b), potential sources of genetic resistance in patchouli (Wahyuno and Sukamto, 2010), and means of control (Sriwati *et al*., 2021) have been initiated. However, little is known about the geographic distribution of *S. pogostemonis* and whether it poses a threat to patchouli production in other regions.

Synchytrium psophocarpi on winged bean (*Psophocarpus tetragonolobus*) crops in Cyprus, Ethiopia, Ghana, Indonesia, Java, Malaysia, Nigeria, Papua New Guinea, Philippines, Tanzania, and Uganda (CABI, 2021c) has the potential to emerge as a serious threat. Indeed, it is potentially spreading as in 2018 it was observed in Taiwan (https://www.inaturalist.org/observations/105293439) where it was previously not reported (CABI, 2021a; Farr and Rossman, 2022). In the 1970s, there was a call to study winged bean as a high-quality protein source that could replace soybeans; however, research was hindered by a lack of resources (Lepcha *et al*., 2017; Tanzi *et al*., 2019). Drinkall (1978), in response to the call to study winged bean, identified *S. psophocarpi* as a major disease in Papua New Guinea and noted that it also occurred in Java, the Philippines, and Malaysia. Price *et al*. (1982) observed that *S. psophocarpi* was present in all areas of Papua New Guinea where winged bean was present, and that all tested strains of winged bean were susceptible. Other researchers have found resistant strains of winged bean (Tanzi *et al*., 2019). Curiously, Price *et al*. (1982) note that winged bean growers in Papua New Guinea would still consume plants infected with *S. psophocarpi* and also noted that growers in Java would purposefully infect their plants before consumption. This would suggest that *S. psophocarpi* may not reduce crop yields; however, just as western civilizations treated *Ustilago maydis*, or corn smut, as a pest, it is likely they will view *S. psophocarpi* infection as something to avoid. Additional research into the ethnobotany of winged bean and *S. psophocarpi* (and subsequent education of western civilizations) and into resistant varieties of winged bean are warranted as there is renewed interest in the large-scale cultivation of winged bean.

Another growing concern is an unidentified zoosporic eufungal pathogen of faba bean (*Vicia faba*) in Ethiopia (Earecho, 2019). This disease was first detected in 2010 (Gorfu *et al*., 2012, as in You *et al*., 2020). It spread rapidly in Ethiopia and became more severe, causing up to 100% crop losses in some parts (You *et al*., 2020). Initially, *Olpidium viciae* was recognized as the causal agent of faba bean gall disease (Meresa and Gebremedhim, 2020). However, the fungus in Ethiopia turned out to be *Physoderma* (Figure 2a, b; Blastocladiomycota), not *Olpidium*, based on morphology and molecular phylogenetic analysis (You *et al*., 2020). *Olpidium viciae* was originally described in Japan (Kusano, 1912) as an endobiotic parasite infecting leaves or stems of *Vicia unijuga*. It was also reported to cause blister disease of broad bean in China (Xin *et al*., 1984). Unfortunately, DNA sequence data of “true” *O. viciae* is not available. The ITS1-5.8S-ITS2 rDNA sequence of *O. viciae* available in GenBank (HQ677595) could be a sequence from a putative contaminated ascomycetous fungus, though currently unverified. Additional studies that include strains from China, additional *Physoderma* species, and strains from the original host of *Olpidium viciae* are needed to clarify whether *Olpidium viciae* should be transferred to *Physoderma* or if the Ethiopian parasite is a novel species.

Olpidium is a genus containing many species of endobiotic parasites of algae and plant roots (Sparrow, 1960). Generally, there are three accepted species that inhabit plant roots: *Olpidium brassicae* on plants in the Brassicales, *O. virulentus* with a broad host range, and *Olpidium bornovanus* on plants in Cucurbitaceae (Rochon, 2016). In most cases, the species that infect plant roots do not cause noticeable disease symptoms or crop loss (but see Stanghellini *et al*., 2010; Aleandri *et al*., 2017; Nishimura *et al*., 2020; Floc’h *et al*., 2020); however, they can serve as vectors for devastating plant viruses (Table 1; Rocha, 2016).

Algal cultivation

The market for algal products is growing, which is creating increased interest in the mass cultivation of algae (Kassinger, 2019). One such class of products are algal derived oils as replacements for crude oil and its products. The demand, and therefore the profitability and investment of resources into research, for such algal derived replacements is heavily dependent on the price of crude oil. For instance, in 2008, the price of crude oil rose to $160 USD per barrel. This prompted over $2 billion USD to be invested in algal biofuel production between 2008 and 2010. The leaders at that time were Sapphire Energy, which focused on photosynthetic algae, and Solazyme, or later TerraVia, which focused on mixotrophic and heterotrophic algae. In 2013, both companies were capable of producing 1 million gallons of algae-derived oil. In 2014-2015, though, hydraulic fracking brought the price of crude oil back to $30 USD per barrel. Sapphire and TerraVia simply could not compete. Both Sapphire and TerraVia were eventually forced to close, though TerraVia had invested in other products and was able to remain open for slightly longer. If the price of crude oil rises again or another reason (e.g., reduction of atmospheric carbon) is identified, there may be renewed interest in algal-derived biofuels (Kassinger, 2019).

As with traditional agricultural crops, the mass cultivation of algae faces the challenge of parasites, including zoosporic eufungi (Table 2; Carney and Lane, 2014; Kassinger, 2019). Most of the published research on zoosporic eufungal parasites of industrially cultivated algae has been taxonomic. This is due in part because taxonomy and systematics are critical for the proper identification and monitoring of pest species, but also because the methods of production are tightly kept trade secrets (Kassinger, 2019). There is a growing body of literature on the effects of pesticides on zoosporic eufungi (e.g., Ortiz-Cañavate *et al*., 2019) and aquatic fungi in general (e.g., Cuco *et al*., 2020). However, past experience tells us that the widespread application of pesticides is not desirable due both to environmental impacts (e.g., Carson, 1962) and the emergence of resistant human pathogens (e.g., Abdolrasouli *et al*., 2018). Plus, leakage of agricultural fungicides into other systems allows for toxic cyanobacteria to bloom by preventing the development of chytrid epidemics (Ortiz-Cañavate *et al*., 2019). Thus, the field would benefit from research into non-pesticide methods of control. Such research would likely benefit from the wealth of literature on the abiotic and biotic factors affecting zoosporic eufungal epidemics in nature (e.g., Ibelings *et al*., 2004, 2011; Schmeller *et al*., 2014; Farthing *et al*., 2021). Alternatively, since zoosporic eufungi are themselves a source of polyunsaturated fatty acids, sterols (Kagami *et al*., 2007a), and polyenoic phospholipid fatty acids (Akinwole *et al*., 2014), perhaps some research should also focus on how to transform epidemics into marketable products as another way to avoid crop loss.

Biological control

Coelomomyces (Figure 3w) is the most well studied of the zoosporic eufungi in terms of a potential biocontrol agent. Members of the genus infect mosquitoes, as well as other aquatic dipterans, usually with high host specificity. Thus, *Coelomomyces* spp. were considered prime candidates for the biological control of mosquitoes that vector human diseases (Couch and Bland, 1985; Scholte *et al*., 2004). However, two factors limit their use. First, their life cycle cannot be completed without the presence of a second host, usually a microcrustacean. For many species, the identity of this second host is not known. Thus, it is currently difficult to mass produce enough resting spores to inoculate mosquito breeding sites (Couch and Bland, 1985; Scholte *et al*., 2004). Second, in many areas, there is already a high incidence of infection in mosquito populations, which means adding additional inoculum would have little effect (Couch and Bland, 1985; Scholte *et al*., 2004). In spite of these challenges, there have been several successful field trials in which *Coelomomyces* spp. were introduced into an uninfected mosquito population and became established (Couch and Bland, 1985; Scholte *et al*., 2004). However, primarily due to the necessity of a microcrustacean host, there has been little further research into the use of *Coelomomyces* as a biocontrol agent (Scholte *et al*., 2004).

Two species of *Synchytrium* have been explored for their potential as biocontrol agents: *S. solstitiale* and *S. minutum*. *Synchytrium solstitiale* was being investigated as a potential biocontrol agent for the yellow star thistle (*Centaurea solstitialis*), which is an invasive, noxious weed in North and South America (Voigt *et al*., 2013). However, difficulties in mass producing enough infectious material have so far limited its usefulness (Widmer, 2006). Li *et al*. (2011) mention *Synchytrium minutum* as a potential biocontrol agent of kudzu, which is also an invasive species in North America. They noted, however, that within kudzu's native range, the parasite was rarely found in wild populations but was frequently observed with a prevalence of 10%-30% in cultivated kudzu populations (Li *et al*., 2011). They also noted that it infected economically important crops but did not list which crops (Li *et al*., 2011). Karling (1964) noted that there were reports of *S. minutum* on velvet beans (*Mucuna* spp.); however, he also noted that they were likely one of several undescribed *Synchytrium* species rather than *S. minutum*. Thus, if *S. minutum* is to be considered as a biocontrol agent of kudzu, its host range will need to be determined.

Batrachochytrium and chytridiomycosis

The genus *Batrachochytrium* (Batrachochytriaceae; Rhizophydiales) is the only zoosporic eufungal taxon known to infect vertebrates, specifically amphibians. The type species, *Batrachochytrium dendrobatidis* (or *Bd*), was discovered concurrently in wild (Berger *et al*., 1998) and captive amphibian populations (Longcore *et al*., 1999) in the late 1990s, as the causative agent of the disease termed chytridiomycosis (Berger *et al*., 1998). The fungus infects keratinized larval mouthparts and superficial epidermal cells of the hosts (Greenspan *et al*., 2012). Infection leads to a disruption of osmoregulation through the host's skin, causing osmotic imbalances, which have been correlated to "cardiac standstill" (Voyles *et al*., 2009). This fungal species is a generalist pathogen, infecting over 500 species of amphibians from over 50 countries (Olson *et al*., 2013). The fungus has been implicated in the complete extinction or extirpation of hundreds of amphibian species (Skerratt *et al*., 2007; Crawford *et al*., 2010; Vredenburg *et al*., 2010), and it is estimated that 41% of amphibians as a whole are threatened by this pathogen (Monastersky 2014).

Fifteen years after the discovery of *B. dendrobatidis*, the species *B. salamandrivorans* (or *Bsal*) was discovered in salamanders from the Netherlands, with the hypothesized introduction of the fungus to have arisen from the Asian commercial pet trade (Martel *et al*., 2013). Unlike the wide host range of *B. dendrobatidis*, *B. salamandrivorans* seems restricted to salamanders, or urodelan amphibians (Martel *et al.,* 2013), though it has been detected on frogs, or anuran amphibians, such as those in trade from Vietnam (Nguyen *et al*., 2017). In contrast to the subtle infection of *B. dendrobatidis*, *B. salamandrivorans* causes erosive skin lesions on its salamander hosts. Thus far it is contained within Asian and European states (González *et al*., 2020), but should the pathogen be introduced to the extremely biodiverse North American salamanders, the risk of decimation would be very high, specifically in the Pacific coast, mid-Atlantic, and southern Appalachian mountain regions (Richgels *et al*., 2016). To prevent the spread of *B. salamandrivorans* within its borders, the United States of America Fish and Wildlife Service has placed restrictive importation regulations on 201 salamander species (Bean, 2016).

The species of *Batrachochytrium* can be cultured on nutrient media (Longcore *et al.*, 1999; Martel *et al.*, 2013), facilitating decades of studies by herpetologists and mycologists worldwide (e.g., Byrne *et al*. 2019). Among the research community, *Batrachochytrium* species and chytridiomycosis have unfortunately become synonymous with “chytrid” or “chytrid fungus”, much to the chagrin of mycologists who are aware of the myriad other species in the Chytridiomycota, much less the entirely of the zoosporic early-diverging eufungal lineages. In truth, study of all zoosporic eufungi flourished in the years after the discovery of *B. dendrobatidis* (James *et al*., 2000, 2006). A reinvigorated interest in these organisms prompted the training of a new generation of zoosporic eufungal systematists (Blackwell 2011) and inspired collaborative research among mycologists, herpetologists, epidemiologists, and ecologists (e.g., Byrne *et al.*, 2019).

The effect of *B. dendrobatidis* on amphibian populations is well-documented and sadly without a foreseeable end, but it has only recently become clear how this fungal pathogen can have far-reaching negative effects, even upon human health. Increasing case numbers of malaria in Costa Rica and Panama are correlated to amphibian population declines (Springborn *et al*., 2022). As amphibian predators have diminished in regions with high incidences of chytridiomycosis, populations of mosquitoes have been allowed to go unchecked. In this absence of predation, these flourishing, disease-vectoring mosquitoes have elevated the transmission potentials of *Plasmodium* spp., the causative agents of malaria. Thus, the detrimental effect of *B. dendrobatidis* on amphibian populations and the interconnected local ecologies is also evident in the indirect effect this pathogen has on human health in these regions (Springborn *et al*., 2022).

Looking toward the future

There are many knowledge gaps concerning the ecology, evolution, and systematics of zoosporic eufungi. Filling in some of these gaps will be critical for understanding the co-evolutionary dynamics of these fungi and the myriad organisms with which they interact. Indeed, zoosporic eufungi can serve as model systems for Red Queen dynamics and evolution in multi-player systems. Filling other knowledge gaps will be critical for understanding how increased pesticide use and climate change will affect HABs and aquatic food webs. As we look for alternatives to fossil fuels and demand for algal products increase, we will need improved methods for identifying and controlling zoosporic eufungi to prevent infestations and yield losses. On the other hand, there is the potential to use zoosporic eufungi as part of integrated pest management programs. Finally, we need to be especially vigilant for emerging agricultural pathogens, such as *Physoderma maydis* (Figure 2a, b) and *Synchytrium psophocarpi*.

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Figure 1.

Cladogram showing the phylogenetic distribution of known parasitic zoosporic eufungi across currently recognized phyla and orders. Images accompanying each order indicate confirmed and suspected host organisms in black and grey, respectively.

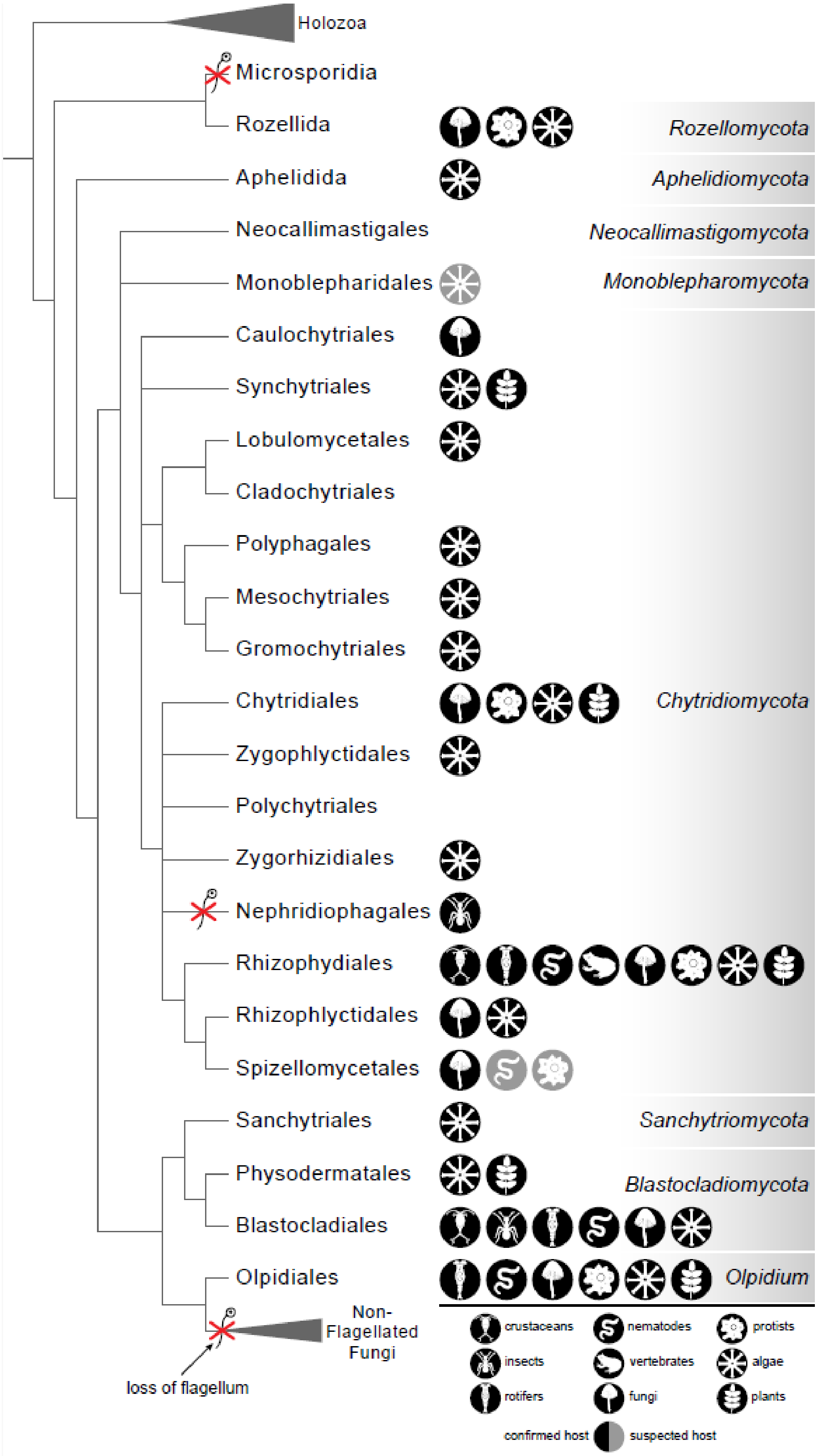
Figure 2.

Diversity of parasitic zoosporic eufungi, including taxa from (a,b) Blastocladiomycota, (c-h, j,k) Chytridiomycota, (i) Monoblepharomycota, (l,m) Sanchytriomycota, and (n) Apehlidiomycota. (a-b) Physoderma maydis. On cultivated corn stalk. (c) Synchytrium papillatum. Red galls on hypertrophied host tissue caused by resistant sporangia. (d) Synchytrium decipiens. Orange resistant sporangia forming galls on Amphicarpaea bracteata. (e) Unidentified chytrid on dead host cell. (f) Empty, (g) mature, and (h) developing zoosporangia of Chytriomyces rhizophydii parasitizing an unidentified saprobic chytrid host. (i) Harpochytrium sp. (arrow) on algal host. (j) Empty zoosporangium of Phlyctochytrium sp. (arrow) (k) Resistant sporangium of Micromyces zygogonii in algal host cell. (l) Multiple developing zoosporangia of Sanchytrium tribonematis (arrows) on host Tribonema gayanum. (m) Multiple developing zoosporangia of Amoeboradix gromovi (arrows) on Tribonema gayanum. (n) Zoospore cyst of Amoeboaphelidium occidentale on host algal cell. Abbreviations: H, host; Zsp, zoosporangium; P, pollen; zc, zoospore cyst.

Figure 3.

Additional diversity of parasitic zoosporic eufungi, including taxa from (a-l,p-s) Chytridiomycota, (m-o) Cryptomycota/Rozellomycota, (v) Olpidium, and (t,u,w) Blastocladiomycota. (a) Developing and (b) mature Collimyces mutans zoosporangia on Microglena sp. (c) Transmission electron (TE) micrograph of a C. mutans germling rhizoid (arrow) penetrating host cell wall. (d) Zygorhizidium willei zoosporangium on host cell. (e) TE micrograph of immature Z. willei zoosporangium parasitizing host cell. Arrow indicates chytrid rhizoids within host. (f) Podochytrium sp. on diatom host. (g) Immature Synchytrium sp. zoosporangia (arrows) on Desmidium. (h) Unidentified chytrid parasite on Melosira sp. (i) Mature zoosporangium of Zygophlyctis melosirae with cleaved zoospores infecting Melosira. (j) Mature zoosporangium of Zygophlyctis asterionellae (arrow) on the colonial diatom host Asterionella formosa. (k) TE and (l) scanning electron micrographs of Z. asterionellae rhizoids penetrating host cell. (m) Resistant sporangium of Rozella apodyae in sporangium of oomycete host, Apodachlya brachynema. (n) Zoospore and (o) resistant sporangia of Rozella allomycis within thallus of blastocladian fungus host Allomyces sp. (p,q) Gaertneriomyces semiglobifer parasitizing azygospores of entomophthoralean fungi. (r,s) Multiple zoosporangia of Septosperma rhizophydii (arrows) on unidentified hosts. (t,u) Myrmecinosporidium durum zoosporangia in the head and thorax of ant host Solenopsis fugax. (v) Endobiotic zoosporangia of Olpidium sp. in rotifer egg. (w) Thick-walled resistant sporangia of Coelomomyces sp. inside larval mosquito host. Abbreviations: H, host; Zsp, zoosporangium; rh, rhizoid; az, azygospore.

Figure 1.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Synchytriales
Lobulomycetales
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Polyphagales
Mesochytriales
Gromochytriales
Chytridiales
Chytridiomycota
Zygophlyctidales
Polychytriales
Zygorhizidiales
Nephridiophagales
Rhizophydiales
Rhizophlyctidales
Spizellomycetales
Sanchytriales
Sanchytriomycota
Physodermatales
Blastocladiomycota
Blastocladiales
Olpidiales
Olpidium
Non-Flagellated Fungi
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crustaceans
nematodes
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algae
rotifers
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confirmed host
suspected host

Figure 2.

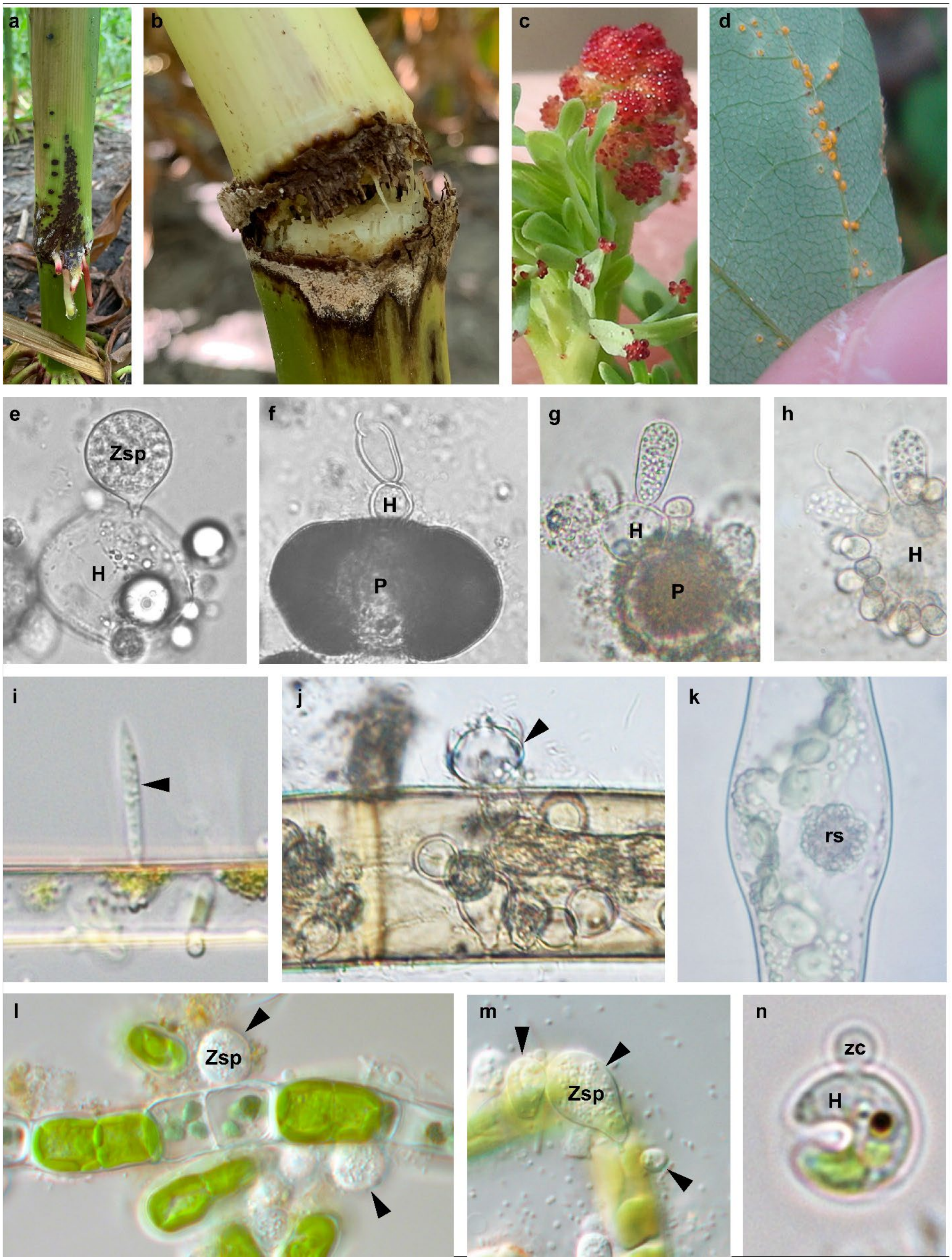
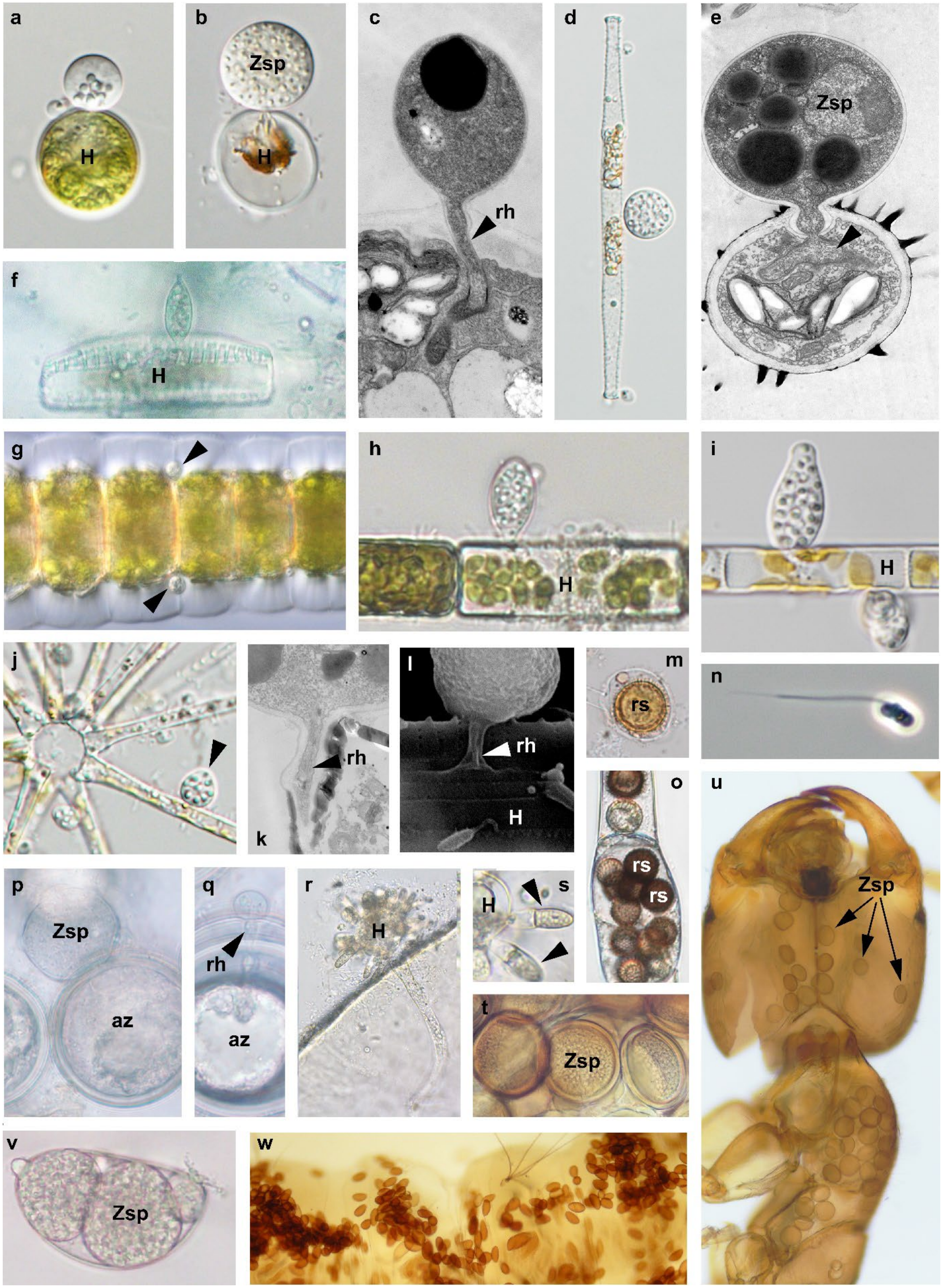


Figure 3.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