An overview on the biology and phylogeny of the early-diverging oomycetes

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Abstract

Holocarpic oomycetes are ubiquitous especially in marine and freshwater environments. These organisms are mostly obligate biotrophic parasites and members of the deep-branching, early-diverging clades of the *Oomycota*, comprising of several genera that had their phylogenetic position only recently investigated (*Miracula*, *Olpidiopsis*, *Eurychasma*, *Haptoglossa*, *Anisolpidium*, *Diatomophthora*, *Pontisma*, *Haliphthoros*) as well as some unresolved genera (*Ducellieria*, *Petersenia*, *Sirolpidium*, *Eurychasmidium*, *Pseudosphaerita*, *Rozellopsis*). Despite their widespread occurrence and importance for understanding the evolution of the oomycetes, knowledge on the biology and ecology of these bizarre organisms is still fragmentary for temperate regions and almost absent for the tropics. Here, an overview on the current state of knowledge on early-diverging oomycetes is presented, with emphasis on the general biology, systematics and ecology.

Keywords: early-diverging clades, *Oomycetes*, *Oomycota*, phylogeny, systematics

Oomycetes

The oomycetes are fungal-like heterotrophic organisms belonging to the Kingdom Straminipila (often informally referred to as "stramenopiles") of the SAR (*Straminipila, Alveolata, Rhizaria)* Superkingdom (Baldauf *et al*., 2000) together with phototrophic organisms, such as the brown seaweeds and diatoms (Silberfeld *et al*., 2014). Sometimes, the kingdom *Straminipila* is also referred to as *Chromista* or *Chromalveolata* (Cavalier-Smith and Chao 2006; Cavalier-Smith 2018), but as the older kingdom concept '*Chromista'* is not monophyletic and as the *Alveolata* and *Straminipila* are both very deeply branching lineages, 'Straminipila' is the preferred kingdom-level designation. The *Oomycota* are sometimes referred to as *Pseudofungi* (Cavalier-Smith 1997; Cavalier-Smith and Chao 2006) but then also including the *Hyphochytriomycota* and *Labyrinthulomycota*. As the latter two groups are often described under the zoological, rather than the

botanical Code of Nomenclature and some bacteriophagic unicellular protists seem to branch within the group (Tong 1995; Kühn *et al*., 2004), the phylum designation as *Oomycota* is preferable. The group is traditionally studied by mycologists, because of superficial similarities due to convergent evolution (Alexopoulos *et al*., 1996; Lévesque 2011). However, there is no immediate phylogenetic relationship with the *Mycota* (Alexopoulos *et al*., 1996; Beakes, Glockling and Sekimoto 2012; Beakes and Thines 2017). Several characters set oomycetes apart from *Mycota*. Asexual reproduction is by means of conidiosporangia or zoosporangia, which often produce heterokont, often kidney or bean shaped zoospores with a posteriorly directed whiplash flagellum and an anteriorly directed tinsel flagellum that is ornamented with tripartite mastigonemes. The flagella are usually subapically or laterally inserted in a groove. Many species, predominantly in the Saprolegniomycetes, produce two morphologically distinct generations of zoospores – primary zoospores that are weak swimmers and often pyriform in shape, and secondary zoospores, which are reniform in shape and efficient swimmers. The reason for this diplanetism is not well understood (Dick 2001; Walker and van West 2007). The cell wall of oomycetes is composed primarily of (1,3) and (1,3;1,6) β-glucans and varying amounts of cellulose rather than chitin (Cooper and Aronson 1967; Bartnicki-Garcia 1968; Lin and Aronson 1970; Wang and Bartnicki-Garcia 1974; Myklestad and Granum 2009); cytoplasmic dense-body or "finger-print" vacuoles with storage of mycolaminarin polysaccharide phosphate (Traquair

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and McKeen 1980; Bortnick *et al*., 1985; Beakes *et al*., 2012); mitochondria with tubular cristae (Alexopoulos *et al*., 1996; Beakes *et al*., 2012) and a different biochemical pathway for the synthesis of amino acid lysine (Vogel 1960, 1961, 1964).

The *Oomycota* are ubiquitous and can be found in almost all types of environments, in both aquatic (lakes, rivers, ponds, mangrove swamps, brackish waters, oceans, arctic, Antarctica) and terrestrial ecosystems (soil, muds, plant parasites) (Sparrow 1960; Dick 2001; Beakes *et al*., 2012; Thines 2014; Beakes and Thines 2017). In aquatic environments, most of the known species were recorded from freshwater, living as saprotrophs or parasites of algae and animals (Sparrow 1960; Marano *et al*., 2016). Only a few species are known from the marine realm, mostly living as obligate biotrophic parasites (Sparrow 1960), saprophytes in coastal environments (e.g. *Halophytophthora*, *Salisapilia*) (Hulvey *et al*., 2010; Marano *et al*., 2016), and others life as facultative anaerobic saprophytes in anoxic water bodies (*e.g.* stagnant ponds, heavily polluted waters) (Emerson and Weston 1967; Emerson and Held 1969; Alabi 1972; Emerson and Natvig 1981). Most of the known terrestrial forms are primarily facultative and obligate biotrophic parasites of many vascular plants in natural and managed ecosystems, which cause devastating outbreaks on several agriculturally and horticulturally important crops (Thines 2014).

To date, the *Oomycota* comprise about 1,700 described species that have been grouped into about 100 genera (Beakes and Thines 2017; Wijayawardene *et al*., 2020). The phylum contains two major classes, Saprolegniomycetes (Thines *et al*., 2015) and Peronosporomycetes (Dick 2001), as well as several early-diverging lineages (*Eurychasmatales, Haliphthorales, Haptoglossales, Miraculales, Olpidiopsidales, Pontismatales*) that are mostly holocarpic marine obligate biotrophic parasites with unresolved phylogenetic relationships to each other (Sparrow 1960; Dick 2001; Sekimoto *et al*., 2007; Beakes and Thines 2017; Buaya *et al*., 2019d). The present taxonomic arrangement of the oomycetes is largely based on the works of Karling (1942), Sparrow (1960) and Dick (2001), but with larger taxonomic revisions over the past 15 years (Thines and Spring 2005; Thines *et al*., 2015; Beakes and Thines 2017; Buaya and Thines 2019b). *Peronosporomycetes* is the largest oomycetes class containing three orders (*Albuginales, Peronosporales, Rhipidiales*) that are saprophytes (*e.g. Sapromyces, Rhipidium, Salispina, Halophytophthora, Phytopythium*) and parasites of various plants (*e.g. Albugo, Bremia, Hyaloperonospora, Peronosclerospora, Peronospora, Phytophthora, Plasmopara, Pseudoperonospora, Pustula, Pythium*), vertebrate and invertebrate animals (*e.g. Lagenidium, Myzocytiopsis*) (Dick 2001; Kamoun 2003; Lamour and Kamoun 2009; Thines 2014; Fawke, Doumane and Schornack

2015; Kamoun *et al*., 2015; Beakes and Thines 2017; Thines and Choi 2016; Derevnina *et al*., 2016).

The *Saprolegniomycetes* (Thines *et al*., 2015) contain two recognised orders (*Saprolegniales, Leptomitales*) mainly saprobes and parasites of plants/algae (*e.g. Aphanomyces, Lagenisma, Ectrogella*), vertebrate (*e.g. Saprolegnia, Achlya*) and invertebrate animals (*e.g. Atkinsiella, Chlamydomyzium, Aquastella, Sommerstorffia, Leptolegnia, Blastulidium, Bolbea*) (Karling 1942; Sparrow 1960; Dick 2001; Duffy *et al*., 2015; Buaya and Thines 2020b). The eucarpic members of the *Saprolegniomycetes* are mostly placed in the *Saprolegniales*, while the holocarpic ones are in the *Leptomitales* clade. The relationships in that clade are largely unclear and several holocarpic genera are assumed to belong to this group. The eucarpic members of the *Saprolegniomycetes* are ubiquitous and abundant in the aquatic environment (freshwater, brackish waters) and moist soil, and are important contributors to organic decomposition and nutrient recycling and can be facultative parasites (Karling 1942; Sparrow 1960; Alexopoulos, Mims and Blackwell 1996; Dick 2001; Beakes and Thines 2017). *Saprolegniomycetes* commonly grow an extensive network of coenocytic mycelium, and undergo both asexual and sexual reproduction (Sparrow 1960; Dick 2001). Asexual reproduction is by means of biflagellate zoospores that are dimorphic and diplanetic or polyplanetic (Sparrow 1960). Sexual reproduction is oogamous, occurring by fusion of a haploid male (antheridium) and a female (oogonium) gametangium, producing one to several diploid oospores (Dick 2001).

The early-diverging orders that branch before the main split between *Peronosporomycetes* and *Saprolegniomycetes* (*Eurychasmatales, Haptoglossales, Olpidiopsidales, Diatomoph -thorales, Miraculales, Anisolpidiales, Haliphthorales*) and a few unresolved families, e.g. *Rozellopsidaceae*, show a great diversity of lifestyles and cytological adaptations and mostly thrive in limnic and marine environments (Beakes and Sekimoto 2009; Beakes *et al*., 2012; Beakes and Thines 2017; Buaya *et al*., 2017, 2019d; Buaya and Thines, 2020a). Most species are holocarpic, and most seem to be, biotrophic parasites and either parasite of phytoplankton and algae, such as *Anisolpidium, Diatomophthora, Eurychasma, Miracula, Olpidiopsis, Petersenia, Pontisma* and *Sirolpidium*, or of invertebrate animals, such as *Haptoglossa, Haliphthoros, Halioticida, Halodaphnea* (Karling 1942; Sparrow 1960; Dick 2001; Hakariya *et al*., 2007; Sekimoto *et al*., 2007, 2008a, 2008b; Gachon *et al*., 2017; Buaya *et al*., 2017, 2019b, 2019d; Buaya and Thines, 2020a). While there is accumulating evidence from environmental sequences that these holocarpic pathogens are ubiquitous, especially in aquatic environments, their ecological roles are widely unknown (Strittmatter *et al*., 2009; Beakes and

Sekimoto 2009; Skovgaard 2014; Scholz *et al.*, 2015; Beakes and Thines 2017; Hassett *et al.*, 2019). However, it is likely these holocarpic oomycetes are significant contributors to the food web stability, functioning both as prey and predator, thereby facilitating energy transfer ("oomycoloop") as well as well as triggering adaptive diversification in their habitats as observed from other biotrophic microorganisms (e.g. chytrids) (Lafferty *et al.*, 2008; Hatcher *et al.*, 2012; Kagami *et al.*, 2014).

Sexual reproduction is known to occur in organisms of the early-diverging lineages (Karling 1942; Sparrow 1960; Dick 2001). But the type of oospores observed for the *Peronosporomycetes* and *Saprolegniomycetes* is an apomorphy of these groups and absent from the early-diverging lineages (Thines 2014; Beakes and Thines 2017). However, some species of *Olpidiopsis* (*e.g. Olpidiopsis saprolegniae* var. *saprolegniae*, *Olpidiopsis achlyae*, *Olpidiopsis varians*) produce oospore-like structures, but their formation is not well understood (Cornu 1872; Barrett 1912; Shanor 1939; McLarty 1941; Sparrow 1960; Buaya *et al.*, 2019d). The classification of early-diverging oomycetes is mainly based on the few morphological characters available and on the development of the holocarpic thallus, zoosporangia and zoospores, as well as the mode of zoospore release and encystment (Sparrow 1960; Dick 2001; Beakes *et al.*, 2012; Beakes and Thines 2017). As these offer only few characteristic states useful for classification, and many might have evolved multiple times, the taxonomy and phylogenetic relationships of the early-diverging oomycetes are poorly resolved as compared to the *Saprolegniales* and *Peronosporales* (Beakes and Thines 2017). Only recently, interest on the taxonomy and systematics of this group has resurged (Fletcher *et al.*, 2015; Klochkova, Shin and Moon 2016; Buaya *et al.*, 2017; Kwak *et al.*, 2017; Klochkova *et al.*, 2017; Garvetto *et al.*, 2018; Badis *et al.*, 2019; Garvetto *et al.*, 2019; Buaya *et al.*, 2019a; Buaya and Thines 2019b; Buaya *et al.*, 2019c, 2019d; Buaya and Thines 2020a; Buaya *et al.*, 2020c). However, investigations of early-diverging oomycetes organisms are challenging due to the obligate biotrophic nature of these parasites, and a huge effort is needed for isolating and establishing a stable dual culture in a defined chemical medium (Buaya *et al.*, 2019c, 2020c). Without pure cultures, sequence data of these organisms are often difficult and challenging to obtain from environmental samples. However, application of advanced molecular techniques, such as single cell genomics (Garvetto *et al.*, 2019) or plasmid cloning (Buaya *et al.*, 2017) can be highly useful to obtain full length sequences of these organisms for taxonomic and phylogenetic investigation.

General biology and characteristics of the early-diverging oomycetes

1) Morphology and Life-cycle

As mentioned earlier in this review, early-diverging lineages of the oomycetes have rather simple morphological characters unlike the morphologically more complex species of the *Saprolegniomycetes* and *Peronosporomycetes*. All known species of the early-diverging oomycetes produce endobiotic holocarpic thalli that subsequently mature into sporangia (Karling 1942; Sparrow 1960; Dick 2001; Beakes and Thines 2017). The typical life-cycle of the early-diverging oomycetes starts as soon as an encysted zoospore attached to its host germinates. After subsequent penetration, growth and elongation, the thallus undergoes rapid differentiation. At early stages of development, the colorless plasmodial thallus is un-walled or very thin-walled, and for most basal oomycetes growth usually starts close to the host nucleus (Karling 1942; Sparrow 1960; Schnepf *et al.*, 1978b; Dick 2001; Beakes *et al.*, 2012; Buaya *et al.*, 2019a), probably to enable a more efficient deployment of pathogenicity effectors. This would be analogous to the movement of the nucleus towards haustoria in obligate biotrophic pathogens (Scheler *et al.*, 2016) where an intimate contact would likewise render host manipulation more efficient, as effectors do not have to travel a long distance to act as transcription factors. This is evident on various early-diverging species especially those that parasitize green or brown algae (*e.g. Olpidiopsis schekiana*, *O. oedogoniarum*, *Eurychasma dicksonii*) and diatoms (*e.g. Miracula helgolandica*, *M. moenusica*, *Diatomophthora drebesii*, *D. gillii*, *D. perforans*), but also the two early-diverging members of the *Saprolegniomycetes* parasitizing diatoms, *Ectrogella bacillariacearum* and *Lagenisma coscinodisci* (Zopf 1884; Scherffel 1925; Sparrow and Ellison 1949; Sparrow 1960; Drebes 1966; Johnson 1966; Schnepf and Drebes 1977; Raghukumar 1980; Schnepf *et al.*, 1978a; Buaya *et al.*, 2017; Buaya and Thines 2019b, 2020a). The majority of the early-diverging oomycetes such as the marine parasitoids of multicellular algae (*e.g. Eurychasma*, *Anisolpidium*, *Pontisma*, *Sirolpidium*, *Petersenia*), diatoms (*e.g. Miracula*, *Diatomophthora*, *Aphanomycopsis*, *Ectrogella*) and aquatic oomycetes (*e.g. Olpidiopsis*) produces unbranched or little-branched thalli that are either tubular or spherical (Zopf 1884; Cornu 1872; Magnus 1905; Petersen 1905; Scherffel 1925; Karling 1943; Feldmann and Feldmann 1955; Sparrow 1960; Buaya *et al.*, 2017; Buaya and Thines 2020a). Other early-diverging lineages produce branched thalli, such as some species that are parasites of invertebrates (*e.g. Haliphthoros*, *Halocrusticida*, *Halodaphnea*), but also *Lagenisma*, a parasite of

centric diatoms, produces branched thalli (Vishniac 1958; Sparrow 1960; Dick 1988; Drebes 1966). The principal chemical composition of the thallus wall of early diverging oomycetes is not fully known, but it is likely to contain significant amounts of cellulose derivatives, since most species across several genera (*e.g. Diatomophthora*, *Miracula*, *Olpidiopsis*) exhibits positive reaction when tested with chloride -zinc and iodine solution (Friedmann 1952; Sparrow 1960; Dick 2001; Buaya *et al.*, 2019a, 2019b).

In several species of *Olpidiopsis* (*e.g. Olpidiopsis saprolegniae*, *O. achlyae*, *O. vexans*, *O. luxurians*, *O. varians*), a number of spherical vacuoles are prominent during the mid-stage of sporangium development (Shanor 1939; Sparrow 1960; Barrett 1912; McLarty 1941). After subsequent differentiation, these vacuoles disappear before roundish zoospores initials and the discharge tube begin to form. The number and length of discharge tube varies and it is unclear, if this character can be used. While many species regularly form a single discharge tube per thallus or thallus segment (*e.g. Diatomophthora gillii, Miracula moenusica, Olpidiopsis saprolegniae, Pontisma lagenidioides*), there are several species that usually form multiple exit tubes (*e.g. Ectrogella bacillariacearum, E. licmophorae, Diatomophthora perforans*) (Zopf 1884; Cornu 1872; Petersen 1905; Scherffel 1925; Buaya *et al.*, 2017, 2019a, 2019b, 2020c). Unlike other early-diverging species, several diatom-infecting oomycetes (e.g. *Ectrogella bacilariacearum, Miracula helgolandica, Diatomophthora perforans* subsp. *pleurosigmae*) show a thickening of the base of the discharge tube (Johnson 1966; Buaya *et al.*, 2017, 2020c). It is likely that these thickenings are formed as a *Spreizapparat* or *Spreizkörper* (Scherffel 1925) for pushing apart the frustule of the diatom host during the development of the thallus into a mature sporangium (Johnson 1966). However, it is unclear and remains to be known if these "thickenings" have significant taxonomic importance (Gavetto *et al.*, 2018). From unpublished observations (Buaya and Thines, unpublished) it seems that this character is highly variable and depends on the actual force needed during discharge tube development.

In addition to the characters mentioned above, the mode of zoospore release also differs among species in the early-diverging lineage (Sparrow 1960). Most holocarpic species of the early diverging *Saprolegniomycetes* and of the species diverging before the main *Peronosporomycetes/ Saprolegniomycetes* split have a zoospore discharge pattern either like *Olpidiopsis* (*e.g. Olpidiopsis saprolegniae*, *Pontisma lagenidioides*), *Saprolegnia* (*e.g. Ectrogella bacillariacearum*, *Lagenisma coscinodisci*), or *Achlya* (*e.g. Aphanomycopsis bacillariacearum*, *Ectrogella monostoma*, *E. licmophorae*) (Cornu 1872; Magnus 1905; Scherffel 1925; Petersen 1905). In

species with olpidiopsis-like and saprolegnia-like zoospores discharge, zoospores immediately swim away and disperse after their release (Sparrow 1960). While the olpidiopsis-like behavior is characterised by spores that swim for some time (sometimes several minutes), in species with saprolegnia-like discharge the spores quickly come to a rest (often within a minute) and form cysts from which a second generation of more vigorously-swimming zoospores emerges. Species with achlya-like discharge first release spores that are non-flagellated (aplanospores), which encyst at the orifice of the discharge tube, and undergo further development before release of zoospores from the cysts (Scherffel 1925; Canter 1949). However, it is still unclear whether those species with an achlya-like zoospores discharge pattern are *bona fide* members of the early-diverging oomycetes since none of them has sequence data available (Beakes and Thines 2017; Buaya *et al.*, 2017).

All early-diverging oomycetes confirmed so far only produce pyriform to grape-seed-shaped primary zoospores that are monomorphic and might change shape, but without forming cysts. Thus, they are considered as monoplanetic or to exhibit an incomplete diplanetism (Dick 2001; Beakes and Sekimoto 2009; Beakes *et al.* 2012; Beakes and Thines 2017). Except for *Anisolpidium*, the zoospores of early-diverging oomycetes contain two anteriorly to sub-lateral inserted flagella, with a forwardly directed tinsel flagellum ornamented with mastigoneme hairs, and a whiplash flagellum trailing behind (Beakes *et al.*, 2012; Beakes and Thines 2017). However, the mastigoneme ornamentation appears to be variable among some lineages such as *Haptoglossa*, which lacks mastigonemes (Beakes and Glockling 1998; Beakes *et al.*, 2012).

Resting spores of early-diverging oomycetes are diverse and derive from various pathogen stages (Sparrow 1960; Dick 2001). In some early-diverging species zoospore cysts are converted into resting spores, e.g. in *Lagenisma coscinodisci* (Schnepf and Drebes 1977). The encysted zoospores can stay dormant for a longer period of time and only germinate under proper environmental conditions. However, in species of the genus *Haptoglossa* the encysted spores germinate into "gun cells" (Barron 1990; Barron 1987; Barron 1989; Beakes and Glockling 1998; Beakes *et al.*, 2012). The gun cell functions like a miniature cannon containing a needle-like harpoon projectile that is capable of rupturing the cuticle of its host (usually *Adineta* rotifers or rhabditid nematodes), establishing a new infection site (Beakes *et al.*, 2012). The ultrastructure and firing mechanism of gun cells has been described in detail by Beakes and Glockling (1998, 2000, 2002) and Barron (1980, 1987). In *Olpidiopsis*, resting spores can either be formed in a manner similar to oospore formation in the crown oomycetes (see below) or from non-discharged thalli that instead of discharge

tubes develop a thick, usually ornamented wall (Cornu 1872; Barrett 1912; Shanor 1939; Karling 1942; Sparrow 1960).

2) Sexual reproduction

Early-diverging oomycete genera do not form oospores in the manner observed in the *Peronosporomycetes* and *Saprolegniomycetes* groups as previously mentioned. The absence of canonical sexual reproduction is likely a key diagnostic feature for all early-diverging species in addition to producing monoplanetic zoospores, probably with the exception of achlyoid spore formation, either endogenous, such as in Eurychasma (Karling 1960) or exogenous (Gavetto *et al*., 2019). However, an obscure form of sexual reproduction is apparently occurring in several species of the genus *Olpidiopsis* sensu Sparrow (1960), *Eurychasma dicksonii*, and *Anisolpidium ectocarpii* (Barrett 1912; Sparrow 1960; Beakes and Thines 2017). This non-canonical reproduction has been reported many times (Cornu 1872; Barrett 1912; Coker 1923; Tokunaga 1933; Shanor 1939; McLarty 1941; Whiffen 1942; Karling 1942; Sparrow 1960), but is still not fully understood. In *Olpidiopsis* s.str. (Buaya and Thines 2019d), sexual reproduction is by the fusion of two thalli of unequal size, in which the smaller thallus (often referred to as companion cells or antheridium) passes its protoplasmic contents into the larger (often referred to as oogonium) (Barrett 1912; Sparrow 1960). Karyogamy is assumed to occur after the protoplasmic fusion between two different thalli (Barrett 1912; McLarty 1941). Subsequently, a thick layer of exospore material is deposited, resulting in a variety of ornamentations, which can be spiny, smooth, tuberculate, fibrillose, or irregular (Sparrow 1960). However, it remains to be demonstrated if sexual reproduction in *Olpidiopsis* is homologous to that of the crown groups or has evolved independently in the genus. So far sexual reproduction in early-diverging oomycetes has been reported or assumed for only few species (Barrett 1912; Coker 1923; Scherffel 1925; McLarty 1941). The most well-documented case of non-oogamous sexual reproduction among holocarpic oomycetes was documented in the diatom parasite, *Lagenisma coscinodisci*, which is a member of the early-diverging *Saprolegniomycetes* (Drebes 1966; Thines *et al*., 2015). In this species, encysted zoospores (zoomeiospores) conjugate forming a diploid zygote that will eventually undergo meiosis, forming several haploid spores (Schnep *et al*., 1978a, 1978b, 1978c). For other species, e.g. *Eurychasma dicksonii*, a similar mode of reproduction has been assumed, but still needs to be ascertained by detailed cytological studies (Magnus 1905; Sparrow 1934; Sparrow 1960; Sekimoto *et al*., 2008a).

Classification and Systematics

1) Phylogenetic Relationships of the Early-diverging Oomycetes

The early-diverging oomycetes currently comprise 8 orders and families (Dick 2001; Beakes and Thines 2017; Buaya *et al*., 2017, 2019d; Buaya and Thines 2020a). These includes the *Miraculales, Olpidiopsidales, Eurychasmatales, Haptoglossales, Anisolpidiales, Diatomophthorales, Pontismatales,* and *Haliphthorales* (Figure 1). The majority of these orders are monogeneric, containing only a single genus (Beakes and Thines 2017; Buaya and Thines 2020a). *Miraculales* probably represents the earliest-diverging lineage, and the order *Haliphthorales* branches just before the main *Saprolegniomycetes/Peronosporomycetes* split (Buaya *et al*., 2017; Sekimoto *et al*., 2007). The molecular phylogeny of the early-diverging oomycetes is mostly based on sequences of the nuclear-encoded small ribosomal subunit (18S/SSU) (Lara and Belbahri 2011; Sekimoto *et al*., 2007; Hakariya *et al*. 2007; Buaya *et al*., 2017, 2019d; Buaya and Thines 2020a) and mitochondrial-encoded cytochrome c-oxidase subunit II (*cox*2) (Hudspeth *et al*., 2000; Hakariya *et al*., 2007; Sekimoto *et al*., 2008a; Choi *et al*., 2015), as well as the cytochrome c oxidase subunit I (*cox*1) (Gachon *et al*., 2017; Garvetto *et al*., 2018). However, the systematics of the early-diverging lineages is still in a state of flux (Beakes and Thines 2017). This is because there are still many species and genera that are supposedly early-diverging, but for which no sequence data are available. Some have not been isolated since their original descriptions. It is also becoming apparent that the classical systematic accounts by Karling (1942), Sparrow (1960) and Dick (2001) are in many aspects not supported by molecular phylogeny and require significant revision.

2) Systematic account of the early-diverging lineages, including Ectrogellaceae and Lagenismataceae (*Leptomitales*)

2.1) *Miraculales: Miraculaceae* (*Miracula*)

Miraculales is a monogeneric order and probably represents the earliest-diverging lineage of the oomycetes (Buaya *et al*., 2017). The two known members of *Miracula* are obligate biotrophic parasites of diatoms (Hanic *et al*., 2009; Buaya *et al*., 2017; Buaya and Thines 2019b) in freshwater (*M. moenusica*, Buaya and Thines 2019b) and marine (*M. helgolandica*, Buaya *et al*., 2017) environments. The type species *M. helgolandica* parasitizes the diatom *Pseudo-nitzschia pungens*, which is known to produce the toxin domoic acid (Bates *et al*., 2018). The cellular ultrastructure of the parasite has revealed structures typical for early-diverging lineages
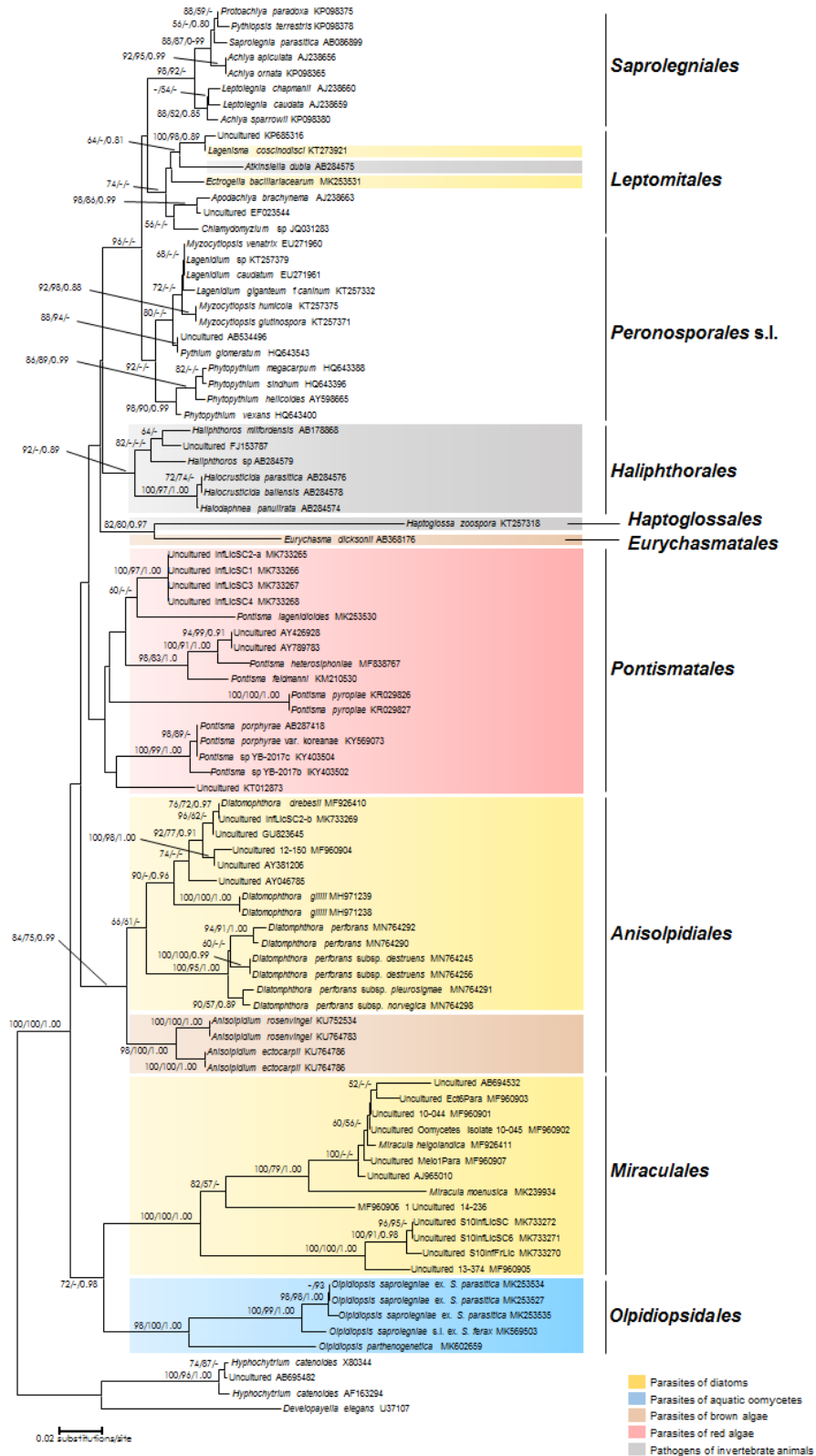
Figure 1. Minimum evolution tree based nrSSU (18S) sequences of the oomycetes. The main oomycetes orders are labelled on the right, highlighted with different colours based on their host type. Numbers on branches denote bootstrap values from minimum evolution, maximum likelihood, and Bayesian analyses, in the respective order. A dash "-" indicates less than 50% bootstrap support for the presented or a conflicting topology. Phylogenetic tree adapted from Buaya e*t al.* (2020c).
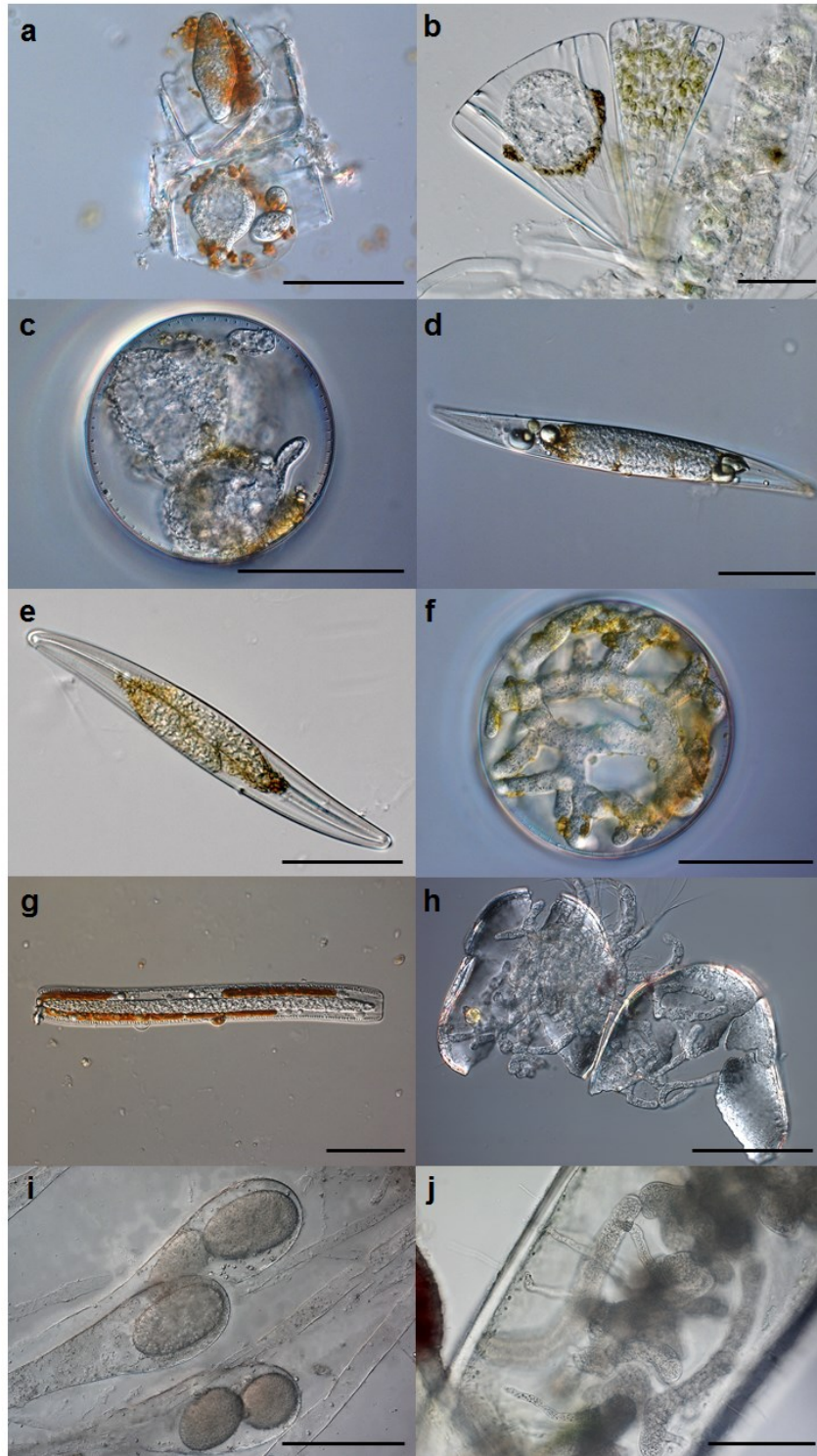
Figure 2. Light micrographs (DIC) of mature thalli of holocarpic oomycetes on various hosts. A. *Miracula moenusica* on the invasive diatom *Pleurosira leavis*; B. *Diatomophthora perforans* on the marine diatom *Licmophora abbreviata* (photo adapted from Buaya *et al*., 2020c); C. *Diatomophthora perforans* subsp. *destruens* on the marine diatom *Coscinodiscus concinnus*; D. *Diatomophthora perforans* subsp. *pleurosigmae* infecting the marine diatom *Pleurosigma intermedium*; E. *Diatomophthora gillii* infecting the freshwater diatom *Gyrosigma acuminatum*; F. *Lagenisma coscinodisci* in the marine diatom *Coscinodiscus granii*; G. *Ectrogella bacillariacearum* in the freshwater diatom *Nitzschia sigmoidea* (photo adapted from Buaya and Thines 2020a); H. *Bolbea parasitica* parasitising a freshwater ostracod (photo adapted from Buaya and Thines 2020b); I. *Olpidiopsis saprolegniae* var. *saprolegniae* parasitising in *Saprolegnia parasitica*; J. *Pontisma lagenidioides* in the marine red alga *Ceramium rubrum* (photo adapted from Buaya *et al*., 2019d). Scale bars: A, B, D, E, G = 50 µm; C, F, H, I, J = 100 µm.

(Hanic *et al*., 2009). The second species, *M. moenusica* (Figure 2A) has been studied less, but it is noteworthy that its host diatom, *Pleurosira laevis* is an invasive species in freshwater aquatic environments (Gherardi 2007; Buaya and Thines 2019b). If *M. moenusica* has been introduced together with its host or the parasitoid has jumped hosts to the alien species, a pattern frequently found in obligate parasites (Thines 2019), needs to be revealed by future studies.

2.2) *Olpidiopsidales*: *Olpidiopsidaceae* (*Olpidiopsis*)

Olpidiopsidales (Dick 2001; Buaya *et al*., 2019d) is also a monogeneric order, and one of the earliest-diverging lineages of the oomycetes. The order has been previously been used as a catch-all for simple holocarpic oomycetes, but has been shown to be largely polyphyletic, leading to substantial revision (Dick 2001; Beakes and Thines 2017; Buaya *et al*. 2019d). The phylogenetic placement of the type species, *O. saprolegniae* from *Saprolegnia parasitica* (Figure 2I), had revealed that *Olpidiopsidales* are largely unrelated to the holocarpic parasites of marine red algae (Buaya *et al*., 2019d). This led to a resurrection of *Pontismatales* and a transfer of all holocarpic parasites of red algae to the genus *Pontisma* (Buaya *et al*., 2019d), as previously suggested by Dick (2001). So far, only two species of *Olpisiopsidales* s.str. have been sequenced, the type species and a newly described species, *O. parthenogenetica*. The type species and other *Olpidiopsis* parasites of aquatic oomycetes are known to be widely occurring in freshwater habitats and moist soil (Karling 1942; Sparrow 1960). The remaining unsequenced *Olpidiopsis* that are obligate endobiotic parasite of aquatic oomycetes and fungi include, *O. saprolegniae* var. *levis*, *O. achlyae*, *O. fusiformis*, *O. braziliensis*, *O. index*, *O. varians*, *O. spinosa*, *O. incrassata*, *O. major*, *O. vexans*, *O. luxurians*, *O. aphanomycis*, *O. gracile*, *O. pythii*, *O. curvispinosa*, *O. brevispinosa*, *O. verrucosa*, *O. myzocytia*, and *O. karlingiae*. For some of these species placements in other genera have been suggested, but without molecular phylogenetic investigations that might help to pin-point synapomorphies, no decision can be made on this. The taxonomic placement of several *Olpidiopsis* species parasitising marine and freshwater algae (*O. schenkiana*, *O. oedogoniarum*, *O. fibrillosa*, *O. appendiculata*, *O. zopfii*, *O. andreei*, *O. magnusii*) remains uncertain, because none were studied for their molecular phylogeny.

2.3) *Eurychasmatales*: *Eurychasmataceae* (*Eurychasma*)

The genus *Eurychasma* has often been placed in the *Saprolegniales*, but phylogenetic investigations have shown that it forms a very early diverging lineage of the oomycetes (Sekimoto *et al*., 2008a; Beakes and Thines 2017), and often

groups with moderate support with the genus *Haptoglossa* (Sekimoto *et al*., 2008a; Beakes and Sekimoto 2009; Strittmatter *et al*., 2013; Buaya and Thines 2020a). The type species *Eurychasma dicksonii* is the only confirmed member of the genus and is a biotrophic parasite of various brown algae (Magnus 1905; Sparrow 1960, Küpper *et al*., 2006; Gachon *et al*., 2009). This parasite is known to be widely distributed in the temperate regions and has been extensively studied with respect to its physiology and cellular ultrastructure (Müller *et al*., 1999; Gachon *et al*., 2009; Tsirigoti *et al*., 2013; Grenville-Briggs *et al*., 2011; Tsirigoti *et al*., 2015; Strittmatter *et al*., 2016). Aside from *E. dicksonii*, *E. succulus* has been described, which is parasitic to the rhodophyte algae *Halosaccion ramentaceum* and *Rhodymenia palmata* (Petersen 1905). However, the taxonomic status of this species is difficult to assess. Petersen, who described the species, later did not consider it as different from *E. dicksonii* (conversation cited in Sparrow 1960), but as the host is unrelated to the host of *E. dicksonii* (red algae vs. brown algae), it would be expected that the species are distinct. However, sequence data for *E. succulus* are needed to clarify this situation.

As the *Eurychasmatales* have not been formally named, as the name "*Eurychasmales*" by Sparrow (1976) lacked a description, this is done here.

Eurychasmatales A. Buaya et Thines ***ord. nov.*** Mycobank MB 835589
Type: *Eurychasma* Magnus, Hedwigia 44: 348 (1905).
Description: Thallus holocarpic, usually leading to an enlargement of the host cell, zoospore cleavage from a large central vacuole, encysting within the thallus as part of their maturation, zoospores hatching from the cysts escape through one to several exit tubes formed during the maturation of zoospores.

2.4) *Haptoglossales*: *Haptoglossaceae* (*Haptoglossa*)

Haptoglossales (Dick 2001; Beakes and Thines 2017) is a monogeneric order often grouping with *Eurychasmatales* (Hakariya *et al*., 2007; Sekimoto *et al*., 2008a; Buaya *et al*., 2019d). The genus *Haptoglossa* contains 12 species (*H. beakesii*, *H. dickii*, *H. elegans*, *H. erumpens*, *H. heteromorpha*, *H. heterospora*, *H. humicola*, *H. intermedia*, *H. mirabilis*, *H. northumbrica*, *H. polymorpha*, and *H. zoospora*), all obligate endobiotic parasites of various rotifers and nematodes (Barron 1990; Glockling and Beakes 2000b, 2001; Glockling and Serpell 2010). All species but *H. heterospora* (Drechsler 1940) are terrestrial (Beakes and Thines 2017). As an apomorphy, *Haptoglossa* species produce "gun cells", which is a specialised infection structure that enables the parasite to penetrate its host

animal (Beakes *et al.*, 2012). Several species in the genus *Haptoglossa* have been studied using electron microscopy, especially with respect to "gun cell" ultrastructure and mechanistic function (Barron 1987; Lee *et al.*, 1992; Glockling and Beakes 2000b, 2002; Beakes *et al.*, 2012). However, there are so far no clear-cut synapomorphies that could be used to differentiate subgroups in the genus.

2.5) *Anisolpidiales*
2.5.1) *Anisolpidiaceae* (*Anisolpidium*)

Anisolpidiaceae is a monogeneric family, and frequently groups with the allied genus, *Diatomophthora* (Gachon *et al.*, 2017; Buaya *et al.*, 2019d, 2020c). If the grouping reflects a host-jump of a common ancestor to members of the *Straminipila* or is coincidental because of the limited knowledge on holocarpic oomycetes needs to be clarified by future studies. So far, only two species of this family have been included in molecular phylogenetic investigations, *A. ectocarpii* and *A. rosenvingei*. The phylogenetic placement of the type species (*A. sphacellarum*) remains unknown (Gachon *et al.*, 2017). The genus contains the species, *A. sphacellarum*, *A. ectocarpii*, *A. rosenvingei*, *A. elongatum*, *A. saprobium*, *A. joklianum*, *A. minutum*, and *A. olpidium*, *A. stigeoclonii*), which are all parasites of marine brown algae (*e.g. Sphacelaria*, *Ectocarpus*, *Pylaiella*) (Karling 1943; Canter 1950; Karling 1968, 1977; Dick 2001).

2.5.2) *Diatomophthoraceae* (*Diatomophthora*)

Diatomophthoraceae is a monogeneric family (Buaya and Thines 2020a). The genus *Diatomophthora* often forms a monophyletic group with *Anisolpidium*, and contains a variety of relatively little-studied parasitoids of diatoms (Buaya and Thines 2020a; Buaya *et al.,* 2020c). *Diatomophthora* has been previously assigned to *Olpidiopsis* together with several species of marine red-algae parasites, an assemblage which was long thought to be polyphyletic or paraphyletic (Beakes and Thines 2017; Buaya *et al.*, 2019d; Buaya and Thines, 2020a). The recent phylogenetic placement of the type species of *Olpidiopsis* (*O. saprolegniae*) shows that the olpidiopsis-like diatom parasitoids are unrelated to *Olpidiopsis* (Buaya and Thines 2020a). It was speculated that the lineage would be related to *Ectrogella* due to host-range similarities and thallus morphology (Garvetto *et al.*, 2018, 2019). However, recent phylogenetic investigations of the type species of *Ectrogella*, *Ectrogella bacillariacearum*, revealed that the genus actually belongs to the early diverging *Saprolegniomycetes* and does not diverge earlier (Buaya and Thines 2020a). Thus, the genus *Diatomophthora* was introduced to accommodate the monophyletic clade containing olpidiopsis-like diatom parasites

(Buaya and Thines 2020a). So far, only six species of this genus have been sequenced, the type species *D. drebesii*, *D. gillii* (Figure 2E) and the recently introduced three subspecies of *D. perforans* (Figure 2B) (*D. perforans* subsp. *norvegica*, *D. perforans* subsp. *destruens* (Figure 2C), *D. perforans* subsp. *pleurosigmae* (Figure 2D)) (Buaya *et al.*, 2017, 2019a, 2020c). There are still several diatom-infecting oomycetes that do not have sequence data for them available, yet, and it is possible that some of these belong to this genus, *Lagenidium*, *Ectrogella*, or *Miracula*. These include several species from the genera *Ectrogella* (*E. monostoma*, *E. gomphonematis*, *E. licmophorae*, *E. eunotiae*), *Aphanomycopsis* (*A. bacillariacearum*) and *Lagenidium* (*L. enecans*, *L. brachystomum*, *L. cyclotellae*) (Zopf 1884; Petersen 1905; Scherffel 1925; Friedmann 1952).

2.6) *Pontismatales*: *Pontismataceae* (*Pontisma*)

The monogeneric order *Pontismatales* (Buaya *et al.*, 2019d) has only been recently introduced. Because of its host-range and "olpidiopsis-like" thallus, many parasites of red algae have been assigned to the *Olpidiopsidales* together with the genera *Olpidiopsis*, *Pontisma*, *Sirolpidium* and *Petersenia* (Petersen 1905; Karling 1942; Sparrow 1960). However, recent phylogenetic investigation of the type species of *Pontisma*, *P. lagenidioides* (Figure 2J), shows that this genus is unrelated to *Olpidiopsidales*, which are probably restricted to oomycete hosts and forms a monophyletic grouping together with other parasites of marine red algae (*P. heterosiphoniae*, *P. feldmanii*, *P. pyropiae*, *P. porphyrae*, *P. porphyrae* var. *koreanae*, *P. bostrychiae*, *P. muelleri*, *P. palmariae*), previously assigned to the genus *Olpidiopsis* (Aleem 1952; Sekimoto *et al.*, 2008b, 2009; Fletcher *et al.*, 2015; Klochkova *et al.*, 2016, 2017; Badis *et al.*, 2019; Buaya *et al.*, 2019d). Thus, all holocarpic oomycete parasites of red algae were transferred to the genus *Pontisma* (Buaya *et al.*, 2019d). Two enigmatic parasites of marine algae remain unsequenced - *Sirolpium* and *Petersenia*. It is likely that *Petersenia* is closely related to *Pontisma* because of its life-cycle and morphological similarities, and the marine green algae parasite *Sirolpidium* might, for the same reason probably be also closely related to *Pontisma*.

2.7) *Haliphthorales*: *Haliphthoraceae* (*Haliphthoros*)

The order *Haliphthorales* is probably monophyletic and might represent the sister group of the *Saprolegniomycetes* and *Peronosporomycetes* oomycetes (Sekimoto *et al.*, 2007; Beakes and Sekimoto 2009; Buaya and Thines 2020a). The type genus of the order is, *Haliphthoros* (*H. milfordensis*, *H. philippinensis*, *H. zoophthorum*, *H. sabahensis*) and contains various crustaceans parasites (Vishniac 1958; Hatai *et al.*, 1980; Dick 2001; Beakes and Thines 2017). The genera *Halioticida* (*H.*

noduliformans), *Halocrusticida* (*H. awabi*, *H. baliensis*, *H. entomophaga*, *H. hamanaensis*, *H. okinawaensis*, *H. parasitica*) and *Halodaphnea* (*H. pinulirata*) are additional members of this group (Kitancharoen and Hatai 1995; Nakamura and Hatai 1995; Hatai et al., 2000; Muroasa *et al*., 2009). However, as there are little to no clear-cut morphological differences between the groups and all have a similar lifestyle, they are probably better considered to be synonymous with *Haliphthoros*. Several species in the genus are likely synonymous, as well (Beakes and Thines 2017). The species belonging to *Haliphthoros* s.l. form irregularly segmented, branched thalli and are the only known members of the early-diverging oomycetes that can be cultured apart from their host (Vishniac 1958; Sekimoto *et al*., 2007; Hatai 2012).

2.8) *Leptomitales*

Even though the *Leptomitales* are not belonging to the early-diverging oomycetes, but are forming the earliest-diverging lineage of the *Saprolegniomycetes* (Buaya & Thines 2020b), the two families *Ectrogellaceae* and *Lagenismatatceae* are discussed here, as they were previously speculated to belong to diverge before the split of the Peronosporomycetes and *Saprolegniomycetes*. Because of the currently unclear phylogenetic relationships within the *Leptomitales* other genera, such as *Blastulidium* and *Clamydomyzium* are not discussed here. For some additional comments on the *Leptomitales*, the reader is referred to Buaya and Thines (2020b). Also the placement in the two separate families needs to be viewed as provisional, as the nomenclature of the *Leptomitales* requires substantial revision after phylogenies with higher resolution and covering more taxa become available.

2.8.1) *Ectrogellaceae* (*Ectrogella*)

Ectrogellaceae is a monogeneric family initially speculated to be a member of the early-diverging oomycetes (Garvetto *et al*., 2018, 2019). However, recent phylogenetic investigations of the type species *E. bacillariacearum* (Figure 2G) shows that this genus belongs to the early-diverging lineages of the *Saprolegniomycetes* (Buaya and Thines 2020a), in line with earlier taxonomic accounts of Karling (1942), Sparrow (1960) and Dick (2001). It remains to be investigated if other diatom-infecting species (*E. monostoma*, *E. gomphonematis*, *E. eunotiae*, *E. brachystoma*, *E. cyclotellae*, *E. licmophorae*, *E. eurychasmoides*) and algal parasites (*E. marina*, *E. lauderia*, *E. dicksonii*, *E. besseyi*) that are traditionally associated to this group are *bona fide* members of this genus, since sequence data are not yet available for these (Petersen 1905; Scherffel 1925; Sparrow and Ellison 1949; Friedmann 1952; Feldmann and Feldmann 1955; Sparrow 1960;

Dick 2001). However, the fact that some of the species, e.g. *E. monostoma* do not exhibit a clear-cut diplanetism casts doubts on their relatedness to the type species, *E. bacilliacearum*.

2.8.2) *Lagenismataceae* (*Lagenisma*)

The family *Lagenismataceae* (Dick 2001) is monotypic, containing a single genus and species, which is an obligate parasite of large marine centric diatoms (Drebes 1966; Thines *et al*., 2015; Beakes and Thines 2017). The parasite is known to occur in both temperate and tropical climates, especially during blooms of its diatom hosts in the genera *Coscinodiscus* (*C. granii*, *C. concinnus*, *C. wailesii*, *C. radiatus*) and *Palmeria* (*P. hardmaniana*) (Parson 1962; Johnson 1966; Gotelli 1971; Grahame 1976; Wetsteyn and Peperzak 1991; Thines *et al*., 2015; Buaya *et al*., 2019c). *Lagenisma* (Figure 2F) was initially speculated to belong to the early-diverging oomycetes because it produces a holocarpic thallus and because of its sexual reproduction by zoomeiospores. However, Thines *et al*., (2015) have shown that it is embedded within the early-diverging lineage of the *Saprolegniomycetes*, close to *Atkinsiella* and *Bolbea* (Figure 2H) (Thines *et al*., 2015; Buaya and Thines 2020b). Later, Buaya and Thines (2020a) have shown that *Ectrogella* belongs to the same group. The parasite produces diplanetic zoospores, which are distinctive characters for species belonging to the *Saprolegniomycetes* (Schnepf and Drebes 1977; Schnepf *et al*., 1978a, 1978b, 1978c; Schnepf and Heinzmann 1980). Some other unsequenced holocarpic species (*e.g. Ectrogella licmophorae*, *Pythiella vernalis*) are also known to produce diplanetic zoospores (Scherffel 1925; Couch 1935; Sparrow 1960). It seems plausible that these species are also members of the *Saprolegniomycetes*, though this needs to be further investigated in future studies.

2.9) Genera *incertae sedis*

There are various genera that so far have not been included in phylogenetic investigations and which morphology does not allow for an unambiguous assignment to one of the groups mentioned above. While the ultrastructure of the pollen parasite *Ducellieria chodatii* supports the view that the species is belonging to the oomycetes and might be diverging after the Peronosporomycetes/Saprolegniomycetes split (Hesse *et al*., 1989), the situation is even less clear for other genera. It is even unclear, if several of these genera, such as *Pseudosphaerita* and *Rozellopsis* are belonging to the oomycetes or are probably better placed in other taxonomic groups. As we feel that speculating regarding this is associated with a high degree of uncertainty, we refrain from doing so.

Ecology and host-range of the early-diverging oomycetes

1) Occurrence and host-range

The early-diverging oomycetes are ubiquitous and widely distributed, especially in the aquatic environment (Karling 1942; Sparrow 1960; Dick 2001; Beakes and Thines 2017). In marine environments, they are known to infect diatoms (Buaya *et al*., 2017; Garvetto *et al*., 2018; Buaya *et al*., 2020c), multicellular algae (rhodophytes, phaeophytes, chlorophytes) (Sekimoto *et al*., 2008a; Klochkova *et al*. 2016, 2017; Badis *et al*., 2019; Buaya *et al*., 2019d) and invertebrate animals (Hatai *et al*., 2000; Leaño 2002; Sekimoto *et al*., 2007). Likewise, these parasites are also widely occurring in freshwater, parasitizing diatoms (Zopf 1884; Gill 1893; Scherffel 1925; Friedmann 1952; Buaya *et al*., 2019a, 2019b), filamentous green algae (de Wildeman 1895, 1896; Canter 1949), and invertebrate animals (Barron 1990; Glockling and Beakes 2000a, 2000b, 2001; Glockling and Serpell 2010). However, despite their widespread occurrence, little is known regarding the ecology of these organisms, especially, on how they interact with other organisms, their occurrence and roles in nature (Skovgaard 2014; Scholz *et al*., 2015). To date, almost all of the known early-diverging oomycetes were recorded from temperate regions, and knowledge about the existence of this group in the tropics is scarce (Grahame 1976; Hatai *et al*., 1980; Raghukumar 1987; Leaño 2002; Chukanhom *et al*., 2003; Strittmatter *et al*., 2009; Raghukumar 2009). In terms of host-range, knowledge is fairly limited as well, and for the past decades there were only a few studies conducted on this aspect (Drebes 1966; Müller *et al*., 1999; Strittmatter *et al*., 2009; Gachon *et al*., 2009). Perhaps the last extensive host-range study was conducted almost eighty years ago on the aquatic, oomycete-parasitic genus *Olpidiopsis* (Shanor 1940). At present, there were only a few host-range studies conducted on two pathogens of marine algae, *Eurychasma dicksonii*, and diatoms, *Lagenisma coscinodisci* (Drebes 1966; Müller et al., 1999; Gachon *et al*., 2009; Strittmatter *et al*., 2009; Buaya *et al*., 2019c). However, it is becoming clearer that a remarkable diversity in terms of host ranges exists. While *Eurychasma dicksonii* seems to have a rather broad host range, at least under laboratory conditions, species of *Olpidiopsis* seem to be more specialised, often even below the genus level (Shanor 1940).

Application of molecular techniques in ecological studies of oomycetes has recently expanded the present understanding on the diversity and distribution of these seemingly intractable organisms (Beakes and Sekimoto 2009). A few community sequencing studies have been conducted on marine oomycetes and revealed environmental sequences that are thought to correspond to some known and many unknown species and higher-level clades of the early diverging lineages, suggesting that these organisms are indeed widespread, with many species still awaiting discovery (Moon-van der Staay *et al*., 2001; Massana *et al*., 2004, 2006; Garvetto *et al*., 2018; Hassett *et al*., 2019)

1.1) Parasites of Algae

Several early-diverging oomycetes species are known to be obligate biotrophic parasites of marine and freshwater algae (Karling 1942; Sparrow 1960; Dick 2001). In marine environments, the majority of these are infecting red-algae (*Pontisma*, *Petersenia*) and a smaller number is parasitic in brown (*Anisolpidium*, *Eurychasma*) or green algae (*Sirolpidium*) (Petersen 1905; Magnus 1905; Karling 1942, 1943; Buaya *et al*., 2019d). In freshwater environments, early-diverging oomycetes were only reported from a small number of species of filamentous green algae, usually as *Olpidiopsis* species (Zopf 1884; de Wildeman 1896; Scherffel 1925). The host-range of most algae-infecting parasites is still not well established, except for *E. dicksonii* (Müller *et al*., 1999; Gachon *et al*., 2009). However, based on morphological identifications, several algal parasites seem to have rather broad host-ranges (*e.g. E. dicksonii*, *P. lagenidioides*), while some are assumed to have rather narrow host-ranges (*e.g. P. bostrychiae*, *P. porphyrae*) (Sekimoto *et al*., 2008b; Strittmatter *et al*., 2009; Sekimoto *et al*., 2009). The genus *Pontisma* is widespread, which is also reflected by the fact that it has the highest number of species recorded (Petersen 1905; Sekimoto *et al*., 2008b, 2009; Klochkova *et al*., 2016, 2017; Badis *et al*., 2019). It is noteworthy that the type species, *P. lagenidioides* (Figure 2a) infects often only old and moribund tissues, which suggests that it has little effect on its host populations. The other species have rarely been reported to cause massive losses in natural ecosystems as well (Petersen 1905; Magnus 1905; Sparrow 1936; Gachon *et al*., 2009; Tsirigoti *et al*., 2013; Gachon *et al*., 2017; Badis *et al*., 2019), indicating a well-balanced host pathogen relationship. If *Petersenia* (*P. lobata*, *P. palmariae*, *P. pollagaster*) is distinct from *Pontisma* remains to be demonstrated. It is conceivable that its lobed thallus represents a beginning compartmentalisation, which is absent in most species of *Pontisma*, but pronounced in *P. lagenidioides*, to which, in term of infection strategy, *Petersenia* is closely connected. Also, *Sirolpdium* (*S. bryopsidis*) seems to favour old thallus parts and has probably only a limited detrimental effect on its host populations. *Anisolpidium* (*A. sphacellarum*, *A. ectocarpii*, *A. rosenvingii*) and *Eurychasma* (*E. dicksonii*) have rarely been recorded (Magnus 1905; Sparrow 1934; Karling 1942, 1943; Sparrow 1943; Pueschel and van der Meer 1985; Dick 2001). The scarcity of the records does not necessarily mean that the

species are indeed rare, it could also be that they are rather attenuated pathogens, so symptoms are not conspicuous, as, e.g. it is possible to co-culture *Eurychasma* and some of its host under optimal growth conditions for several months (Ploch and Thines, unpublished experiments).

1.2) Parasites of Diatoms

Diatom-infecting early-diverging oomycetes are widely occurring, containing more than a dozen species in various genera (Karling 1942; Sparrow 1960; Dick 2001). Most of these parasites were recorded from marine environments and almost all were isolated from temperate regions (Sparrow 1960). The ecological role and occurrence of these parasitoids remains largely speculative (Scholz *et al*., 2015). In both freshwater and marine habitats, the occurrence of these parasites often seems to coincide with the bloom of their respective host, and most species seem to favour cooler temperatures, occurring in high abundance during spring or autumn (Sparrow 1936, 1960; Hanic *et al*., 2009; Beakes and Thines 2017; Buaya *et al*., 2017, 2019a, 2019b). However, this remains to be proven systematically, since reports of diatom parasitoids are rather rare. The bulk of the known species has been assigned to the genus *Ectrogella* (Zopf 1884). However, the phylogenetic affinity of most of these remains unresolved since many have not yet been investigated for their molecular phylogeny. The host-range of these parasitoids remains also largely unknown, even though it has been speculated that there is some degree of host specificity (Sparrow 1936; Drebes 1966; Gotelli 1971; Wetsteyn and Peperzak, 1991; Garvetto *et al*., 2018), and to date, only three species (*L. coscinodisci*, *D. perforans* subsp. *destruens*, *D. perforans* subsp. *pleurosigmae*) has been successfully cultivated together with its host diatom (Schnepf and Drebes 1977; Buaya *et al*., 2019d, 2020c) over longer periods of time.

1.3) Parasites of Aquatic Oomycetes

Early-diverging oomycetes that are obligate parasites of aquatic oomycetes (*Saprolegniales, Pythiales*) are widely distributed in various freshwater environments (Karling 1942; Sparrow 1960; Dick 2001). The majority of these parasitoids are members of the genus *Olpidiopsis*, but also *Lagenidium destruens*, *Petersenia irregulare*, *Pythiella besseyi*, *P. vernalis*, and *Pythium utriculoba* have been reported as parasites of aquatic oomycetes (Cornu 1872; Maurizio 1895; Barrett 1912; Coker 1923; Tokunaga 1933; Shanor 1939; McLarty 1941; Karling 1942; Whiffen 1942; Sparrow 1960; Miller 1962). The ecological role of these organisms with respect to regulating the pathogen pressure on e.g. invertebrates remains largely unknown. In a cross-infection study conducted with five

parasite species (*O. saprolegniae*, *O. varians*, *O. fusiformis*, *O. incrassata*, *O. luxurians*, *O. aphanomycis*), results have shown that a few are able to affect a broader host range, while others apparently infect only single host species (Shanor 1940). The genus *Rozellopsis*, is another interesting group of aquatic oomycetes parasites, that is likely to be a member of the early-diverging lineages (Karling 1942). This genus contains four species that are biotrophic parasites of *Saprolegniaceae* (*R. septigena, R. simulans*), and *Pythiaceae* (*R. inflata, R. waterhouseii*) (Fischer, 1882; Butler, 1907; Karling, 1942). However, taxonomic placement of the genus still remains unresolved, since none of the species has been included in molecular phylogenies to date, and it can even not be excluded that the genus does not belong to the oomycetes.

1.4) Parasites of Invertebrate Animals

Early-diverging oomycetes that parasitize invertebrate animals are also ubiquitous and widely occurring in aquatic and terrestrial environments (Sparrow 1960; Beakes and Sekimoto 2009; Beakes and Thines 2017). Among the hosts of marine species of the genus *Haliphthoros* s.l. are several crustaceans (*e.g.* *Homarus americanus*, *Penaeus monodon*, *Haliotis sieboldii*) cultivated in aquaculture or with economic importance in fishing (Fisher *et al*., 1975; Kitancharoen and Hatai 1995; Chukanhom *et al*., 2003). The genus *Haptoglossa* is a widespread, mostly terrestrial obligate endobiotic parasite of invertebrate animals (Beakes *et al*., 2012). Most of the species of *Haptoglossa* parasitize nematodes (*e.g. H. beakesii, H. erumpens*), and a few others are parasitic to rotifers (*H. mirabilis, H. elegans*) (Beakes and Sekimoto 2009). Their regulating effects on their often abundant host populations are poorly understood, but the widespread nature, species-richness of the genus, and the deep divergence of the lineages within suggests that there is a longstanding evolutionary equilibrium between the parasitoids and their respective hosts.

2) *Methods of Study and Cultivation*

Most of the early-diverging oomycetes are widely distributed and can be readily isolated from their natural environments after a thorough screening process. Methods for the collection, isolation and culturing these parasites can be found in Karling (1942), Sparrow (1960) and Dick (2001). Fresh aquatic samples (*e.g.* water, mud, filamentous algae, floating organic debris, insect carcasses) can be directly collected from the field. Field collection of basal oomycetes infecting phytoplankton are usually done using a plankton net, preferably with mesh size of 20 *μm* (Hanic *et al*., 2009; Thines *et al*., 2015; Buaya *et al*., 2017). Screening for parasites and isolation is probably most efficient using an inverted light microscope

(Buaya *et al.*, 2017, 2019c, 2019d; Buaya and Thines 2020a). Early-diverging oomycetes that are parasites of diatoms (*e.g. Miracula helgolandica*, *Diatomophthora gillii*, *Ectrogella bacillariacearum*, *Diatomophthora perforans*) and algae (*e.g. Pontisma lagenidioides*, *Eurychasma dicksonii*) can be directly isolated using pipettes and scalpels, respectively (Müller *et al.*, 2008; Buaya *et al.*, 2017, 2019a, 2019d; Buaya and Thines 2020a; Buaya *et al.*, 2020c). Others require some additional techniques for isolation such as baiting (Karling 1942; Sparrow 1960; Karling 1981). Baiting is especially useful for isolating *Olpidiopsis* (*e.g. O. saprolegniae*, *O. achlyae*) species (Barrett 1912; Coker 1923; Shanor 1939; McLarty 1941; Buaya *et al.*, 2019d). Samples (*e.g.* water, mud, soil sediments, organic substance) are diluted with autoclaved pond water, baited with various seeds (*e.g.* sesame, hemp) and then incubated for several days (Sparrow 1960; Karling 1981; Beakes and Thines 2017). Baiting is also useful for the isolation of invertebrate animal parasites such as *Haptoglossa* (Beakes and Thines 2017). Removal of the bacterial or fungal contaminants can be achieved by the addition of antibiotics to the medium or through stepwise rinsing using sterile water (Sparrow 1960). After isolation, specimens can be processed for morphological characterisation and also for molecular investigations. So far, only a handful of the early-diverging holocarpic oomycetes can be cultivated in agar medium. These include species that are marine parasites of various crustaceans from the genus *Haliphthoros* s.l. (*H. milfordensis*, *H. philippinensis*), which can be cultivated using PYG medium (peptone, yeast extract and glucose agar) or synthetic sea-water medium containing glucose and sodium aspartate dissolved in sterile sea water (Vishniac 1958; Hatai *et al.*, 1980; Chukanhom *et al.*, 2003). A few early-diverging oomycetes species were also cultivated together with their host, such as *Olpidiopsis* spp., *Eurychasma dicksonii*, and the diatom-infecting oomycetes *Lagenisma coscinodisci* (Shanor 1940; Müller *et al.*, 2008; Buaya *et al.*, 2019c) and *Diatomophthora* (Buaya *et al.*, 2020c). If (temporal) cultures are aimed for, it is important to first isolate some healthy hosts and to establish their culture, before dividing it in half and inoculating half of the culture for each asexual cycle of the parasites.

Practical and economic importance

Only a few early-diverging oomycetes are known to infect various economically important marine algae and crustaceans (Strittmatter *et al.*, 2009; Beakes and Thines 2017). In marine algae, the widely cultivated red-algae *Porphyra* spp. is periodically parasitised by two *Pontisma* species (*P. porphyrae*, *P. bostrychiae*) causing a disease known as "chytrid blight" (Sekimoto *et al.*, 2008b, 2009; Li *et al.*, 2010; Klochkova *et al.*, 2012). *Porphyra* spp. are widely cultivated in East Asia (Japan, Korea, China), where they are used for nori production (Pereira and Yarish 2008; Baweja *et al.*, 2016). *Pontisma* spp. cause spots, holes and discolorations, affecting the quality and yield of the diseased crop (Ding and Ma 2005; Sekimoto *et al.*, 2008b, 2009; Strittmatter et al., 2009).

The eucarpic oomycete *Pythium porphyrae* is also known to infect *Porphyra*, occurring simultaneously with the *Ponstima porphyrae* and *P. bostrychiae* causing a "red-rot" disease (Kawamura *et al.*, 2005; Park *et al.*, 2006; Park and Hwang 2015). Aside from marine algae, as mentioned before, a few species of the genus *Haliphthoros* s.l. (*H. milfordensis*, *H. philippinensis*, *H. sabahensis*, *H. okinawaensis*) are also known to have economic impact on marketed marine crustaceans (shrimp, lobster, mud crab) (Vishniac 1958; Hatai *et al.*, 1980; Nakamura and Hatai 1995; Strittmatter *et al.*, 2009; Lee *et al.*, 2017). These parasites usually attack the larvae of crustaceans causing mycotic infections subsequently killing the larvae (Fisher *et al.*, 1975; Tharp and Bland 1977; Leaño 2002). Apart from these negative impacts, it can be assumed that some holocarpic oomycetes affecting toxic diatoms have a positive economic impact by controlling harmful algal blooms (Hanic *et al.*, 2009; Lelong *et al.*, 2012; Trainer *et al.*, 2012; Buaya *et al.*, 2017; Garvetto *et al.*, 2018; Bates *et al.*, 2018)

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