Hyphochytriomycota and Oomycota

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Gordon W. Beakes and Marco Thines

Abstract

The anteriorally uniflagellate Hyphochytriomycota and biflagellate Oomycota are in the Kingdom Straminipila (commonly referred to as stramenopiles) which are part of the SAR superkingdom. Both appear to be basal to the large assemblage of golden-brown algae, the Ochrophyta. Both feature osmotrophic nutrition and have traditionally been considered as zoosporic "fungi," but are unrelated to organisms in the monophyletic kingdom Mycota. The Hyphochytriomycota is a small group encompassing around half a dozen genera, which have simple nonmycelial, holocarpic thalli, traditionally encompassing three families: the endobiotic Anisolpidiaceae, the polycentric Hyphochytriaceae, and the monocentric Rhizidiomycetaceae. Recently the former have been shown to be placed among the early diverging Oomycota, leaving just the latter two families in the monophyletic Hyphochytriomycota clade. Hyphochytriomycota are widespread in occurrence, and most are saprotrophs or parasites, infecting the resting spores of Oomycota and Glomeromycota. In contrast, the Oomycota are a large and diverse assemblage, consisting of two major (class level) clades, the Saprolegniomycetes and Peronosporomycetes, and several early diverging classes most of which are simple holocarpic organisms that lack mycelial organisation. Many of these early-diverging clades are as yet poorly resolved because of sparse taxon

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sampling. The early-diverging orders include the Eurychasmales and Olpidiopsidales, both of which are marine seaweed parasites, the nematode infecting Haptoglossales and crustacean infecting Haliphthorales. The Saprolegniomycetes mostly have fungal-like mycelial thalli and include the orders Atkinsiellales s.lat., Leptomitales, and Saprolegniales, which are mostly saprophytes or parasites of invertebrates and, occasionally, vertebrates such as fish and amphibians. A few species in the Saprolegniales are root infecting parasites of plants. The Peronosporomycetes are the second major fungal-like class, and include the largely saprotrophic Rhipidiales, the facultively parasitic Pythiales s.lat., which can infect both animals and plants and the predominantly plant pathogenic Albuginales and Peronosporales sensu lato. Indeed, the Oomycota are significant parasites of both animals and plants, impacting both natural ecosystems and causing significant economic losses in both aquacultural and agricultural systems. The molecular systematics of the Oomycota is still in a state of flux, and in this account a relatively conservative approach has been taken. It is apparent that most of the early-diverging genera are almost exclusively marine and that the Peronosporales represents the main terrestrial and plant pathogenic lineage. Most early-diverging genera lack the oogamous sexual reproduction that characterizes this group and suggests that the oogenesis evolved around the time of emmergence from the sea to the land and freshwater ecosystems. It is also clear that obligate biotrophy in the white blister rusts (Albuginales) and downy mildews (Peronosporales s.str.) has evolved independently.

Keywords

Albugo; *Aphanomyces* • Biflagellate zoospore • Oogamy • Biotrophy • Ecology • Evolution • *Hyphochytrium* • Oomycetes • *Phytophthora* • *Pythium* • Plant pathogen; *Rhizidiomyces* • RxLR-effectors • *Saprolegnia* • Stramenopile • Systematics • Zoosporogenesis • Zoospore ultrastructure

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Where s. lat. is used after a name, there are significant subclades which suggests this taxon will require splitting, although at present the low statistical support, or incomplete taxon sampling means it cannot be done with confidence.
Where names are placed between " " means names have not been formally published.
~Before the name means this Order, Family or genus appears to be para- or polyphyletic and will require taxonomic revision.
[a]Indicates Family or species has not been sequenced, so taxonomic position not confirmed by molecular data.
[b]Recent multigene trees, suggest this clade may merit a new order and family rank (Paralagenidiales, Paralagenidiaceae) (Spies et al. 2016).
[c]This family's Order placement still not fully resolved.
[d]Recent multigene trees, suggest this clade may merit order rank (Pythiales), but may also require further splitting (Spies et al. 2016).
[e]Recent multigene trees, suggest this clade may merit order rank as Peronosporales s. str. (Spies et al. 2016).

Introduction

General Characteristics

Historically, the zoosporic fungi studied by mycologists encompassed chytrids, hyphochytrids, labyrinthulids, thraustochytrids, oomycetes, and plasmodiophorids. All generally had walled thalli that fed by osmotrophic absorption, although many had small holocarpic thalli rather than a typical mycelium. These organisms are a polyphyletic assemblage with only the Chytridiomycota now included in the kingdom Fungi (Fig. 1a; Adl et al. 2012). The Plasmodiophorids are now placed in the Cercozoa, a sister clade to Rhizaria (Heuhauser et al. 2010), which together with all other biflagellate fungal-like groups fall within the recently defined "SAR" (Straminipila, Alveolata, Rhizaria) superkingdom (Fig. 1a; Burki et al. 2007, 2008; Burki and Keeling 2014). Molecular studies confirm that both the anteriorly uniflagellate Hyphochytriomycota and the biflagellate Oomycota (Fig. 1b; Tsui et al. 2009; Van der Auwera et al. 1995) are part of the same lineage as the chlorophyll c containing Ochrophyta (Cavalier-Smith and Chao 2006), which together form the sister clade to the Labyrinthulomycota and Opalinids (Tsui et al. 2009). Dick (2001)

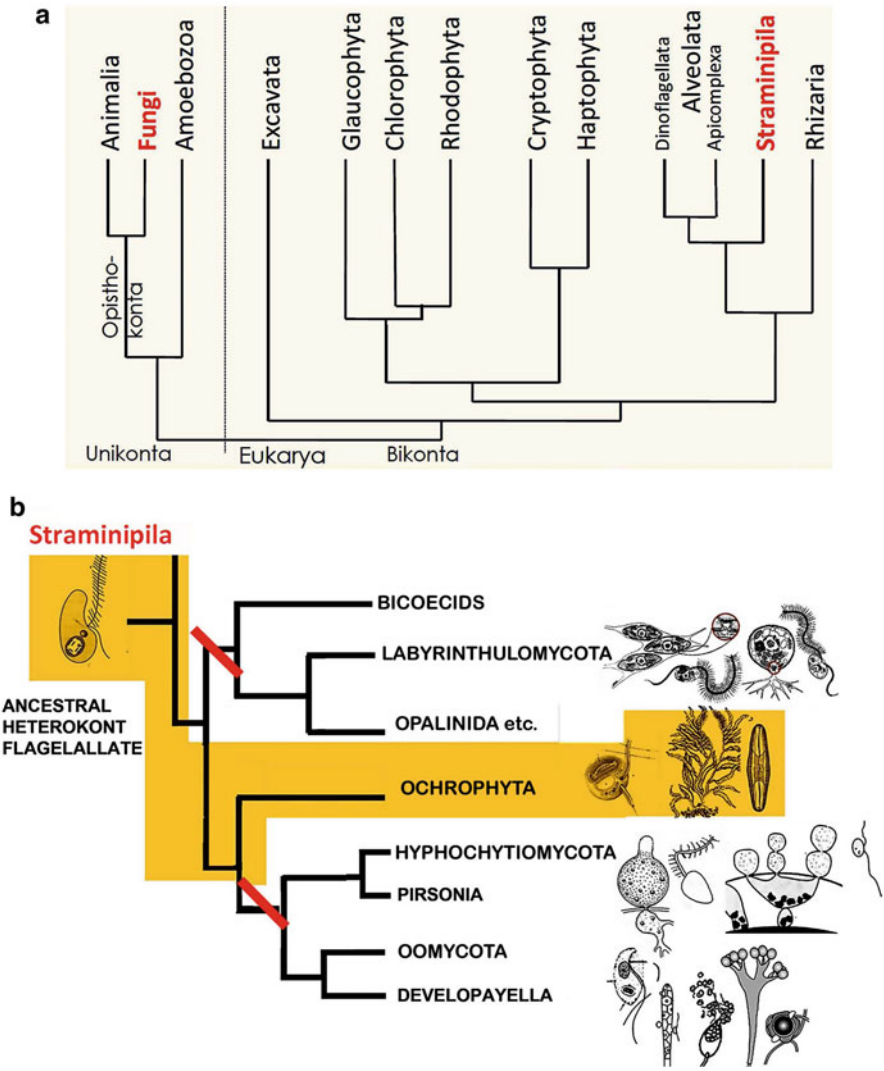

Fig. 1 General phylogeny. (**a**) Overview summary tree of main Eukaryote supergroup clades, showing relative phylogenetic postions of the Fungi and Straminipila, which is part of the Straminipila, Alveolata, Rhizaria (SAR) superclade (Based on Burki et al. 2008). (**b**) Schematic tree of the Straminipila clade, showing probable relationships between the Hyphochytriomycota and Oomycota, with respect to other members of the clade. The *red bars* represent possible plastid loss events as proposed by Tsui et al. (2009) on which Figure is based. However, not all data supports multiple plastid losses, others have proposed multiple plastid acquisitions rather than losses (see Beakes et al. 2014a) (Adapted from Beakes et al. (2011) from *Protoplasma* with permission)

placed all of these mastigonate fungal-like groups in his revised Kingdom Straminipila, while Cavalier-Smith and Chao (2006) placed the Hyphochytriomycota and Oomycota in the phylum Pseudofungi, together with a number of protists, including the bacteriotrophic flagellate *Developayella* (Leipe et al. 1994) and the parasitoid *Pirsonia* (Kühn et al. 2004).

Members of the Hyphochytriomycota are characterized by their small holocarpic, chytrid-like thalli and zoospores with a single, anteriorly-directed flagellum (Figs. 2a and 7a). At the end of a motile period, the zoospores encyst, germinate, and grow to form simple epi- or endobiontic chytrid-like thalli (Fig. 2a–e). Hyphochytriomycota is a small phylum/subphylum consisting of a single order (Hyphochytriales) containing only four or five described genera encompassing around two dozen species. These were grouped by Karling (1942, 1977) into three families: the Anisolpidiaceae, Rhizidiomycetaceae, and Hyphochytriaceae. Molecular sequencing studies of *Hyphochytrium catenoides* (Van der Auwera et al. 1995) and *Rhizidomyces inflatus* (Hausner et al. 2000) confirmed that the Hyphochytriomycota form a well-defined clade sister to the Oomycota (Fig. 1b). However, recent sequence data for the marine phaeophyte parasite *Anisolpidium ectocarpi* have revealed that the Anisolpidiaceae fall within the basal Oomycota, close to *Olpidiopsis spp.* (Gachon et al. 2015), and thus, are excluded from the Hyphochytriomycota (Table 1).

In contrast, the Oomycota is a large and diverse phylum/subphylum containing mostly fungal-like organisms (Fig. 2q, r–u; Money 1998; Richards et al. 2006). There are around 1500 or more species grouped into about a 100 genera, the majority of which, however, contain fewer than five species (Table 1; Dick 2001). They typically produce biflagellate zoospores (Fig. 7b–e) and many saprolegniomycete genera produce two generations of zoospores (diplanetic; Fig. 7b, d) or aplanospores and zoospores. The anterior flagellum is mastigonate (Fig. 7e), while the posterior flagellum is smooth with a terminal acroneme (Fig. 7c; Vlk 1939; Manton et al. 1951; Fig. 2). Characteristics that separate Oomycota from true Fungi include having a diploid rather than haploid vegetative thallus (Win-Tin and Dick 1975), cell wall microfibrils composed of cellulose and glucans rather than chitin (Bartnick-Garcia 1970), and a different biochemical pathway for lysine biosynthesis (Vogel 1960). In addition, they store β1–3 mycolaminarins rather than glycogen as their main carbohydrate reserve (Wang and Bartnicki-Garcia 1974). Molecular phylogeny based on ribosomal subunit genes confirmed that the Oomycota share the same common ancestor as the Ochrophyte algae (Fig. 1b: Adl et al. 2012; Cavalier-Smith and Chao 2006; Förster et al. 1990; Gunderson et al. 1987; Leipe et al. 1994; Rilsberg et al. 2009).

Occurrence

The Hyphochytriomycota are found in both soil and water in freshwater, marine, and terrestrial environments and are cosmopolitan in distribution (Fuller 1990, 2001; Gleason et al. 2009). There are both saprotrophs and low-impact parasites, particularly of other chromistans (Oomycota and Phaeophyta) and possibly of crustacea. Although relatively small numbers of species have been described, environmental

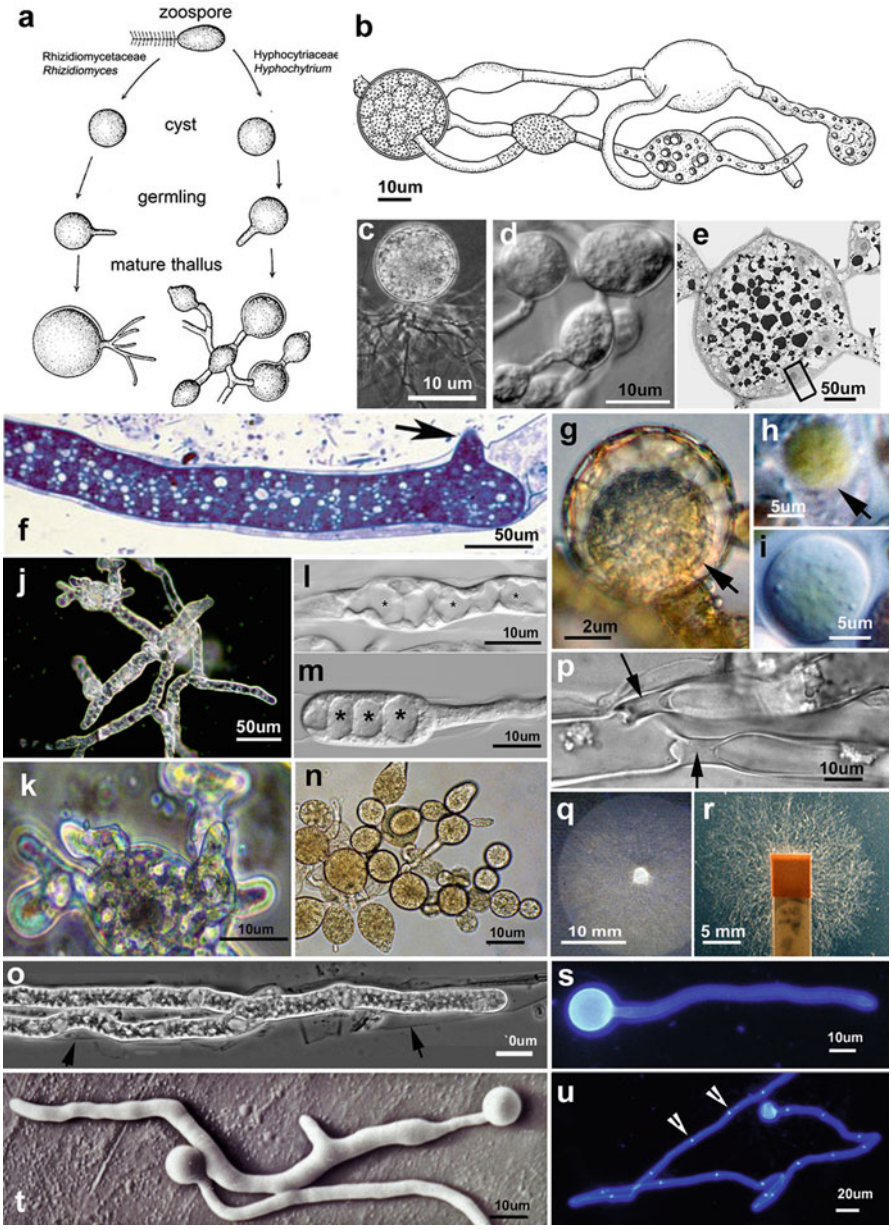

Fig. 2 The vegetative thallus. (**a**) Schematic hyphochytridiomycete life style diagram showing monocentric thallus development in *Rhizidiomyces* and polycentric development in *Hyphochytrium* (Adapted from Fuller 1990, with permission*) (**b**) Diagram of the polycentric thallus of *Hyphochytrium catenoides* showing swollen thalli, interconnectd by short hyphal-like segments (From Karling (1977), with permission of Charles Lubrecht) **(c)** Light micrograph of *Rhizidiomyces apophysatus*, showing spherical thallus, with basal rhizoids (From Fuller and Jaworkski (1987) with

sequencing from both marine (Diéz et al. 2001; Massana and Pedró-Alió 2008; Massana et al. 2002, 2004, 2006) and freshwater (Richards et al. 2012) environments has revealed many unknowns that fall within the hyphochytrid clade, suggesting that as a group they are both more diverse and widespread than generally appreciated. Hyphochytrid cultures are not widely available although both *H. catenoides* and *R. inflatus* are listed in the American Type Culture Collection (ATCC).

Oomycetes are also ubiquitous in marine, freshwater, and terrestrial ecoystems, where they occur as widespread saprotrophs infesting decaying plant and animal detritus (Dick 1990, 2001; Hulvey et al. 2010; Newell and Fell 1995; Riethmüller and Langer 2004) or as necrotrophic and biotrophic pathogens of a wide range of animals (Fig. 3a–k: Karling 1981; Phillips et al. 2008) and plants (Fig. 4a–v: Constantinescu 1991; Dick 2001; Thines 2014; Voglmayr 2008). Plant pathogenic species (Fig. 4a–v) show the greatest diversity, and recent molecular studies have explored the phylogenetic relationships between these pathogens and their hosts (Choi and Thines 2015; Göker et al. 2007; Thines et al. 2008, 2009a; Voglmayr 2003, 2008). Many oomycete plant pathogens, notably *Albugo* and *Hyaloperonospora* infecting

Fig. 2 (continued) permission) (**d**) Light micrographs of mature polycentric thallus of *H. catenoides* in culture (From Gleason et al. (2009) with permission *J. Euk. Microbiol.*) (**e**) TEM of developing thallus showing central vacuole system with electron dense inclusions (From Clay et al. (1991) with permission *Mycol. Res.*) (**f**) A toluidineblue-stained thallus of *Haptoglossa polymorpha*, infecting a rhabditid nematode, showing dense cytoplasm and short discharge tubes (From Beakes et al. (2011) with permission *Protoplasma.*) (**g**) Light micrograph of a naked thallus of *Eurychasma dicksonii*, strain Euo5within a hyperplasic infected cell of the host *Ectocarpus*. (**h**–**i**) Light micrographs of young developing thalli of holocarpic oomycete *Olpidiopsis porphyrae*, in thallus of *Porphyra* (All from Sekimoto (2008) with permission *Protist*) (**j**–**k**) Darkfield and phase contrast light microgrphs of the irregularly lobed thallus of the early diverging, crustacean parasite *Halocrusticida* (syn. *Halodaphnea*) *okinawensis*, Beakes, unpublished micrographs. (**l**–**m**) Differential interference contrast (DIC) light micrographs of crustacean parasite *Haliphthoros* sp. showing irregularly swollen, vacuolate (*) thallus, with peripheral spore initials developing. Photo courtesy Satoshi Sekimoto. (**n**) Irregularly beaded thallus of an in vitro culture of the early diverging saprolegniomycete parasite of nematodes, *Chlamydomyzium oviparasiticum* (From Glockling and Beakes (2006b) with permission *Mycol. Res.*) (**o**) Phase contrast light micrograph showing the elongate holocarpic (sparsely branched) thallus of the related species *Ch. dictyuchoides in vivo*. The digested remnants of nematode cuticle are arrowed (From Beakes et al. (2014b) with permission *Fung. Biol.*) (**p**) Part of a branched sporulating mycelium of *Sapromyces elongatus* (Rhipidiales) showing constricted thalli, sealed with thick cell wall plugs. Beakes, unpublished. (**q**) A colony of *Saprolegnia parasitica*, growing on agar media, showing typical fungal-like colony of advanced Oomycote. Beakes unpublished. (**r**) A colony of *Phytophthora cinnamomi*, growing over surface of agar from a soil incubated dipstick bait. Courtesy of Adrienne Hardham. (**s**) Calcofluor stained, UV-fluorescence light micrograph of a germinating cyst of *Saprolegnia diclina*, showing typical narrow hyphal-like germ tube. (**t**) Low temperature SEM of germinating cysts of *S. diclina* showing beginning of branched mycelial-thallus. (**u**) Calcofluor stained, UV-fluorescence light micrograph of a germinating cyst of *S. parasitica,* showing septate (plugged – *arrows*) hyphae characteristic of this species. **s**–**u**. Beakes unpublished

Table 1 A provisional taxonomic framework for the Hyphochytiomycota and Oomycota based on molecular data

Kingdom: Straminipila	Superphylum: Pseudofungi
Phylum: Hyphochytriomycota	
Class: Hyphochytriomycetes	
Order: Hyphochytriales	
Family Hyphochytriaceae	*Canteriomyces, Cystochytrium*, ***Hyphochytrium***
Family Rhizidiomycetaceae	*Latrostium, Reesia,* ***Rhizidiomyces***
Phylum: Oomycota	
Basal orders – Class(es) incertae sedis	
Order Eurychasmales	
Family Eurychasmaceae	***Eurychasma***[a]
Order Haptoglossales	
Family Haptoglossaceae	***~Haptoglossa***
Order Olpidiopsidales s.lat.	
Family Anisolpidiaceae	***Anisolpidium***
Family Olpidiopsidacae s.lat.	***~Olpidiopsis***
?Family Pontismataceae	*Petersenia, Pontisma*
?Family Sirolpidiaceae	*Sirolpidium*
Order "Haliphthorales"	
Family Haliphthoraceae	***~Haliphthoros, Halocrusticida (****syn. Halodaphnea****),***
Order and Family incertae sedis	***Halioticida***
Rozellopsidaceae	*Rozellopsis*
Ectrogellaceae	*Ectrogella*
Class: Saprolegniomycetes	
Order Atkinsiellales s.lat.	
Family "Atkinisellaceae"	***Atkinsiella***
Family Crypticolaceae	***Crypticola***
Family Lagenismatacae	***Lagenisma***
Order and Family incertae sedis	***~Chlamydomyzium, ~Cornumyces,***
Order Leptomitales	
Family Leptomitaceae	***Apodachlya,*** *Apodachyella*, ***Blastulidium, Leptomitus***
Family incertae sedis	
Leptolegniellaceae	*Aphanomycopsis, Brevilegniella, Ducellieria, Eurychasmopsis, Leptolegniella, Nematophthora, Pythiella*
Order Saprolegniales	
Family Verrucalvaceae	***~Aphanomyces, Aquastella,*** *Pachymetra,* ***Plectospira, Sommerstorffia, Verrucalvus***
Family Saprolegniaceae s.lat. Clade spp. with eccentric oospores	***~Achlya, Brevilegnia, Dictyuchus, Thraustotheca***

(*continued*)

Table 1 (continued)

Kingdom: Straminipila	Superphylum: Pseudofungi
Clade spp. centric oospores	***Aplanes, Aplanopsis, Calyptralegnia,*** *Couchia*, ***Isoachlya, Newbya, Protoachlya, Pythiopsis, ~Saprolegnia,*** *Scoliolegnia*
Clade - uni-oosporiate, centric oospores	***Geolegnia, ~Leptolegnia***
Class: Peronosporomycetes	
Order and Family incertae sedis	***Salispina***
Order Rhipidiales	
Family Rhipidiaceae	*Araiospora, Aqualinderella, Mindeniella, Nellymyces, Rhipidium*, ***Sapromyces***
Order "Paralagenidales"	
?"Paralagenidiaceae"	***Paralagenidium***
Order Albuginales	
Family Albuginaceae	***Albugo****,* ***Pustula, Wilsoniana***
Order Peronosporales s.lat.	
Salisapiliaceae[a]	***Salisapilia***
Family Pythiaceae s. lat. subclades ?Myzocytiopsidaceae subclade	Holocarpic or eucarpic with narrow filamentous sporangia, many with vesiculate zoospore differentiation *Gominocheate,* ***~Myzocytiopsis (part)***
?Salilagenidiaceae subclade	***Salilagenidium (marine Lagenidium spp.)***
?Lagenidiaceae subclade	***~Lagenidium, Myzocytiopsis (part)***
?Lagenaceae s.lat. subclade	*~****Lagena****,* ***Lagenidium*** *(part),* ***Pythiogeton, Pythium*** *(part),* ***Myzocytiopsis*** *(part),*
?Pythiaceae s.str. subclade	Subclades with spp. with filamentous sporangia
	Lagenidium (part), Pythium **s.str,**
Family Peronosporaceae s.lat. subclades	Subclades with more or less globose to ovoid sporangia, zoospore differentiation often intra-sporangial with transient vesicle or without (downy mildews)
Section 1 subclade Globose to elongate sporangia formerly in *Pythium*.	***Globisporangium, Elongisporangium***
Halophytophthora sp. clade marine saprotrophs	***~Halophytophthora*** s.lat.
Section 2a,b subclades: Saprotrophs,	***Phytopythium*** *(syn. Ovatsporangium), Calycofera*
facultative stem and leaf pathogens, many of which produce elicitors	***Pilasporangium*** ***~Phytophthora***
Section 3 subclades Downy Mildews: 3a Graminicolus downy mildews (GDM)	Obligate biotrophs of Angiosperms ***Baobabopsis, Eraphthora, Graminivora, Peronosclerospora, Poakatesthia Sclerospora, Scleropthora, Viennotia***
3b: Brassicolous downy mildews (BDM)	***Hyaloperonospora, Perofascia***

(*continued*)

Table 1 (continued)

Kingdom: Straminipila	Superphylum: Pseudofungi
3c: Downy mildews with coloured conidia (DMCC)	***Pseudoperonospora, Peronospora***
3d: Downy mildews with pyriform haustoria (DMPH)	***Basidiophora, Benua, Bremia, Novotelnova Paraperonospora, Plasmopara, Plasmoverna, Protobremia,***

Those genera that are not emboldened have not been included in molecular phylogenies until the end of 2016
Those prefixed by a ~ appear to be paraphyletic or polyphyletic and are in need of revision
Families prefixed with a ? are in Dick (2001) and although reflected by clades, but it is uncertain whether all will eventually be given family level designation. These subclades are mostly based on a recent unpublished study of Spies et al. (2014, 2016)
Those Orders and Families in quotation marks " ", have not been formally published
[a]The phylogenetic position of this family/genus still not fully resolved. Some analyses have it as sister clade to *Halophytophthora* in the Peronsporaceae s. lat. clade

Arabidopsis, have provided model systems for exploring the molecular interactions between biotrophic pathogens and their hosts (Jiang and Tyler 2012; Kemen and Jones 2012; Thines and Kamoun 2010; Thines et al. 2009c). The occurrence and diversity of marine oomycetes have been greatly underestimated (Hulvey et al. 2010; Nigrelli and Thines 2013), and many recent studies on marine picoplankton samples have revealed many unknown stramenopiles within the Oomycota clade (Diéz et al. 2001; Massana and Pedró-Alió 2008; Massana et al. 2002, 2004, 2006; Richards et al. 2012).

Culture collection holdings of oomycetes are largely confined to the saprophytic and facultatively parasitic species with the largest collections held in the major culture collections such as the American Type Culture Collection (ATCC), Maryland; the Commonweath Agricultural Bureau International fungal collection (CABI), Egham; the Centraalbureau voor Schimmelcultures (CBS), Baarn, and the National Biological Resource Centre (NBRC), Chiba. Some academic institutions hold specialist collections, mainly of *Phytophthora* and *Pythium* isolates, such as the World Oomycete Genetic Resource Collection at the University of California, Riverside; the Department of Agriculture Mycology Culture Collection Ottawa; and a collection of *Aphanomyces* and fish-pathogenic *Saprolegnia* isolates in the Oomycete Culture Collection, Real Jardin Botanico (CSIC), Madrid. The Culture Collection for Algae and Protozoa (CCAP) in Oban has recently established a small collection of dual clonal cultures of marine oomycetes on their seaweed hosts (Strittmatter et al. 2013).

Literature and History of Knowledge

While there have been no dedicated monographs on the Hyphochytriomycota, they were included by Karling (1977) in his richly illustrated monograph of the chytrids sensu *lato*. In this he illustrates over half of the 23 accepted species and gives the

Fig. 3 **Animal pathogenic Oomycota**. (**a**–**d**) Achelminth pathogens. (**a**–**b**) DIC micrograph of a zoosporic *Haptoglossa* sp., infecting rhabditid nematodes showing both zoospore initials and in situ encysted spores that have formed infective gun cells (**b**). Courtesy S. Glockling (**c**) Encysted zoospores of *Ch. dictyuchoides* germinating around the mouth orifice of a rhabditid nematode host (From Beakes et al. 2014b with permission *Fungal Biol.*) (**d**) Tapered thallus lobes of a glutaraldehyde preserved thallus of *Aquastella acicularis*, infecting the rotifer *Polyarthra vulgaris*, an example of holocarpic relative of *Aphanomyces.* Beakes unpublished. (**e**) European white-clawed crayfish (*Austropotomobius pallipes*) that have been challenged and killed by crayfish plague, *Aphanomyces astaci.* (**f**) Sporulating mycelium of *Ap. astaci*, showing undifferentiated hyphae and discharged cluster of primary cysts. (**g**) detail of the underside of the body segments of an infected animal, showing white discolouration. (**e**–**g**) Beakes unpublished. (**h**) Atlantic salmon (*Salmo salar*) eggs, infected with *Saprolegnia diclina*, showing typical white fungal-like vegetative mycelia. Beakes unpublished. (**i**) A wild brown trout (*Salmo trutta*) infected with *Saprolegnia parasitica*, showing extensive white mycelial lesions on the skin. (**j**) Secondary cyst of *S. parasitica*, showing hooped bundles of boathook spines that characterize fish-lesion isolates. (**i**–**j**) Bruno et al. (2011) with permission. (**k**) Winter saprolegniasis, gizzard shad (*Dorosoma cepedianum*) from Murray River showing small irregular lesions typical of *S. parasitica* infections of coarse fish. Courtesy of James Puckridge

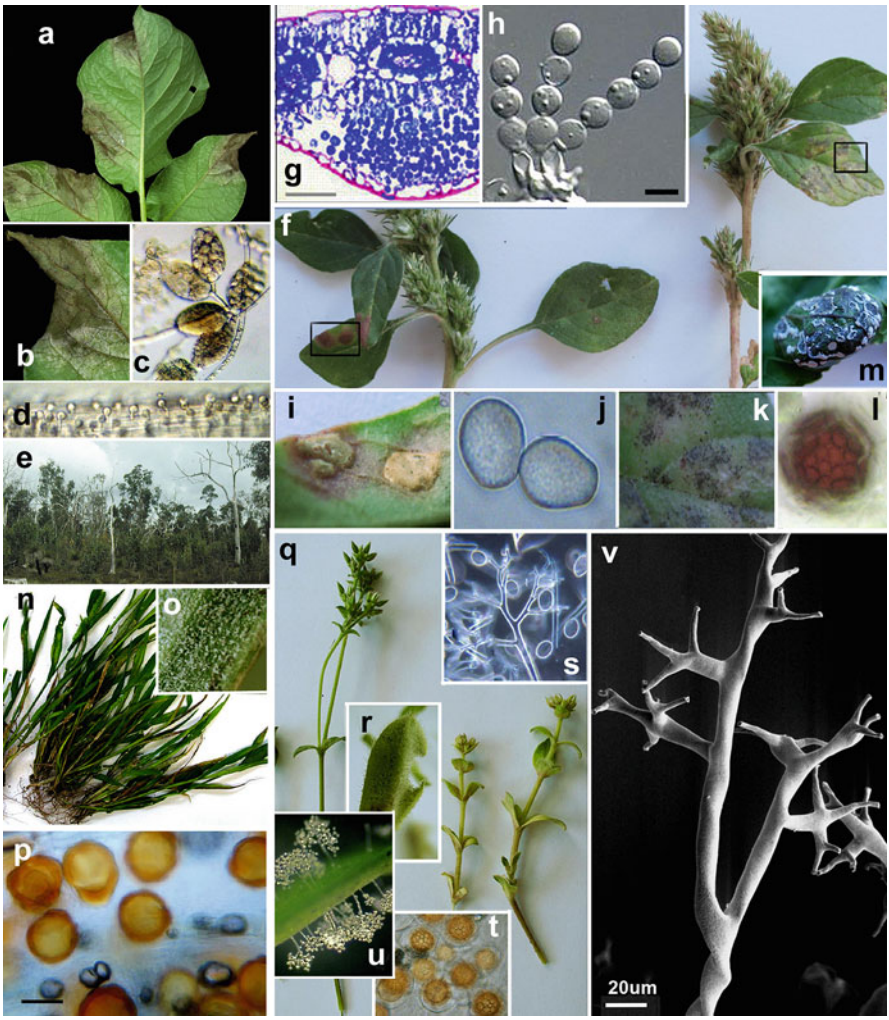

Fig. 4 Plant pathogenic Oomycota(all images unless otherwise stated Thines, unpublished): (**a**–**b**) Leaf lesions caused by the hemibiotrophic late blight pathogen, *Phytophthora infestans* on *Solanum tuberosum.* Courtesy of David Cooke. (**c**–**e**) The root infecting, *Ph. cinnamomi*. e. Mature sporangia showing zoospore release (**c**) and encysted zoospores, germinating on a eucalyptus root surface. (**d**) Native jarrah Forest dieback caused by *Ph. cinnamomi.* (**d**–**e**) courtesy of Adrienne Hardham. (**f**–**m**) The obligate biotrophic white blister rusts (Albuginales). (**g**–**l**) *Amaranthus* infected with *Wilsonia bliti* (f) General view of infected plants showing general symptoms of infections, with lesions shown by boxes. (**g**) Cross section through infected leaf showing pustule with parallel chains of condiosporangia (courtesy Annerose Heller), which are shown in detail in the DIC micrograph (h) of a chains of conidia (courtesy Young-Joon Choi). (**i**) Detail of blister like pustules on the underside of leaves. (**j**) Pear-shaped dispersive (secondary) conidia. (**k**) Detail of

important references for their study. Other reviews of this phylum include those by Fuller (1990, 2001), Dick (2001), and Beakes et al. (2014a). The first observations of zoosporic fungi possessing a single anterior flagellum were first made in the late nineteenth century (Zopf 1884), although the hyphochytrids were not formally separated from the posteriorly flagellate chytrids until later (Karling 1939, 1943).

The most recent comprehensive monograph of the Oomycota is the scholarly overview by Dick (2001) which lists much of the extensive taxonomic and general biological literature up to end of the millennium. Two important plant pathogenic genera, *Pythium* and *Phytophthora*, have been previously monographed, respectively, by Plaats-Niterink (1981) and Waterhouse (1970). The former is currently being comprehensively updated (previewed by de Cock et al. 2012). Recent literature sources for the plant pathogenic downy mildews can be found in Thines and Choi (2016), Lebeda and Spencer-Phillips (2007), Thines (2014), Thines et al. (2009a, b), and Voglmayr (2008). A review of the updated taxonomy of the Albuginaceae is given in Choi et al. (2006, 2008) and Thines and Voglmayr (2009). The three principal genera in the Saprolegniales (*Achlya*, *Aphanomyces* and *Saprolegnia*) have been monographed, respectively, by Johnson (1956), Scott (1961), and Johnson et al. (2002 updated from Seymour 1970). For other taxa, particularly the holocarpic species, reference should be made to Dick (2001), Karling (1981), and Sparrow (1960).

Detailed accounts of the extensive historical studies on the Oomycota have been given by both Dick (2001) and Johnson et al. (2002) and only highlights will be covered here. During the late eighteenth century, there were a number of reports of what we now recognize to be *Saprolegnia* infections of fish (reviewed by Hughes 1994). Similarly the first documented plant pathogenic oomycete was by Persoon who described the white blister rust *Aecidium candidum*, which was subsequently transferred by de Roussel in 1806 to the genus *Albugo* (Choi et al. 2007), although at that time it was still not recognized as an oomycete (Dick 2001). Much of the early documentation of the Oomycota stems from the pioneering researches of Pringsheim, de Bary, Regel, and Tulasne among others (Dick 2001). The higher oomycete taxa were recognized almost as soon as sufficient species had been described to put them into groups. De Bary separated the "Peronsporei" from the mucoraceous phycomycetes and shortly after proposed the "saprolegnieen" and "peronosporeen" family

Fig. 4 (continued) upper leaf showing dark fleck-like oospores within tissue. (**l**) Mature oospore of *W. bliti* showing reticulate oospore ornamentation. (**m**) Blister-like leaf lesion of *Albugo "armoraciae"*. (**n**–**p**) Graminicolousdowny mildews – *Sclerospora graminicola*. (**n**–**o**) Infected plants of *Setaria viridis* and details of leaf surface showing white conidiophores. Detail of orange-pigmented thick-walled angular oospores, typical of these mildews. (**q**–**v**) Downy mildews of herbaceous angiospermae. (**q**–**u**) *Cerastium* sp. infected with *Peronospora* sp. (**q**) plants (unifected *left*, infected *right*) showing stunting and chlorosis. (**r**) Detail of lower surface of a leaf, showing darker regions in areas where oospores have formed. (**s**) Branched sporangiophores (darkfield), with terminal disarticulating conidiosporangia. **t**. Mature reticulate oospores within infected leaf tissue. (**u**) Cotyledons of *Microthlaspi erraticum*, showing abundant condiophores of *Hyaloperonospora thlaspeos-perfoliat*ion both upper and lower surfaces. (**v**) SEM micrographof conidiophore of *Plasmopara nivea*, showing branchlets that bore the now-detached conidiosporangia

concepts (de Bary 1881). *Albugo* was eventually recognized as an oomycete when its sexual stages were described by Léveillé (1847) and subsequently placed in the "peronosporeen group" by de Bary (1881). The first attributable oomycete parasites of aquatic plants, protozoa and invertebrate animals were described by Schenk (1858), Cornu (1872), and Zopf (1884). The first plant pathogenic member of the oomycetes to be described was *Albugo candida* (Persoon, in Gmelin 1792). By the mid nineteenth century, there had also been descriptions of the first three downy mildew genera: *Peronospora* (Corda 1837), *Bremia* (Regel 1843), and *Basidiophora* (Roze and Cornu 1869). However, it was not until the end of the century that Schröter (1893) placed these plant pathogenic species into their own separate family, the Peronosporaceae.

In the latter half of the twentieth century, the taxonomic synthesis of the Oomycota was forged by three outstanding scholars of zoosporic fungi: Dick (1973a, b; 2001), Karling (1981), and Sparrow (1960, 1976). In the second edition of "*Aquatic Phycomycetes,*" Sparrow (1960) listed four major oomycete orders, the Saprolegniales, Leptomitales, Lagenidiales, and Peronosporales. In his final synthesis, Sparrow (1976) proposed splitting of the oomycetes into two 'galaxies', which Dick (2001) later formalized into the subclasses Saprolegniomycetidae and Peronosporomycetidae and also introduced a new order the Eurychasmales, in which he placed a number of little known marine taxa. He considered this new order to be part of the "saprolegnian galaxy" together with the Leptomitales and Saprolegniales. His "peronosporalean galaxy" included the orders Peronosporales, which encompassed most important plant pathogens, and Lagenidiales, which encompassed most of the holocarpic parasites of invertebrates and algae. Dick had continued to refine the classification of the Oomycota (Dick 1976a, b, 1997, 1998; Dick et al. 1984) culminating in his final synthesis which he outlined in his encyclopaedic treatise, "*Straminipilous Fungi*" in which he expanded the number of orders to around a dozen (Dick 2001). However, as a result of subsequent molecular studies, a substantial revision of Dick's (2001) scheme has recently been proposed (Beakes et al. 2014a).

Economic and Practical Importance

No hyphochytrid (i.e., excluding *Anisolpidium*) is known to cause any economically significant disease of plants or animals. Artemchuk and Zelezinskaya (1969) described a species (*Hyphochytrium peniliae*) that caused a severe mycosis of a freshwater crawfish, but there have been no subsequent reports of this disease, and Dick (2001) questioned whether this organism was even a hyphochytrid. Both *Rhizidiomyces* spp. and *Hyphochytrium catenoides* are known to parasitize oospores of plant pathogenic oomycetes (Ayers and Lumsden 1977; Sneh et al. 1977; Wynn and Epton 1979), and *Rhizidiomycopsis stomatosa* (Sparrow 1977) infects the resting spores of the endomycorrhizal fungus *Gigaspora margarita* (Schenck and Nicolson 1977; Sparrow 1977). Hyphochytrids may, therefore, adversely affect populations of both potentially harmful oomycetes and beneficial mycorrhizal fungi in soil ecosystems (Sneh et al. 1977). The closely related parasitoids belonging to the genus *Pirsonia* infect centric diatoms and bring about a decline in planktonic

blooms (Kühn 1997; Schnepf et al. 1990). Members of the genus *Anisolpidium* infect both freshwater algae (Canter 1950) and filamentous phaeophyte seaweeds (Karling 1943; Küpper and Müller 1999); however, this genus is now thought to be an oomycete (Gachon et al. 2015).

In contrast, the economic importance of the Oomycota is well known. Many are devastating and economically important plant pathogens (Fig. 4a–v), with even threatening natural ecoystems such as the Jarrah forest in Australia (Fig. 4e). In the mid-nineteenth century, de Bary and Berkeley established that the species we now know as *Phytophthora infestans* (Fig. 4a, b) was the causal agent of the devastating potato blight epidemic responsible for the great Irish famine (Berkeley 1846; de Bary 1876; Yoshida et al. 2013). Other species cause serious losses to wild and farmed fish (Fig. 3i, k) and crustaceans (Fig. 3e, g), and there are a few species that can opportunistically infect mammals, including humans (Bruno et al. 2011; de Grooters et al. 2013; Mendoza 2005; Phillips et al. 2008; Schurko et al. 2004; Van West 2006). Economically important genera include the obligate biotrophic white blister rusts (*Albugo*; Fig. 4f–l) and the downy mildews (e.g., *Bremia*, *Peronospora*, *Sclerospora* etc.; Fig. 4n–v) and facultatively parasitic genera such as *Aphanomyces, Phytophthora* (Fig. 4a–e)*, Pythium* and *Saprolegnia*. White blister rusts (Fig. 4f–l) and downy mildews (Fig. 4n–v) infect plants, the latter often causing stunting (Fig. 4f, q) and may result in significant yield losses to many economically important crop plants (Constantinescu 1991; Thines and Choi 2016; Van Wyk et al. 1995). The graminicolous downy mildews (GDM; Fig. 4n, o) in particular pose a serious threat to agriculture in the semi-arid tropics (Bock et al. 2000; Kenneth 1981; Telle et al. 2012; Vilgoen et al. 1997). Many *Phytophthora* species cause economically and ecologically devastating dieback diseases of trees and scrubs, such as sudden oak death caused by *Phytophthora ramorum* (Davidson et al. 2003) and jarrah forest dieback (Fig. 4e) caused by *Phytophthora cinnamomii* (Newhook and Podger 1972; Podger 1972). *Aphanomyces euteiches* causes serious economic losses by infecting the roots of leguminous crops such as peas and beans (Gaulin et al. 2007). Comprehensive catalogues of oomycete diseases of crop plants have been given by, among others, Dick (2001) and Constantinescu (1991).

Both *Nematophthora,* which infects nematode eggs (Dick 2001), and *Lagenidium giganteum,* which infects mosquito larvae (Kerwin 2007), have been explored as potential biocontrol agents. Marine species such as *Atkinsiella*, *Haliphthoros* (Fig. 2l, m)*, Halodaphnea* (Fig. 2j, k), and *Salilagenidium* spp. can cause serious economic losses to cultured crustaceans (crabs and prawns etc.) in coastal aquaculture systems (Hatai 2012; Hatai et al. 1980). *Aphanomyces astaci* (Fig. 3e–g), which was introduced to Europe around a century ago on imported signal crayfish (*Pacifastacus leniusculus*) from north America, now threatens to wipe out the native European white-clawed crayfish (*Astacus astacus*) which has no innate resistance to this pathogen (Cerenius et al. 1988; Edgerton et al. 2004).

Saprolegnia infections of fish and their eggs have been extensively documented and are responsible for significant losses to salmonids worldwide (Bruno et al. 2011; Van West 2006). Epizotoic ulcerative syndrome (EUS) caused by *Aphanomyces invadans* (syn *A. piscida*) is an emerging disease of farmed fish in warmer countries,

from the Indian subcontinent eastwards (Johnson et al. 2004; Lilley et al. 1998). Equine phycomycosis is an opportunistic pathogen of mammals caused by *Pythium insidiosum* (Krajaejum et al. 2011; Schurko et al. 2004), which, although largely affecting domesticated livestock in tropical countries, can cause potentially fatal infections to humans (Mendoza 2005). A newly recognized holocarpic lagenidiaceous species (*Paralagenidium karlingii*) has recently been shown to be the cause of fatal mycoses in dogs (de Grooters et al. 2013). In contrast to their importance as pathogens, no hyphochytrid or oomycete is known as a source for any economically important product, although, as with other heterokonts, they are able to synthesize valuable fatty acids (Domergue et al. 2005), but have not so far been commercially exploited.

Habitats And Ecology

Hyphochytriomycota, in common with the Chytridiomycota and Oomycota, are likely to be encountered in soil and water samples from any area of the world (Gleason et al. 2009; Thines 2014). Soil samples baited with pollen and boiled grasses commonly yield isolates of *Rhizidiomyces* (Figs. 2c, 6a–b) and *Hyphochytrium* (Fig. 2b, d). Gleason et al. (2009) demonstrated that *H. catenoides* is capable of surviving extreme environmental conditions. Viable colonies were recovered after subjecting dried material to extremes of pH (2.8–11.2), hypersalinity and freezing temperatures. Species belonging to the genera *Hyphochytrium, Latrostium,* and *Rhizidiomyces* have all been reported to infect algal thalli (Canter 1950). *Hyphochytrium infestans* was isolated from the decaying ascocarps of ascomycetous fungi, while both *Hyphochytrium* and *Rhizidiomyces* spp. infect oogonia of *Saprolegnia* and *Pythium* spp. and the resting spores of endomycorrhizal fungi (Fuller 2001; Schenck and Nicolson 1977; Sparrow 1977).

The Oomycota are likewise ubiquitous in marine, terrestrial, and aquatic ecosystems worldwide. Water moulds in the Saprolegniales have been recovered from almost every freshwater ecosystem but appear most abundant at the margins of lakes and ponds (Dick 1976; Johnson et al. 2002; Willoughby 1962; Wood and Willoughby 1986). In general population levels of saprolegniaceous water molds appear higher in cooler and wetter seasons, often showing peaks in spring and autumn (Ali-Shtayeh et al. 1986; Dick and Ali-Shtayeh 1986). Stagnant water and anaerobic environments also have their own distinctive communities of oomycetes, in which members of the Leptomitales and Rhipidiales (such as *Sapromyces*, Fig. 2p) predominate, and these fungi are often referred to as sewage fungi (Emerson and Natvig 1981; Riethmüller and Langer 2004). In coastal ecosystems, genera such as *Halophytophthora* and *Salisapilia* are now known to play a major role in the initial colonization, degradation and recycling of organic substrates, such as cord grass and mangrove leaves (Hulvey et al. 2010; Nakagiri et al. 1994; Newell and Fell 1995; Nigrelli and Thines 2013). Oomycota also infect a wide range of invertebrate animals such as crustaceans (Fig. 3e–g; Duffey et al. 2015; Hatai et al. 1980, 1992), insects (Frances et al. 1989; Kerwin 2007; Martin 1977), nematodes

(Figs. 2f, o; 3a–c; Dick 2001; Glockling and Beakes 2000a; Karling 1981), and rotifers (Fig. 3d; Molloy et al. 2014).

Oomycota play significant roles in terrestrial ecosystems. In soils, saprotrophic or facultatively pathogenic genera such as *Aphanomyces, Phytophthora*, and *Pythium* spp. predominate (Ali-Shtayeh et al. 1986; Arcate et al. 2006; Duncan 1990; Gaulin et al. 2007). Many oomycetes are obligate plant pathogens infecting annual or perennial herbs (Fig. 4f, q) and grasses (Fig. 4n). The white blister rusts (Fig. 4f–l) are found almost exclusively on herbaceous angiosperm hosts (Dick 2001; Choi et al. 2008; Constantinescu and Fetehi 2002; Spencer 1981; Spencer and Dick 2001; Thines 2009; Thines and Voglmayr 2009; Volgmayr and Riethmüller 2006; Van Wyk et al. 1995) with genera that appear to be restricted to specific host lineages (e.g., *Albugo* s.str. to the Rosidae, *Albugo* s.lat. to the Solanales, *Pustula* to the Asteridae, and *Wilsoniana* to the Caryphyllidae; Thines and Voglmayr 2009). Recent molecular phylogenetic studies have revealed downy mildew and white blister rust species that are restricted to a single host species (Choi and Thines 2015; Choi et al. 2007, 2008; García-Blázquez et al. 2008; Göker et al. 2004; Ploch et al. 2010; Thines et al. 2009b; Voglmayr 2003; Voglmayr et al. 2004). In contrast, some downy mildew genera such as *Peronospora* and *Plasmopara* have a very wide host ranges (Voglmayr and Constantinescu 2008; Voglmayr et al. 2004). While a few species of downy mildews are known to be parasitic to trees (e.g., *Plasmopara cercidis*, *Pseudoperonospora celtidis*), shrubs, and lianae (e.g., *Plasmopara viburni*, *Plasmopara viticola*, *Plasmopara australis*, *Pseudoperonospora humuli*, *Peronospora sparsa*), it is the hemibiotrophic genus *Phytophthora* that is more commonly encountered as pathogens of woody plants (Fig. 4e; Davidson et al. 2003; Newhook and Podger 1972).

Characterization and Recognition

Thallus Organization

Spore germination in monocenric hyphochytrids such as *Rhizidiomyces* results in the formation of a primary rhizoid from which the basal rhizoidal system develops, while the spore body expands to form the main vegetative thallus (Fig. 2a, c; Karling 1971; Sparrow 1960). In the polycentric *Hyphochytrium*, a much broader germ tube emerges, into which a nucleus moves and divides, and develops into a rhizomycelium of interconnected thalli (Fig. 2a, b, d; Wells 1982; Karling 1977). Young thalli of *Hyphochytrium* contain many small vacuoles with electron-dense inclusion bodies (Fig. 2e; Clay et al. 1991). Hyphochytriomyota are characterized by the presence of both chitin and cellulose in their cell walls (Bartnick-Garcia 1970; Clay et al. 1991; Fuller 1960). Immunogold labeling reveals the vegetative thallus walls are predominantly composed of cellulose, while chitin is principally located in the septa and the sporangial discharge tubes and restraining vesicle (Clay et al. 1991).

Many early-diverging Oomycota also have simple endobiotic holocarpic thalli, which directly differentiate into sporangia on maturity (Figs. 5b, c, f; 6a, b). Many

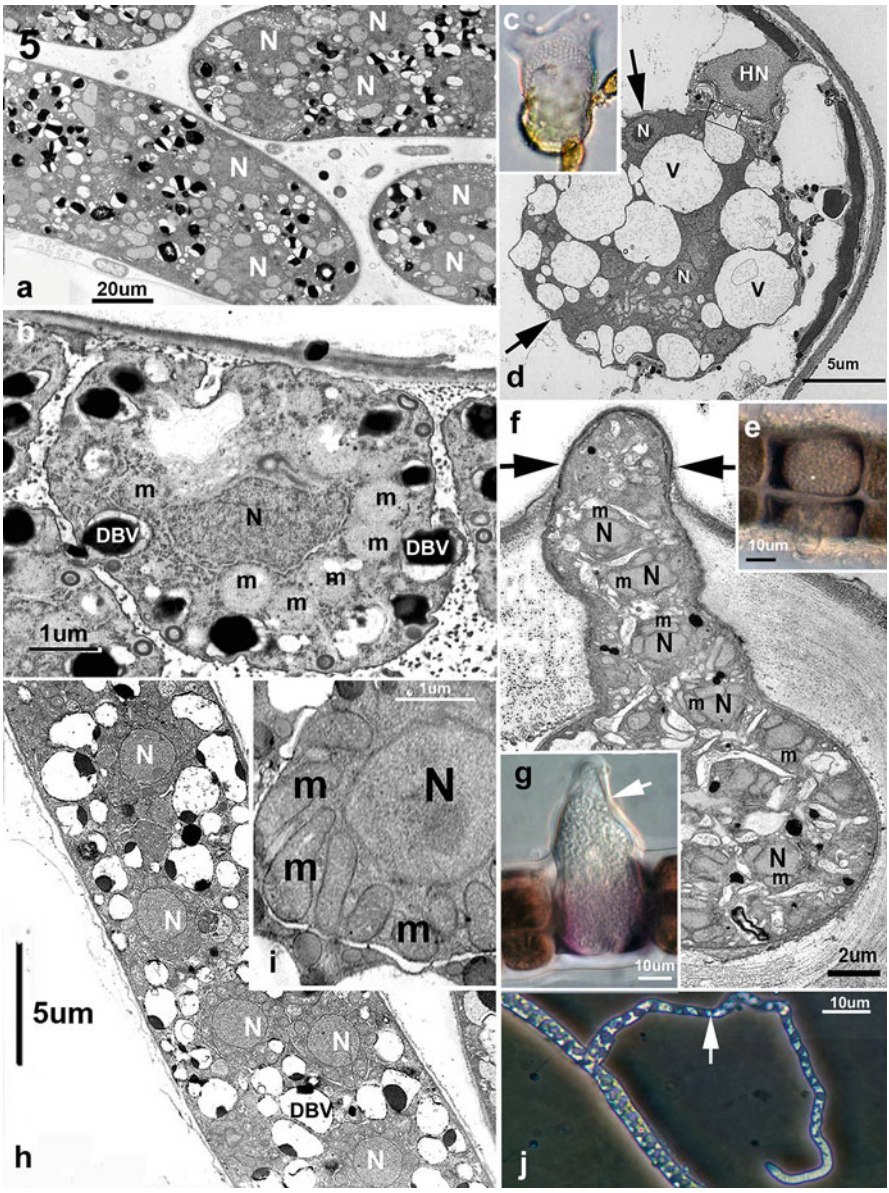

Fig. 5 Thalli of early-diverging Oomycota. (**a**) TEM of a series of young thalli of *Ha. heterospora* showing densely packed non vacuolated cytoplasm scattered with dense body vesicles, mitochondria and nuclei. (**b**) TEM detail of a developing zoospore of a zoosporic *Haptoglossa* sp. showing characteristic zonation of mitochondria (m) and peripheral DBV around the central nucleus (N). Courtesy Sally Glockling. (**c**) Mature thallus of *Eurychasma dicksonii* infecting *Ectocarpus* filament, showing characteristic peripheral net of primary cysts from which zoospores have been released and escaped. (**d**) TEM section of a young thallus of *E. dicksonii* in an expanded vacuolated host cell. Note close proximity of host nucleus (HN) and unwalled nature of the

holocarpic oomycetes, such as the parasities of algae *Ectrogella* (Ragukumar 1980), *Eurychasma* (Sekimoto et al. 2008a), and *Olpidiopsis* (Sekimoto et al. 2008b), have naked plasmodia stages during the earliest stages of infection (Fig. 5d). Taxa that have more extensive lobed, branched or segmented thalli (Fig. 2j, k, n) include the marine crustacean parasites, such as *Atkinsiella* (Karling 1981), *Haliphthoros, Halodaphnea* (Sekimoto et al. 2007), and algal parasites, such as *Lagenisma* (Schnepf et al. 1977, 1978a, b, c; Thines et al. 2015a) and *Petersenia* (Molina 1981; Pueschel and van der Meer 1985) as well as terrestrial genera such as *Chlamydomyzium* (Beakes et al. 2014b; Glockling and Beakes 2006b) and *Cornumyces* (Inaba and Hariyama 2006). Although none of these species produce typical hyphal-like thalli, most can be cultured on solid artificial media, where they form slow-growing irregular colonies (Glockling and Beakes 2006b; Sekimoto et al. 2007). Most thalli in the Rhipidiales (Fig. 2p) and Leptomitales form more typical fungal-like colonies on solid media, although they still have segmented thalli with regular constrictions. It appears that as in the Hyphochytriomycota, the Oomycota also have the capacity to synthesize chitin or chitin-like analogues, as evidenced by the widespread presence of chitin synthase genes within the phylum (Badreddine et al. 2008). In the Leptomitales, the pores in the constricted regions are plugged with refractile chitin-containing cellulin granules (Huizar and Aronson 1986).

The majority saprolegniomycete and peronosporomycete species have branched filamentous mycelial thalli that grow as fungus-like colonies on agar media (Fig. 2q, r). The hyphal tips contain accumulations of vesicles although they lack a well-defined Spitzenkörper analog found in most Fungi (Bartnicki-Garcia 1996). Hyphae vary in diameter from around 2 μm in genera such as *Pythiogeton* and *Verrucalvus* to nearly 150 μm in many genera in the Saprolegniaceae (Dick 2001). Hyphal vacuoles contain soluble β1–3 glucans (mycolaminarins), which are a major storage reserve in the Oomycota (Bartnicki-Garcia and Wang 1983; Wang and Bartnicki-Garcia 1974) as in the Ochrophyta. Most obligate biotrophic plant pathogens produce extensive intercellular hyphae in the infected leaf tissues from which haustoria intrude into the surrounding host cells (Hickey and Coffey 1977, 1978). The hyphae of the relatively

Fig. 5 (continued) pathogen thallus (*arrowed*). From Sekimoto et al. 2008a, *Protist* with permission. (**e**) Mature sporangium of *E. dicksonii*, showing peripheral network of primary cystospores, which is a characteristic feature of this genus. From Sekimoto et al. 2008a, *Protist*with permission. (**e**–**g**) LM showing a young and mature holocarpic thallus of *Olpidiopsis. bostrychiae*, infecting cells of the red seaweed *Bostrychia moritziana*. Note in mature thalli, the distended cell with elongate discharge tube terminated by a cap of wall material (*arrowed*, **g**). Beakes, unpublished. (**g**) Near-median TEM micrograph of *Olpidiopsis porphyrae* infecting ared seaweed of the genus *Porphyra*. The cytoplasm is fully differentiated in zoospore initials typical of holocarpic species. From Sekimoto et al. (2008b), *Mycol. Res*. with permission. (**h**) None-median TEM through thallus of *H. milfordensis* showing peripheral uninucleate (N) spore initials separated by vacuoles. (**i**) Detail of a zoospore initial showing regular array of mitochondria (m) around the central nucleus. Both Beakes unpublished. (**j**) Phase contrast micrograph of sporulating thallus of *H. milfordensis*, showing well formed refractile spore initials and elongate, hyphal-like, discharge tube (*arrowed*). Beakes and Sekimoto unpublished.

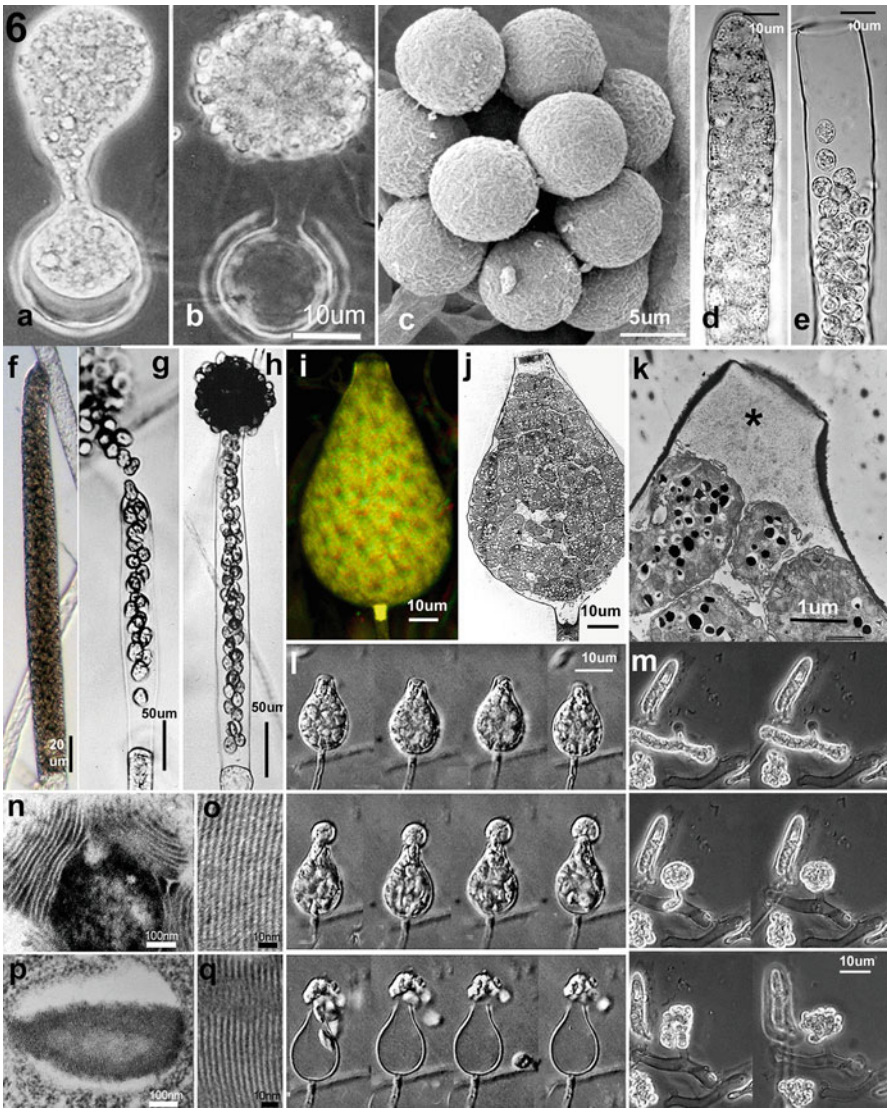

Fig. 6 **Asexual zoosporogenesis**. (**a**–**b**) Sporogenesis in the Hyphochytriomycota. Light micrograph of *Rhizidiomyces apophysatus*, showing cytoplasmic discharge from a mature thallus and formation of a zoospore-filled vesicle. From Fuller and Jaworkski (1987) with permission. (**c**–**h**) Sporogenesis in the Saprolegniales (**c**) SEM of a discharged ball of primary cysts in *Aphanomyces leavis.* Beakes and Lilley unpublished. (**d**) A mature sporangium of *Thraustotheca*, in which the encysted spores are released by gradual dissolution of the entire original sporangium wall. (**e**) A partially discharged sporangium of *Calyptralegnia*, in which the apex of the sporangium dissolves allowing the encysted spores to gradually escape (Beakes unpublished). (**f**) A mature zoosporangium of *Saprolegnia ferax* packed with zoospores. (**g**) A discharging zoosporangia of *S. diclina* and (**h**) *Achlya flagellata*, showing acumulating primary spore ball at mouth of sporangium. Courtesy Dr. N.P. Money. (**i**–**m**) Sporogenesis in the Peronosporales (all Beakes unpublished).

early diverging white-blister rusts, such as *Albugo*, form small stalked globose haustoria (Coffey 1975; Mims and Richardson 2002; Soylu et al. 2003), whereas *Phytophthora* (Coffey and Wilson 1983) and the downy mildews form generally larger digit-like to globose saccoid haustoria (Göker et al. 2003; Voglmayr et al. 2004).

Sporogenesis

In the Hyphochytriomycota, the expanded thallus is directly converted into simple zoosporangia. The cytoplasm then differentiates into uninucleate and uniflagellate zoospores during the zoosporogenesis phase of development (Karling 1977). In *Rhizidiomyces*, the sporangial cytoplasm flows into an external vesicle (Fig. 6a) where the completion of zoospore differentiation takes place (Fig. 6b; Clay et al. 1991; Fuller and Jaworksi 1987). In *Hyphochytrium*, the zoospores form within the sporangium and are released via open discharge tubes (Karling 1977).

Asexual reproductive structures provide many of the morphological characters which have been traditionally used to define genera (Dick 2001; Coker 1923; Johnson et al. 2002; Sparrow 1960), although recent molecular studies have revealed the inherent unreliability of many of these traditional morphological characters (Thines 2006). In early diverging Oomycota genera with plasmodial thalli, the thallus becomes walled prior to spore differentiation (Fig. 5f; Molina 1981; Raghukumar 1980; Schnepf et al. 1978b; Sekimoto et al. 2008a, b). Holocarpic endobiotic species usually form one or more elongate exit tubes (Figs. 2f, 3a, 5g, f, j) to facilitate the release of their spores from their hosts (Glockling and Beakes 2000a; Karling 1981). In species such as *Haliphthoros milfordensis*, these discharge tubes may be very long and hyphal-like in appearance (Fig. 5j). In *Aphanomyces*, primary aplanospores differentiate within what appear to be undifferentiated hyphae (Hoch and Mitchell 1972, Johnson et al. 2002). However, most species with eucarpic thalli form septum-delimited sporangia with a characteristic morphology (Fig. 6f–j) that are typically formed terminally (Johnson et al. 2002; Sparrow 1960). In the

Fig. 6 (continued) (**i**) Stereo z-series projection of mature zoosporangium of *Halophytophthora vesicula* containing fully differentiated zoospores and highly refractile basal plug. **j**. Median LS TEM of a mature zoosporangium of *Hp. vesicula* tightly packed zoospores and callose-like plug delimiting the sporangium. (**k**) Detail of sporangium apex of *Hp. vesiscula*, showing loosely fibriallar material, which forms the apical papillum (asterisked). (**l**) Video sequence showing vesiculate discharge of zoospores in *Hp. vesicula*. (**m**) Video sequqence showing discharge of spore mass into vesicle in a lagenidiaceous *Myzocytiopsis* sp. It takes about 10 min before the zoospores become fully motile and the vesicle ruptures. (**n**–**q**) Electron micrographs of the dense-body (DB)/finger-print (FP) vesicles associated with sporogenesis (all Beakes unpublished). (**n**) Densebody vesicle from primary cyst of *Achlya* (Saprolegniaceae), showing cap of lamellate material associated with the dense vesicle inclusion body. (**o**) High magnification detail of regular lamellate arrays from a oosphere DBV in Saprolegniaceaeshowing a periodicity of ca. 15 nm. (**p**) A finger-print vesicle from zoospore of *Pythium* Pythiaceae) showing reticulate array of lamellate material. (**q**) High magnification detail of regular lamellate arrays from a cyst of *Phytophthora* (Peronosporaceae) showing a periodicity of ca. 15 nm

Saprolegniales, sporangia are delimited by a double-walled septum (Gay and Greenwood 1966), whereas in the Peronosporales they are separated by a callose plug (Fig. 6i, j; Hohl and Hammamoto 1967). There are a significant number of taxa that produce nonmotile primary aplanospores (e.g., *Achlya*: Fig. 6h; *Aphanomyces*: Figs. 3f, 6c; *Calyptralegnia*: Fig. 6d, *Eurychasma*: Fig. 5c, *Protascus*: Fig. 7n, and *Thraustotheca* Fig. 6e). Many downy mildew genera in the Peronosporaceae such as *Bremia*, *Hyaloperonospora* (Fig. 4u) and *Peronospora* (Fig. 4s) form condiosporangia that germinate directly by means of germ tubes.

Zoospores or aplanospores are released (Fig. 6g, h, l) following the dissolution of the apical papillum wall (Beakes 1987; Gay and Greenwood 1966). In the Peronosporales, the papillum usually contains a plug (Fig. 6k, m), which often gives rise to extra-sporangial vesicles into which partially differentiated cytoplasm (Fig. 6m) or fully differentiated zoospores (Fig. 6l) are released (Beakes 1987; Glockling and Beakes 2006b; Lunney and Bland 1976). In the hyphochytrid *Rhizidiomyces* (Fig. 6a, b; Fuller and Reichle 1965) and some Peronosporomycete genera, such as ~*Lagenidium* (Gotelli 1974), *Myzocytiopsis* (Fig. 6m; Glockling and Beakes 2006a), and *Pythium* (Lunney and Bland 1976), the final stages of zoospore differentiation take place within the extra-sporangial vesicle, outside of the thallus. In other Peronosporomycete genera, such as *Phytophthora* and *Halophytophthora* (Fig. 6l), fully motile zoospores form within the sporangium and are also released into a transient restraining vesicle (Hyde et al. 1991a), while in downy mildew species such as *Plasmopara* spp. and *Pseudoperonospora* spp., zoospores are directly released from the sporangium (Thines 2006). In most downy mildews, the sporangia are formed on determinate sporangiophores of distinctive branched morphology (Fig. 4s, v). In most leaf-borne plant pathogens, the mature reproductive structures are disseminated by disarticulation (Fig. 4s) and dispersed by wind and rain splash (Dick 2001, Thines 2006). In the white blister rusts, basipetally maturing chains of conidia/sporangia are produced subepidermally by sporogenous hyphae (Fig. 4g, h), remiscent to true rusts, and again disseminated by disarticulation after lysis of the plant epiermis (Fig. 4j; Heller and Thines 2009; Kemen and Jones 2012; Mims and Richardson 2002).

In the genus *Saprolegnia*, two morphologically distinct types of zoospore are produced, traditionally referred to as primary and secondary zoospores (Beakes 1987; Coker 1923; Holloway and Heath 1977a; Sparrow 1960). Primary zoospores simply serve to disperse the spores from the immediate vicinity of the parent sporangium and are generally weak swimmers. They are usually pip or pear shaped and have apically inserted flagella (Fig. 7b)) which are retracted upon encystment (Holloway and Heath 1977a). The resulting primary cysts (Fig. 7o) typically release the stronger swimming dispersive secondary zoospores (Fig. 7d) which are typically reniform in shape and have laterally inserted flagella (Fig. 7d, g, i) that are shed upon encystment (Holloway and Heath 1977a). This ability to produce two generations of zoospore appears to have been lost in many Saprolegniomycete genera (Beakes et al. 2014a; Johnson et al. 2002), such as where the primary spore initials encyst at the mouth of the exit tube as in *Aphanomyces* (Fig. 3f, 6c) and *Achlya* (Fig. 6h) or within the sporangium as in *Dictyuchus* and *Thraustotheca* (Fig. 6d).

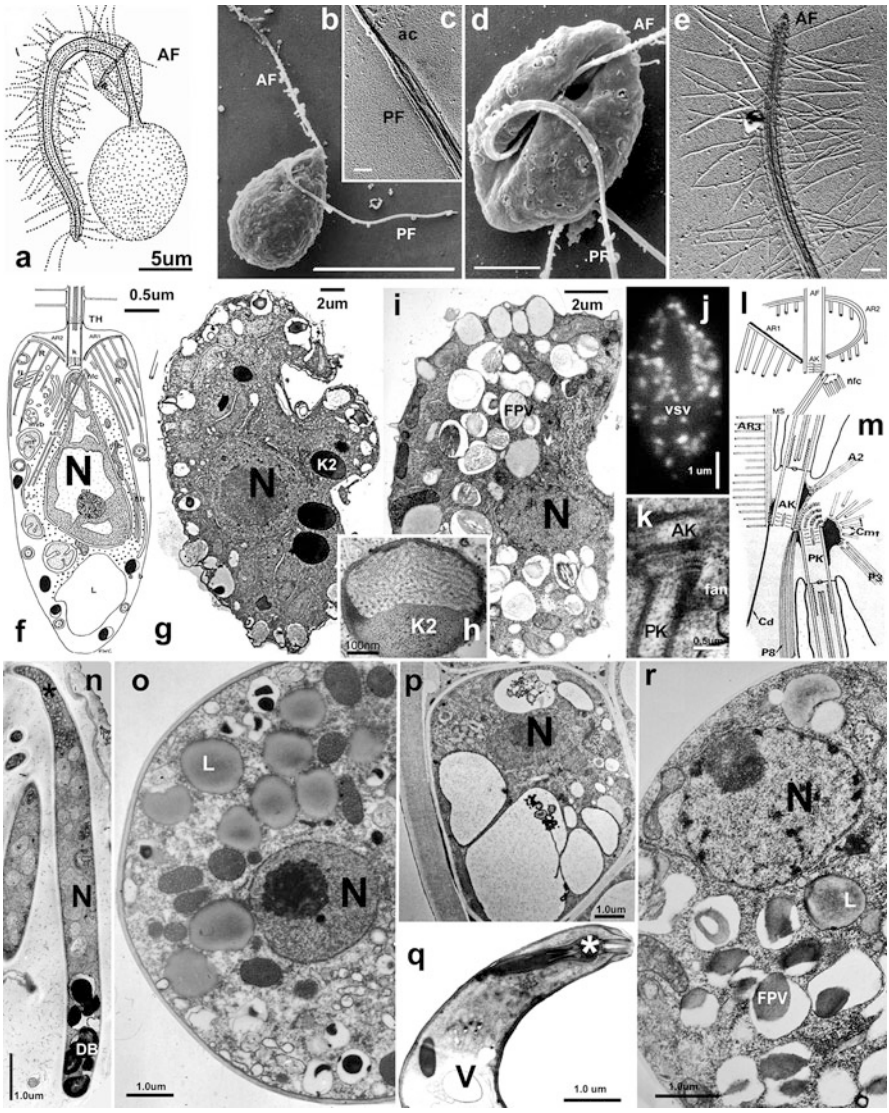

Fig. 7 Zoospore and cyst structure. (**a**) Drawing based on a whole-mount preparation of a Hyphochytriomycota zoospore (*Rhizdiomyces apophysatus*). From Karling (1977) with permission of Charles Lubrecht. (**b**) SEM of a primary zoospore of *Saprolegnia parasitica*, showing anterior (AF) and posterior (PF) flagella attached at apex of pip shaped spore. (**c**) Shadowed TEM whole mount of terminal acronme of posterior flagellum (PF) of *S. ferax*. (**d**) SEM of secondary zoospore of *S. parasitica*, showing ventral grove from which anterior (AF) and posterior (PF) flagella emmergee. Shadowed TEM whole mount of anterior flagellum (AF) of *S. ferax* showing tripartite mastigonene hairs, that give the straminipiles their name **b**–**e**; **g**–**h**: From Beakes (1989), Oxford Clarendon Press with permission. (**f**) Schematic diagram of TEM longitudinal profile of a zoospore of *Hyphochytrium catenoides*. From Fuller 1990. From Cooney et al. (1985) *Can. J. Bot*. with permission. (**g**) Longitudinal LS section of a secondary zoospore of *S. parasitica*, showing central

The ability to produce both primary zoospores (Fig. 7b) and cysts (Fig. 7o) has been entirely lost in Peronosporomycetes, which only form secondary type zoospores and cysts (Fig. 7i, n–r; Beakes 1987; Dick 2001; Hohl and Hammamoto 1967; Lunney and Bland 1976; Sparrow 1960). In the downy mildews, the complete loss of zoospore production has taken place independently in several genera (e.g., *Bremia*, *Hyaloperonospora*, *Paraperonospora*, *Peronosclerpospora*, and *Peronospora*; Göker et al. 2007; Thines 2006; Thines et al. 2009a; Voglmayr et al. 2004). The recent finding of a complete absence of genes associated with flagellum formation and function in the genome of *Hyaloperonospora* indicates that, in some downy mildews at least, this is an irreversible loss (Baxter et al. 2010).

In order to maximize zoospore production, sporangium proliferation frequently occurs throughout the Oomycota following zoospore discharge. Regrowth may take place through the basal septum (internal renewal), or from a lateral branch (cymose renewal) or by outgrowth of the sporangiophore from sites where sporangia were discharged as in some *Phytophthora* species and the grass parasite *Viennotia* (Thines et al. 2007; Thines 2009). In the Albuginales, sporangia are produced in basipetal sequence by the sporogenous hyphae as occurs in true rust fungi (Fig. 4g, h; Heller and Thines 2009; Kemen and Jones 2012; Mims and Richardson 2002).

Encysted zoospores in Oomycota (cysts; Fig. 7o–r) are typically spherical, although in some nematode infecting species, such as *Protoascus* (Fig. 7n), may be elongate and spindle-shaped. They are typically uninucleate and thin walled and contain abundant lipid and vacuolar dense-body/fingerprint vesicles (Fig. 7n–r). Most secondary cysts germinate directly by means of a vegetative germ tube, thus completing the asexual life cycle (Fig. 2s–u). However, the encysted zoospores of the nematode-infecting genus *Haptoglossa* (Beakes and Glockling 1998, 2000, 2002) germinate to produce specialized infection structures known as gun cells

Fig. 7 (continued) nucleus (N) and electron-dense kinetosome-associated bodies (K2) adjacent to the ventral groove. (**h**) TEM detail of a kinetosome associated K-body from *Achlya flagellata* (Saprolegniaceae). (**i**) Near median LS through zoospore of *Phytophthora palmivora*, showing disposition of fingerprint vesicles and lipid around the nucleus. (**g**–**i**) From Beakes (1989), Oxford Clarendon Press, with permission. (**j**) Fixed zoospore of *Phytophthora cinnamomi*, stained with FITC labeled monoclonal antibody (vsv-1) which labels the ventral vesicle fraction. (**k**) Kinetosomes associated with spore of *Haptoglossa erumpens*, showing both anterior (AK) and posterior (PK) kinetosomes and intervening striate fan structure. (**j**, **k**) Beakes unpublished. (**l**–**m**) Schematic diagrams showing basal bodies and rootlet system associated with secondary zoospores of *Hyphochytrium catenoides* (**l**) and *Phytophthora* (**m**). From Barr and Allen (1985) *Can. J. Bot.* with permission). (**n**) Elongate cyst of nematode parasite *Protascus subuliforme*, showing apical vesicles (asterisk), basal cluster of dense body vesicles (DB) and central nucleus (N). Courtesy Sally Glockling. (**o**) Section of a primary cyst of *Achlya flagellata*, showing nucleus and dispersed lipid bodies and mitochondria. (**p**) Cyst of Sapromyces elongatus that had encysted with sporangium. Note single nucleus and basal vacuoles (V) derived from coalesced dense body vesicles (Beakes unpublished). (**q**) Infection gun cell of *Haptoglossa erumpens*, showing basal vacuole (V) and inverted injection tube (asterisked). From Beakes and Glockling (2002), *Fung. Genet and Biol.* with permission). (**r**) Cyst of *Phytophthora palmivora*, showing nucleus (N) and array of finger-print vesicles (FPV). Beakes unpublished.

(Fig. 7q; Robb and Barron 1982). These cells contain a needle-like structure within an inverted tube (Beakes and Glocklng 1998, 2000, 2002). Upon contact with a suitable host, the tube everts and the needle ruptures the host cuticle, resulting in the injection of a minute infective sporidium into the body cavity of the nematode (Glockling and Beakes 2000b).

Most Oomycota also produce vegetative resting structures, variously referred to as chlamydospores in the Peronosporomycetes (Hemmes 1983) and gemmae in Saprolegniomycetes (Dick 2001; Johnson et al. 2002). These structures are delimited by similar septa to sporangia but are thicker-walled. They typically contain abundant storage reserves, particularly lipid (Beakes 1994; Hemmes 1983). When environmental conditions become favorable, they either germinate by producing germ tubes or convert into zoosporangia.

Sexual Reproduction

Sexuality has never been documented in the Hyphochytriomycota sensu stricto (i.e., excluding Anisolpidiaceae; Karling 1977), although structures that have been described as resistant sporangia have been reported in *Rhizidiomyces* spp. and *H. catenoides* (Karling 1977) which might explain why these species appears to be able to survive extreme environmental conditions (Gleason et al. 2009).

Most early diverging Oomycota (Table 1) are usually stated to lack a sexual stage (Sparrow 1976; Karling 1981). However, as Sparrow (1976) points out it seems improbable that all such species are genuinely asexual and suggested that they must have some form of cryptic (i.e., non oogamous) sexual reproduction. The best documented evidence supporting this comes from *Lagenisma coscinodisci*, which has recently been established to be an early diverging member of the Saprolegniomycetes closely related to *Atkinsiella* (Thines et al. 2015a). This species produces zoomeiospores which form cysts that conjugate to form the diploid resting zygote (Schnepf et al. 1977). Recent unpublished observations suggest that this might also be the form of sexual reproduction in *Eurychasma,* although this has only been observed on certain host seaweeds (Gachon, personal communication). Further support that conjugative, nonoogamous, sexual reproduction is prevalent in early diverging Oomycota also comes from *Anisolpidium ectocarpii* (Johnson 1957; Karling 1943, 1981). This species has recently been shown to be an early diverging member of the Oomycota closely related to marine *Olpidiopsis* spp. (Gachon et al. 2015) and reproduces by the fusion of adjacent protoplasts, derived from different cysts (Johnson 1957). Plasmogamy is immediately followed by nuclear fusion (karyogamy). The resulting zygote nucleus divides repeatedly as the cell enlarges and the wall thickens (Johnson 1957). All of these recent observations suggest that oogamy might have evolved at around the time of the Peronosporomycete divergence (Fig. 9a, b) and may even have arisen independently in saprolegniomycete and peronosporomycete lines (Thines et al. 2015a). However, the paraphyletic/polyphyletic genus *Olpidiopsis* needs further investigation in this respect, as

oogenesis has been reported in freshwater species such as *Olpidiopsis varians* (Martin and Miller 1986c) but not in any of the marine species (Sekimoto et al. 2008b, 2009).

In holocarpic Peronosporomycete species, such as *Lagenidium* and *Myzocytiopsis* adjacent thallus segments differentiate into male and female gametangia which have been interpreted as antheridial and oogonial segments, and give rise to a typical oosporic zygote (Dick 1995; Glockling and Beakes 2006a; Karling 1981; Martin and Miller 1986c). In the holocarpic, basal saprolegniomycete genus *Chlam ydomyzium* thick-walled oospore-like structures are formed, but without the apparent involvement of antheridial segments (Beakes et al. 2014b; Glockling and Beakes 2006b). Unfortunately, no information is available regarding nuclear changes that take place during resting spore formation in this genus to confirm whether this is a genuine sexual process, such as described in *Saprolegnia* species that lack antheridia (Beakes 1980b).

Oomycota as a group were named after their distinctive oogamous sexual reproduction present in the vast majority of species, involving the production of spherical to ovoid female oogonia, containing one (Fig. 8i) to several (Fig. 8a, f) large eggs (oospheres), and the associated male antheridia (Fig. 8f, i). In the diploid Oomycota gametangial meiosis preceeds gamete formation (Beakes and Gay 1977; Dick and Win-Tin 1973; Howard and Moore 1970). The female oosphere nuclei and male antheridial nuclei are the only haploid stages in the life cycle (Howard and Moore 1970; Beakes 1980b). The diploid state is restored by the fusion of the gamete nuclei, which normally takes place before the oospores (zygotes) have reached maturity (Beakes 1980b; Beakes and Gay 1977; Howard and Moore 1970). The morphology of gametangia (Fig. 8a, f, i) and oospores (Fig. 8g, h, k–p) have been widely used as key taxonomic characters (Dick 1969, 1990, 2001; Sparrow 1960). In the genus *Saprolegnia*, but also in the Albuginales, species identification is almost entirely dependent upon sexual characters (Choi et al. 2007, 2008; Coker 1923; Johnson et al. 2002; Ploch et al. 2010; Thines et al. 2009c; Voglmayr and Riethmüller 2006). It seems likely that in the Oomycota gametangium differentiation is regulated and coordinated by diffusible steroid hormones (antheridiols and oogoniols), whose functions have been well documented particularly in *Achlya bisexualis* (McMorris and Barksdale 1967; Raper 1939) and certain *Phytophthora* spp. (Ko 1988). In contrast to Saprolegniomycetes, several Peronosporomycetes were reported not to be able to synthesise their own sterols and require these as supplements in order to reproduce sexually (Jee and Ko 1997; Kerwin and Washino 1983). The male antheridia typically are formed on either subtending branches (monoclinous; Fig. 8a) or hyphal compartments (hypogynous) or from separate hyphae produced either on the same thallus (diclinous; Fig. 8f) or in the case of heterothallic species from separate thalli (Dick 1972, 1995, 2001). Many *Phytophthora* species show a unique type of amphigynous antheridium-oogonium association, where the oogonium penetrates the young antheridium which then forms a collar around the base of the oogonium (Fig. 8i; Hemmes and Bartnick-García 1975; Beakes et al. 1998).

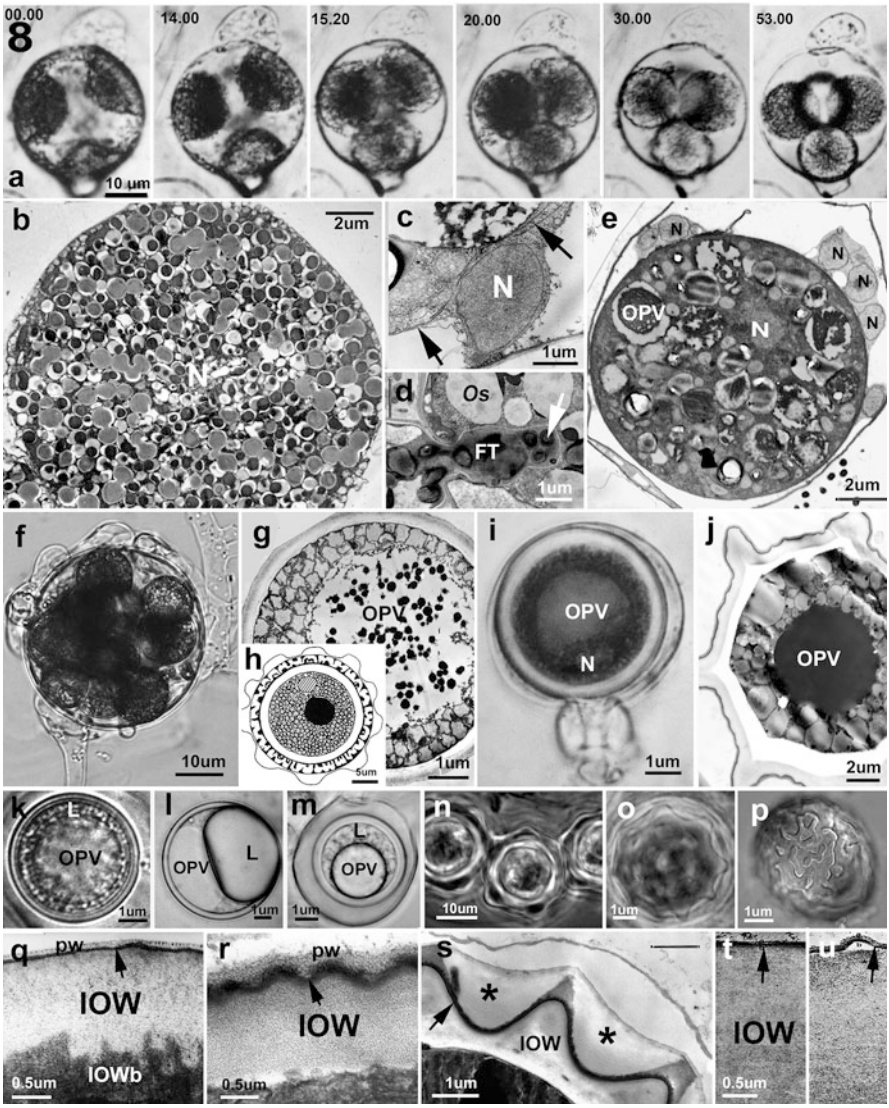

Fig. 8 Sexual reproduction. (**a**–**b**) Differentiating oospheres in *Saprolegnia furcata* (Saprolegniales). (**a**) Timelapse sequence over 53 min showing oosphere formation resulting from the fusion of the tonoplast with the plasma membranes, resulting in naked (unwalled) oospheres that initially swell (<20 min). As the oosphere primary wall forms, the oospheres achieve their final volume (around 30 min) and this is followed by fertilization tube formation from the attached antheridium (53 min). (**b**) TEM section through a newly formed, naked oosphere of S. furcata, showing interspersed lipid and densebody vesicles and central nucleus. (**a**–**b**) From Beakes and Gay (1977),*Trans. Br. Mycol. Soc.* with permission. (**c**–**e**) Differentiationg oospheres in *Myzocytiopsis spp.* (Peronosporales). Detail of a periplasmic nucleus (N) and part of a differentiated oosphere, separated by a double membraned envelope (*arrow*). (**d**) TEM of a developing fertilization tube (FT) extending into the oosphere (Os). The fertilization tube is bounded by a thin wall

In the Saprolegniomycetes, egg (oosphere) differentiation occurs as a result of the fusion of the central tonoplast membrane with the plasma membrane (Fig. 8a) resulting in naked oospheres (Fig. 8b), which within 30 minutes acquire an outer primary oosphere wall (Fig. 8a; Beakes and Gay 1978b). Following fertilization (Fig. 8a, d) thick inner oospore wall layers are accreted below a thin intervening electron-dense layer. In contrast in all Peronosporomycetes, a uninucleate oosphere (Fig. 8e) is cleaved from the cytoplasmic mass, surrounded by an outer periplasmic layer containing supernumerary nuclei (Fig. 8c; Beakes 1981; Hemmes and Bartnicki-Garcia 1975; Stevens 1901), which also contributes to the oospore formation by the the formation of an outer wall of the oospore.

Fig. 8 (continued) (*white arrow*). **e**. TEM of fully differentiated oosphere surrounded by a multinucleate (N) periplasm, typical of all Peronosporomycetes. The central nucleus (N) is surrounded by lipid and coalescing ooplast vesicles (OPV). All from Glockling and Beakes (2006a) *Mycol. Res.* with permission. (**f**) Light micrograph a mature oogonium of *Saprolegnia australis*, showing multiple oospores and diclinously attached antheridia. Beakes and Dieguez-Uribeondo unpublished. (**g**) TEM section through a mature oospore of *S. furcata*, showing central ooplast vacuole (OPV) containing densebody granules, surrounded by a lipid rich peripheral cytoplasm (From Beakes and Gay (1978a) *Trans Br. Mycol. Soc.* with permission) (**h**) Diagram of a mature oospore of *Albugo candida*(Albuginales) showing complex mutli-layered verrucose wall, and rather small ooplast vacuole surrounded by lipid-rich cytoplasm (adapted from Beakes (1981)) (**i**) Mature oogonium of *Phytophthora megasperma* (Peronosporales), showing amphigynous antheridium forming a collar around the the oogonium stalk and single oospore with a homogenous large central ooplast vacuole (OPV) and single zygotic nucleus (N). Beakes unpublished. (**j**) Near media profile of a mature oospore of *Myzocytiopsis venatrix,* showing lipid packed cytoplasm surrounding the homogenous central ooplast vacuole (OPV). Beakes and Glockling unpublished. (**k**) Light micrograph of a near mature centric oospore of *S. furcata* showing ooplast vacuole (OPV) is still homogeneous, but will eventually appear granular due to the dense body granules undergoing Brownian motion. (**l**) Mature eccentric oospore of *Leptomitus* (Leptomitales) showing transleucent ooplast vacuole and single large lipid globule. m. Sub eccentric oospore of *Apodachlya* (Leptomitales) showing homogenous ooplast vacuole (OPV) surrounded by a layer of fairly large lipid droplets (L). (**k**–**m**) Beakes unpublished. (**n**) Chain of stellate oospores of *Chlamydomyzium dictyuchoides* (Atkinsiellales s. lat.), showing punctate thick walls (From Beakes et al. (2014b) *Fung. Biol.* with permission) (**o**) Phase contrast LM of mature oospore of *M. vermicola* (Pythiaceae), showing punctate wall. Glockling and Beakes (2006a), *Mycol. Soc.* with permission. (**p**) DIC light micrograph of mature oospore of *Albugo* "*armoraciae*" (Albuginales), showing complex ornamentation that varies from species to species. Thines unpublished. (**q**) Oospore wall of *Saprolegnia furcata* (Saprolegniales) showing outer exospore wall layer (pw), electron-dense epispore layer (*arrow*) and thick inner endospore wall (IOW), which in this genus has an irregular electron dense inner zone (IOWb). Beakes and Gay (1978b) *Trans. Br. Mycol. Soc*. with permission. (**r**) Mature oospore wall of *Cornumyces* (Saprolegniomycetes), which shows similar layers to above, except for the absence of the inner electron dense zone to the endospore wall. Beakes unpublished. **s**. TEM through mature oospore wall of *Myzocytiopsis vermicola*(Peronosporomycetes) showing that punctate spines are the result of the uneven thickening (*asterisked*) of the endospore layer. The outer electron leucent exospore layer is laid down early in oospore maturation before the formation of the electron dense epispore layer (From Glockling and Beakes (2006a) *Mycol. Res*., with permission) (**t**–**u**) TEM through mature oospore walls of *Ph. megasperma*, fixed with glutaraldehyde and osmium (**t**) and additianlly stained with permanganate (**u**) showing outer electron-dense epispore (*arrowed*) and homogeneous, but finely fibrillar endospore wall (IOW) (From Beakes and Bartnicki-Garcia (1989). *Mycol. Res.*with permission)

Ultrastructure

Mitosis in the Hyphochytiomycota has only been described at the ultrastructural level in *Rhizidiomyces* (Barstow et al. 1989). During prophase the centrioles of unequal length divide and migrate to the poles of the nucleus. During metaphase small polar fenestrae (gaps) develop in the nuclear envelope, allowing the spindle microtubules to span the nucleus. By metaphase the chromosomes are grouped equatorially and vesicles appear and fuse with each other on the poleward side of chromosomes (Barstow et al. 1989). At metaphase the nucleolus is located in a pocket to the side of the chromosomes, after which it disperses completely. During anaphase the intranuclear cisternae migrate ahead of the advancing chromosomes. A perinuclear endoplasmic reticulum and microbodies surround dividing nuclei during anaphase and telophase. During telophase, offspring nuclei are formed by the addition of new envelope to existing membranes and the mid-region of the original nucleus is excluded (Barstow et al. 1989).

This contrasts with the completely closed mitosis described in most Oomycota (Beakes 1980c). Mitosis has been documented at the ultrastructural level in *Albugo* (Khan 1976), *Lagenisma* (Schnepf et al. 1978a), *Olpidiopsis* (Martin and Miller 1986a), *Phytophthora* (Hemmes and Hohl 1973) and *Saprolegnia* (Beakes 1980b, c; Heath and Greenwood 1970a). In most, the nuclear membrane persists throughout mitosis and an intranuclear spindle forms between pairs of polar or sub-polar centrioles, which are usually oriented at 180° (end to end) to each other. Only in *Olpidiopsis varians* are small polar fenestrae reported to form during prophase (Martin and Miller 1986a).

The vegetative thallus in both the Hyphochytriomycota and Oomycota is filled with large somatic vacuoles, which contain osmiophilic inclusion bodies of unknown composition that are often associated with the tonoplast membrane (Figs 2e, 5a, h). Nuclei and other cytoplasmic organelles are distributed throughout the peripheral cytoplasm (Fig. 5a, f, h). In both groups mitochondria have prominent tubular cristae (Fig. 5i), which are a characteristic feature of the chromalveolate lineage (Cavalier-Smith and Chao 2006). In vegetative hyphae and young sporangia in the Saprolegniales, the Golgi dictyosomes are associated with mitochondria and an intervening cisternum of endoplasmic reticulum (ER), a feature shared with many diatoms (Beakes 1989).

During sporangium differentiation in both the Saprolegniales and Peronosporales vacuolar dense body/fingerprint vesicles (DBV/FPV) increase (Beakes 1980a, 1994; Gay and Greenwood 1966; Glockling and Beakes 2006a) and their osmiophilic inclusion bodies become associated with lamellate material of regular periodicity (Fig. 6n–q). In *Phytophthora* phosphorylated glucan derivatives (phospho-mycolaminarin) have been shown to co-localize with isolated FPV (Powell and Bracker 1977). However, no lamellate DBV have been observed in early diverging genera (Beakes and Glockling 2000; Sekimoto 2008; Sekimoto et al. 2008a, b, 2009), which may indicate phosphorylated mycolaminarins are not synthesised by these species, although this needs experimental confirmation.

In most species spore formation involves the division (cleavage) of the multinucleate protoplast into uninucleate spore initials each with a defined complement of organelles. In early diverging genera such as *Eurychasma* (Sekimoto et al. 2008a), *Haliphthoros* (Fig. 5i), *Haptoglossa* (Fig. 5b; Beakes and Glockling 2000), *Olpidiopsis* (Martin and Miller 1986b; Sekimoto et al. 2008b, 2009) and *Petersenia* (Molina 1981) there is a tight association mitochondria around nuclei prior to cytoplasmic cleavage. Cytoplasmic cleavage in the Oomycota follows one of two general patterns (Beakes 1994; Dick 2001). The first, usually referred to as centrifugal cleavage (Beakes 1989, 1994) is found in most early diverging genera (Sekimoto 2008) and Saprolegniomycetes (Beakes et al. 2014a). A central vacuole expands delimiting a peripheral layer of uninucleate initials (Fig. 5h) and spore initial formation is effected by the fusion of the tonoplast with the plasma membrane (Gay and Greenwood 1966; Sekimoto et al. 2008b, 2009), as occurs in oosphere differentiation illustrated in Fig. 8a. In most Saprolegniomycetes flagellum formation occurs after the zoospore initials have differentiated (Beakes 1987; Gay and Greenwood 1966; Glockling and Beakes 2006b).

The second pattern, described as centripetal cleavage (Beakes 1994), predominantly occurs in the Peronosporomycetes (and probably Hyphochytriomycota). The uninucleate zoospore initials are delimited by the progressive disposition of a system of narrow Golgi-derived cleavage vesicles/cisternae, occasionally with additional infurrowing of the plasma membrane as occurs in *Albugo* (Khan 1976, 1977), *Phytophthora* (Hemmes 1983; Hohl and Hammamoto 1967; Hyde et al. 1991a, b) and *Pythium* (Lunney and Bland 1976). This leads to the concurrent, rather than sequential, formation of zoospore initials and flagella (Hohl and Hammamoto 1967; Hyde et al. 1991a, b; Lunney and Bland 1976). As a consequence beating flagella can often be observed in differentiating sporangia or extrasporangial vesicles even before the formation of individual zoospores.

Zoospore Ultrastructure

The ultrastructure of motile cells has traditionally been widely used to provide taxonomically and phylogenetically informative characters in protists and is still important in helping to define clades of chytrid fungi (Powell and Letcher 2014). In the Hyphochytriomycota and Oomycota, zoospores are also a rich source of phylogenetically informative characters (reviewed by Beakes 1987, 1989). Hyphochytriomycota zoospore ultrastructure has been documented for both *R. apophysatus* (Fuller and Reichle 1965) and *H. catenoides* (Barr and Désaulniers 1989; Cooney et al. 1985; Lange and Olson 1979: see Fig. 7f). In common with other members of the stramenopile lineage (Cavalier-Smith and Chao 2006) there is a helically coiled double transitional helix (TH) located just above the basal plate of the flagellum (Fig. 7f). In the Hyphochytriomycota the anterior flagellum is associated with two microtubular rootlets consisting of single (AR1) and doublet (AR2) type, both of which have rib-like microtubules extending from them, providing a cytoskeletal framework for the zoospore (Fig. 7l; Barr and Désaulniers 1989; Beakes et al. 2014a; Dick 2001). In addition, there is a third doublet rootlet (designated as multistranded

root, MS), which originates between the two basal bodies and extends to the spore posterior (Fig. 7l; Barr and Désaulniers 1989).

In the Hyphochytriomycota, the ribosomes in the zoospores are aggregated around the posterior region of the nucleus and are surrounded by a zone of mitochondria (Fig. 7f; Cooney et al. 1985; Fuller 1966; Fuller and Reichle 1965; Lange and Olson 1979). Lipid bodies and microbodies and assorted vesicles, including those containing mastigoneme tubules, are also scattered throughout peripheral zoospore cytoplasm (Fig. 7f). When Hyphochytriomycota zoospores encyst, the axoneme of the flagellum is retracted into the body of the cyst (Fuller and Reichle 1965; Wells 1982). The outer cyst coat is derived from the discharge of structured peripheral vesicles (Fuller 1966) which are similar to the encystment vesicles described in the Oomycota (Beakes 1987, 1989).

The structure and orientation of the four microtubular flagellar rootlets in Oomycota zoospores has been meticulously documented from serial section reconstructions in *Saprolegnia* (Fig. 7m; Barr and Allan 1985; Barr and Désaulniers 1987, 1989; Holloway and Heath 1977b) and *Phytophthora* (Barr and Allan 1985; Hardham 1987) and appears broadly similar to other biflagellate stramenopiles (Anderson et al. 1991; Barr 1981). Most Oomycota zoospores have the expected double TH in the flagellum base (Beakes et al. 2014a; Barr 1981; Dick 2001) although in *Olpidiopsis saprolegniae* it has only a single gyre (Bortnick et al. 1985), and it is apparantly absent in a few species, including the Peronosporomycete *Lagena radicola* (Barr and Désaulniers 1989). Zoospores contain an array of peripheral vesicles (Fig. 7g–j), which upon encystment are discharged to form both a ventral pad of adhesive and the outermost cyst coat layers (Beakes 1983, 1989, 1994; Gubler and Hardham 1988; Lehnen and Powell 1989). In Saprolegniomycetes, this system includes the larger kinetosome-associated (K-bodies) vesicles (Fig. 7h; Beakes 1989; Holloway and Heath 1977b; Randolph and Powell 1992) which upon encystment discharge to form a ventral pad of adhesive material (Burr and Beakes 1994; Lehnen and Powell 1989). In Peronosporomycetes the homologous vesicles are smaller and generally located along the rim of the ventral zoospore groove rather than immediately adjacent to the kinetosomes (Fig. 7j Gubler et al. 1990), and are often morphologically indistinguishable from the dorsal vesicle fraction. Saprolegniomycete genera also contain a second vesicle fraction, which in *Saprolegnia ferax* were called bar-bodies (Heath and Greenwood 1970b), although in other genera such as *Apodachlya* are spherical in profile (Randolph and Powell 1992). Upon discharge the peripheral component of these vesicles give rise to the thin outer electron-dense primary cyst coat (Beakes 1983, 1989; Randolph and Powell 1992). The corresponding vesicles in secondary zoospores of genera such as *Dictyuchus* and *Saprolegnia* contain, respectively, conspicuous tapered spines or boathook spines (Beakes 1983; Burr and Beakes 1994; Heath and Greenwood 1970b) that on release decorate the secondary cyst coat (Fig. 3j). In other genera such as *Apodachlya*, *Aphanomyces*, and *Achlya* the equivalent vesicles are spherical or ovoid in shape and have granular contents rather than tubules or spines and form only the thin outer electron-dense layer to the cyst wall (Beakes 1989). Morphologically similar encystment vesicles also occur in the zoospores of many of

the early diverging oomycetes, including *Eurychasma* (Sekimoto et al. 2008a), *Lagenisma* (Schnepf et al. 1978c), *Haliphthoros* (Overton et al. 1983; Sekimoto 2008), *Haptoglossa* (Beakes and Glockling 2000), *Olpidiopsis spp.* (Sekimoto et al. 2008b, 2009), and *Petersenia* (Pueschel and van der Meer 1985). In contrast, in Peronosporomycetes, the homologous vesicle fraction are the so-called dorsal small vesicles (dsv), which are often morphologically indisguishable from the ventral vesicle fraction, and upon encystment form a structurally diffuse sticky glycoprotein coat (Gubler and Hardham 1988; Gubler et al. 1990).

Mature Oospore Ultrastructure

Following nuclear transfer and fusion (karyogamy) the fertilized oosphere matures into the thick-walled resting zygote, the oospore (Fig. 8g–p; Beakes 1980a; Beakes and Gay 1978a; Hemmes and Bartnicki-Garcia 1975; Tewari and Skoropad 1977). Following fertilisation a thick electron-dense wall layer is layed down (Fig. 8q–u), to which further wall layers may be added both internally from egg cytoplasm and externally from the periplasm (Fig. 8q–u; reviewed by Beakes 1981). This "epispore" layer appears to represent the transition from oosphere to oospore, and after its formation, the mature eggs are much more recalcitrant to TEM fixation (Fig. 8g, j). The overall organization of the cytoplasmic components in mature oospores was described by Dick (1969) and has proven to be a useful taxonomic character. In all species the oospore protoplasm contains a prominent ooplast vacuole (Dick 1969; Fig. 8g–m) derived from the fusion and expansion of the oosphere DBV system (Beakes 1980a; Beakes and Gay 1978a; Beakes et al. 1986; Hemmes and Bartnicki-Garcia 1975; Howard and Moore 1970). This vacuole is usually surrounded by the peripheral cytoplasm containing oil reserves, which may be organized into many small droplets (in centric, subcentric or plerotic oospores; Fig. 8g, h, j) or these may coalesce into a small number of large droplets (as in the eccentric oospores of *Leptomitus*; Fig. 8l). In the genus *Saprolegnia* the mature ooplast vacuole contains small granules which are in constant Brownian motion (granular ooplast; Fig. 8g, k) whereas in the Leptomitales (Fig. 8l; Dick 1969, 1973a) and Peronosporomycete species the ooplast vacuole usually has a uniform refractile appearance (Fig. 8i; Beakes et al. 1986) and appears as a homogenously electron-dense matrix in the transmission electron-microscope (Fig. 8j; Beakes 1981; Beakes et al. 1986).

Oospores are mostly not shed from the oogonium wall which provides an additional protective outer layer to the zygote. It is often thick and multilayered (Beakes and Bartnicki-Garcia 1989; Hemmes and Bartnicki-Garcia 1975) and in many genera can be papillate (e.g in *Chlamydomyzium dictyuchoides*: Fig. 8n; *Sclerospora stellatus*: Fig. 8o) or ornamented (e.g., Fig. 8p; *Albugo ipomoeae-panduratae*; Voglmayr and Riethmüller 2006). In *Saprolegnia* there are often thinner-walled pit regions through which the germ tube hyphae escape. Mature oospore walls are also thick multi-layered structures and contain a large amount of storage carbohydrates (and probably lipids) that are mobilized upon germination (Beakes and Bartnicki-Garcia 1989; Bartnicki-Garcia and Wang 1983). The thick (2–3 μm) innermost endospore wall layer may be multilayered as in the genus *Saprolegnia* (Fig. 8q Beakes and Gay 1978b) or relatively homogeneous as in

Cornumyces (Fig. 8r) and most Peronosporomycete species (Fig. 8t, u; Beakes 1981; Beakes and Bartnicki-Garcia 1989; Hemmes and Bartnicki-Garcia 1975). In the Peronosporomycetes, the outermost oospore wall layer (the exospore layer; Beakes 1981) may at least be partially derived from the residual periplasm (Fig. 8s) and is particularly thick and complex in the Albuginales (Fig. 8h; Stevens 1901; Tewari and Skoropad 1977). In the Albuginales and many Peronosporales species (such as *Peronospora tomentosa*, Fig. 4l and *Myzocytiopsis vermicola*, Fig. 8o; Glockling and Beakes 2006a) the exospore is unevenly thickened, which gives the oospores their ornamented appearance (Fig. 8n–p).

The onset of germination is indicated by the rapid digestion and reabsorption of the thick inner endospore wall (Beakes 1980b; Beakes and Bartnicki-Garcia 1989) followed by the breakdown of the electron-dense ooplast globule material as the central vacuole expands. The broad germ tube hypha is often terminated by a zoosporangium (Ruben and Stangellini 1978). In *Albugo* also the swollen oospore may be converted directly into a zoosporangium, as depicted by Schröter (1893).

Genomic Studies

So far, there are no genome sequences for any Hyphochytriomycota in the public domain, although *Hyphochytrium catenoides* is being sequenced by Tom Richards, University of Exeter, and as part of the ATCC 18717 genome project. Some prelimary data for this organism has been included in publications, exploring horizontal gene transfer into the Oomycota (Richards et al. 2011; Savory et al. 2015). The top ten Oomycota pathogens, which genomes have been sequenced (even though some have not been released to the public domain so far) and which have been extensively studied in molecular plant pathology have recently been reviewed by Kamoun et al. (2015). Six are *Phytophthora* species, with the potato blight pathogen, *Ph. infestans* coming top of the list. The remaining places, were taken by two downy mildews (*Hyaloperonospora arabidopsis* and *Plasmopara viticola*), and a single *Albugo* and *Pythium* (Kamoun et al. 2015). The downy mildew *Hyaloperonospora arabidopsidis* and white blister rust *Albugo laibachii* both infect the model plant *Arabidopsis,* and have provided excellent systems in which to explore host pathogen interactions at the molecular level (Kemen and Jones 2012; Thines et al. 2009a). Much recent effort has been directed at unravelling the molecular basis of pathogenicity in economically important plant pathogenic oomycetes (see reviews by Jiang and Tyler 2012; Thines and Kamoun 2010). However, compared with the Fungi, genetic manipulation of stramenopiles has generally proven difficult and frustrating. With a few exceptions, such as *Phytophthora capsici*, it has been difficult to routinely transform Oomycota (Judelson and Ah-Fong 2009). Gene silencing techniques have often been the only tool available to explore gene functions (Whisson et al. 2009).

Representatives of the phytopathogenic genera *Albugo* (Kemen et al. 2011, Links et al. 2011), *Hyaloperonospora* (Baxter et al. 2010), *Peronospora* (Derevnina et al. 2015), *Plasmopara* (Sharma et al. 2015a), several *Phytophthora species* (e.g., Haas

et al. 2009; Judelson 2012; Tyler et al. 2006), *Pseudoperonospora* (Tian et al. 2011) and *Pythium ultimum* (Cheung et al. 2008; Lévesque et al. 2010) and the fish pathogen, *Saprolegnia parasitica*, have had their full or partial genome sequences released. Comparative genomics is promising to unlock many interesting secrets about these organisms (see Greville-Briggs et al. 2011; Judelson 2012; Lamour et al. 2007; Pais et al. 2013; Seidl et al. 2012; Sharma et al. 2015a, b). Features of genome evolution in the Oomycota, has revealed repeat-driven expansions, deletions, gene fusions and horizontal gene-transfer (Judelson 2012; Haas et al. 2009; Savory et al. 2015; Tyler et al. 2006). One surprising discovery appears to be the extent to which the genomes of oomycetes contain genes derived from other prokaryotes and eukaryotes, suggesting horizontal gene transfer (HGT) from bacteria, fungi and red and green algal endosymbionts (Jiang and Tyler 2012; Maruyama et al. 2009; Richards et al. 2006; Soanes et al. 2007). Genes of green algal ancestry have been discovered in oomycetes (Richards et al. 2011; Jiang and Tyler 2012). This might suggest that the single plastid acquisition-multiple loss interpretation related to evolution of non-photosynthetic organisms, such as Oomycota, from a photosynthetic ancestor needs further evaluation (Dorrell and Smith 2011; Maruyama et al. 2009; Stiller et al. 2009).

Recent genomic studies on non-biotrophic pathogens in genera such as *Aphanomyces* (Gaulin et al. 2007; Krajaejun et al. 2011), *Saprolegnia* (Torto-Alalibo et al. 2005; Wavra et al. 2012) and *Pythium* (Cheung et al. 2008; Lévesque et al. 2010) show these organisms contain a formidable array of glucanase and proteinase encoding genes, which have enabled them to so successfully exploit a wide range of plant and animal substrates (Jiang and Tyler 2012). Genomic studies have also revealed a startling array of pathogenicity factors and effector molecules, which presumably have enabled *Phytophthora* species (Judelson 2012; Lamour et al. 2007; Morgan and Kamoun 2007; Qutob et al. 2002; Sharma 2015a), downy mildew species (Baxter et al. 2010, Derevnina et al. 2015, Sharma et al. 2015a, b), and white blister rusts (Kemen et al. 2011; Links et al. 2011) to become such effective plant pathogens. The independent evolution of obligate biotrophy in the white blister rusts is also reflected by the fact that *Albugo laibachii,* the white blister rust pathogen of *Arabidopsis thaliana* (Thines et al. 2009c), has a much smaller genome compared with obligate parasites in the Peronosporales (Kemen and Jones 2012; Kemen et al. 2011) and has evolved a novel group of CHxC/CxHC effectors that are unique to this clade (Kemen et al. 2011; Links et al. 2011).

Classification

Karling (1977) presents what is probably the most realistic systematic treatment of the Hyphochytriomycota. He questioned Sparrow's (1973) classification that placed emphasis on zoospore cleavage patterns and rejected *Canteriomyces* and *Rhizidiomycopsis* as independent genera. In this account the Hyphochytriomycota have been treated as a phylum in their own right, which may also include the phagotrophic protist, *Pirsonia* (Kühn et al. 2004), which we will consider to be of *incertae sedis*.

The most recent formal systematic account of the Oomycota was by Dick (2001) and is largely based on a critical and scholarly evaluation of morphological characters. Since this account was published there have been many molecular phylogenetic studies on oomycetes (see review by Beakes et al. 2014a). Most of these have compared genes such as those encoding the small (SSU) and large ribosomal subunits (LSU) and the intervening internal transcribed spacer region (ITS), beta-tubulin, NADH and the mitochondrially-encoded cytochrome c oxidase subunit II genes (*cox*2). Some studies have concentrated on higher level taxonomic boundaries and general phylogenic relationships (e.g.; Choi et al. 2015; Dick et al. 1999; Göker et al. 2007; Hudspeth et al. 2000; Lara and Belbahri 2011; Léclerc et al. 2000; Petersen and Rosendahl 2000; Riethmüller et al. 1999; Thines et al. 2008, 2015b), whilst others have been concerned with resolving species clades within the main genera (e.g., *Albugo* Choi et al. 2007, 2008; Ploch et al. 2010; Thines et al. 2009c: *Aphanomyces* Diéguez-Uribeonodo et al. 2009; Levenfors and Fatehi 2004; Lilley et al. 2003; *Haliphthoros* Sekimoto et al. 2007; *Basidiophora* Sökücü and Thines 2014; *Hyaloperonospora* Göker et al. 2004, *Peronospora* Voglmayr 2003; *Peronosclerospora* (Telle et al. 2011), *Phytophthora* Blair et al. 2008; Cooke et al. 2000; Förster et al. 2000; Runge et al. 2011; *Pseudoperonospora* Choi et al. 2005, Runge et al. 2011; *Pythium* Lévesque and de Cock 2004; Martin 2000; *Saprolegnia* Diéguez-Uribeondo et al. 2009; Hulvey et al. 2007; Inaba and Tokumasu 2002; Léclerc et al. 2000; Sandoval-Sierra et al. 2014; Steicow et al. 2013, 2014). As a result of these studies it is now clear that many of the taxonomic changes that were introduced by Dick (1997, 2001) are not supported by molecular data and require substantial revision. It is also becoming apparent that many of the ordinal, family and generic circumscriptions in Oomycota require re-evaluation and that many traditional morphological characters used in taxonomy (such as patterns of asexual spore formation in the Saprolegniceae, patterns of antheridium attachment in *Phytophthora* and conidiophore development in the downy mildews etc.) are not reliable indicators of genetic relatedness.

A revised taxonomic framework of the Hyphochytriomycota and Oomycota based on molecular data is summarised in Table 1. We have refrained from making formal taxonomic descriptions, but will use working names, indicated by “ ” when first used for likely new classes, orders and families. Those taxa that we consider not to be monophyletic and consider are in need of revision are indicated by the ~ before them. We have assumed that the Oomycota form a phylum in their own right and consequently have raised to full class rank the sub-orders proposed by Dick (2001). The placement of the taxa (Rhipidiales, Leptomitales and “Atkinsiellales”) which lie at the cusp of the divergence of the main groups, the Saprolegniomycetes and Peronosporomycetes, have proven particularly problematic and their taxon sampling under-represented, as is the case with many of the smaller marine and holocarpic genera (Table 1).

The majority of Oomycota genera listed in Table 1 fall into one of two major clades with a high degree of statistical support (Fig. 9b). These have been assigned as separate classes the Saprolegniomycetes and Peronosporomycetes (Beakes et al. 2014a, Thines et al. 2015a), which approximate to the galaxies proposed by Sparrow

(1976) and assigned sub-class status by Dick (1997, 2001). Molecular studies have also revealed a number of early diverging basal clades, mostly encompassing marine species (Cook et al. 2001; Küpper et al. 2006; Sekimoto et al. 2007, 2008a, b). However, because of the limited or complete absence of molecular data for many genera in these early-diverging clades, we have refrained from assigning them to new classes at present and therefore they are placed under class(es) *incertae sedis* (Table 1).

Phylum Hyphochytriomycota

Class Hyphochytriomycetes

Order Hyphochytriales

Fuller (1990, 2001) considered that the Hyphochytriomycota consisted of one class (Hyphochytriomycetes), one order (Hyphochytriales), and three families (Anisolpidiaceae, Rhizidiomycetaceae, and Hyphochytriaceae). The Rhizidiomycetaceae have simple monocentric thalli and release their zoospores into a vesicle (Fig. 6b), consisting of 3 genera (Dick 2001; Fuller 2001). The Hyphochytriaceae have polycentric thalli and zoospores differentiate fully within the sporangium and are not released into a transient vesicle and at present also contains 3 genera (Dick 2001; Fuller 2001). Only two Hyphochytiomycota genera, *Hyphochytrium* and *Rhizidiomyces*, have so far been sequenced and together form a well supported clade that is well separated from the Oomycota (Fig. 1b). Recent molecular sequencing has shown that *Anisolpidium* belongs within the Oomycota (Gachon et al. 2015) and will be excluded from the Hyphochytiomycota in this account.

Phylum Oomycota Arx

Basal Class(es) – incertae sedis

Order "Eurychasmales"

The "Eurychasmales" (Table 1, Fig. 9b; Sparrow 1976) are a monotypic order of holocarpic parasites of seaweeds. Although three *Eurychasma* species have been described, most is known about *E. dicksonii* (Fig. 5c) a widespread parasite of filamentous brown seaweeds (Greville-Briggs et al. 2011; Küpper and Müller 1999). In all phylogenetic trees where it is included, *Eurychasma* is the earliest-diverging clade (Küpper et al. 2006; Sekimoto et al. 2008a; Strittmatter et al. 2013).

Order Haptoglossales M.W. Dick

The Haptoglossales (Dick 2001) forms a second early-diverging order (Table 1, Fig. 9b), which may ultimately form a new class together with the Eurychasmales as they both appear to share a common ancestor, but always with long branch separation (Beakes et al. 2006). This monotypic order and family contains a dozen or so species, all of which are parasites of bacterivorous nematodes and rotifers (Beakes and Glockling 1998, 2000, 2002; Glockling and Beakes 2000b, c; Hakariya et al.

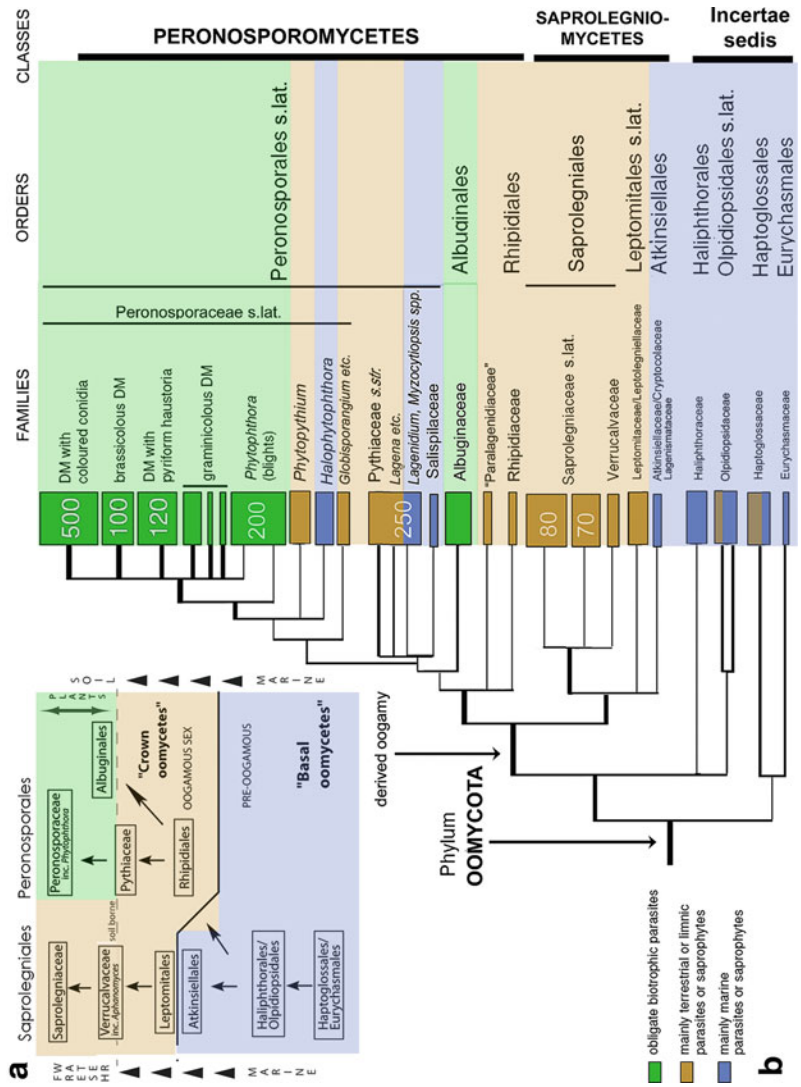

Fig. 9 Oomycete phylogeny diagrammatic summaries. (**a**) Diagram summarizing likely evolutionary path way of the Oomycota, indicating, for illustration, taxonomic clades (Adapted from Beakes et al. (2012). *Protoplasma*, with permission). (**b**) Schematic phylogenetic tree showing main taxonomic clades with an indication of taxon diversity (numbers in *boxes*) and predominant ecology of clades

2002, 2007). *Haptoglossa* (Figs. 2f, 3a, b, 5) is unusual amongst the genera in the early diverging clades of Oomycota in that it is a predominantly terrestrial genus, although *H. heterospora* has also been reported to infect marine nematodes (Newell et al. 1977). This genus produces unique infection 'gun cells' (Figs. 3b, 7q; Beakes and Glockling 1998; Robb and Barron 1982). Recent studies have revealed a number of species, such as *H. erumpens* (Beakes and Glockling 2002) and *H. heteromorpha* (Glockling and Beakes 2000c), which produce several morphological types of gun cells, which suggest they may have evolved to infect multiple hosts. Species within *Haptoglossa* clade also appear deeply diverging (Hakariya et al. 2007) and this genus will require revision.

Order ~Olpidiopsidales s. lat. M.W. Dick

The ~Olpidiopsidales (Fig. 5e–g) as currently defined is a paraphyletic or polyphyletic order of predominantly marine genera that are mostly parasites of marine algae (Fig. 5e–f). This order traditionally encompased three families, the Olpidiopsidaceae, Sirolpidiaceae and Pontismataceae (Dick 2001) but so far only representatives of the first family have been sequenced. The different species of marine *Olpidiopsis* for which sequence data have so far been published fall into two closely related clades, one with *O. porphyrae* and *O. pyropiae* (Klochclova et al. 2015; Sekimoto et al. 2008b) and the second with *O. bostrychiae* and *O. feldmanni* (Fletcher et al. 2015; Sekimoto et al. 2009) (Table 1). However, the type of the genus, *O. saprolegniae,* a freshwater endoparasite of saprolegniaceous water moulds (Bortnick et al. 1985), does not form a monophyletic clade with the marine species (Sekimoto and Inaba, unpublished sequences). This means the marine species will most likely have to be renamed. Recently, Gachon and colleagues (personal communication) have shown that two *Anisolpidium* species (*A. ectocarp, A. rosenvingei*) also forms a discrete clade nested between the marine *Olpidiopsis* spp. and the "Haliphthorales" clade. Therefore, it seems likely that as currently constituted even the genus *Olpidiopsis* is probably polyphyletic and will need significant revision, with new genera names required for the marine species.

Order "Haliphthorales"

The "Haliphthorales" (Figs. 2j–m, 5h) has not been formally described and among others contains the parasites of marine crustacea, *Haliphthoros* and *Halocrusticida* (renamed as *Halodaphnea* by Dick in 1998, but without supporting molecular data). These species can be cultured on agar media, have constricted segmented thalli (Hatai 2012; Hatai et al. 1980, 1992; Sekimoto et al. 2007), and form rather long (often >100 um) hyphal like discharge tubes (Fig. 5j). At present a single order (not as yet not formally described) and family (Haliphthoraceae) contains three or four poorly circumscribed genera (Sekimoto et al. 2007), including the recently described parasite of abalone, *Halioticida* (Maurosa et al. 2009). *Haliphthoros* as currently recognised appears to be a paraphyletic genus, with some "*Haliphthoros*-like" isolates apparently occuring within the crown Oomycota clade close to *Atkinsiella* (Sekimoto et al. 2007; Gachon, personal communication). Clearly much more research is required on this order.

It also seems possible that *Petersenia* and *Pontisma* in the Pontismataceae and *Sirolpidium* in the Sirolpidiacae will also turn out to be related to these two early-diverging marine orders or the basal lineages of the Saprolegniomycetes, currently they are placed as orders *incertae sedis* until sequence data become available (Taxonomic Summary; Table 1). The Ectrogellaceae (Dick 2001; Karling 1981) has been traditionally considered as part of the Saprolegniomycete line (Sparrow 1973, 1976) and also forms 'naked' plasmodial thalli in their diatom hosts similar to *Lagenisma* (Raghukumar 1980 – see below). However *Ectogella* has not yet been sequenced and therefore the Ectrogellaceae must also be considered as a family *incertae sedis*.

Class Saprolegniomycetes Thines et Beakes

The Saprolegniomycetes (Table 1; Fig. 9b), are characterized by the formation of two morphologically distinct generations of zoospore or aplanospore (Figs. 6c, 7a, d), a phenomenon usually referred to as diplanetism (see Dick 2001; Johnson et al. 2002). Fully differentiated zoospores or aplanospores are released directly from the sporangium (Fig. 6g, h). Both zoospores (Figs. 6f–h, 7b, d) and oospores are formed as a result of centrifugal cleavage (Fig. 8a) without the differentiation of a peripheral periplasmic layer of cytoplasm. Saprolegniomycetes are able to synthesize the sterols they require for oogenesis and generally utilize ammonium as a source of nitrogen and may also use organic sulphur (Gleason 1976). We have taken a conservative approach to their taxonomy, recognizing three orders within the class, the "Atkinsiellales", Leptomitales s. lat., and Saprolegniales (Fig. 9, Table 1).

Order "Atkinsiellales" and closely related taxa.

The order Atkinsiellales contains a handful of relatively little studied parasites of marine crustaceans and terrestrial invertebrates and contains two families as defined by Dick (1998, 2001), the Atkinsiellaceae and Crypticolaceae. *Atkinsiella dubia* forms a highly distinct clade (Fig. 16) at the base of the Saprolegniomycetes (Cook et al. 2001; Sekimoto 2008; Sekimoto et al. 2007, Thines et al. 2015a). A second species, *Atkinsiella entomophaga,* a parasite of dipteran larvae described by Martin (1977), was transferred by Dick (1998) to the previously monotypic genus *Crypticola*. The latter had been created for *C. clavulifera,* a parasite of mosquito larvae described by Frances et al. (1989). *C. clavulifera* forms a clade with *A. dubia* in *cox*2 analyses (Deborah Hudspeth, personal communication), which suggests the Crypticolaceae should also be included in this order, although family cirumscriptions require more data.

The diatom pathogen *Lagenisma coscinodisci,* which Dick (2001) placed in its own family, the Lagenismataceae, has been shown to form an early diverging Saprolegniomycete clade with some affinity to *Atkinsiella* (Thines et al. 2015a). We have therefore included this family in the Atkinsiellales (Table 1). The paraphyletic genus *Chlamydomyzium* (Dick 2001), which has both Saprolegniomycete and Peronosporomycete characteristics (Glockling and Beakes 2006b; Beakes et al. 2014), also forms clades amongst these early diverging Saprolegniomycete genera (Beakes et al. 2006; Beakes et al. 2014a). Isolates of the genus *Cornumyces* obtained

from keratin baits appears to be closely related to the nematode parasite *Chlamydomyzium* (Fig. 2o; Inaba unpublished trees) as well as to the Leptomitales clade (Inaba and Hariyama 2006). Dick (2001) also transferred *Lagenidium pygmeaum* to *Cornumyces* in absence of molecular data supporing this. He considered *Cornumyces* might belong in the Leptolegnielliaceae for which there is as yet no supporting sequence data. It is clear that much more work is required on these little studied basal Saprolegniomycetes before their formal taxonomy can be fully resolved.

Order Leptomitales Kanouse

The Leptomitales is a long-standing order that formerly included two families, the Leptomitaceae and Rhipidiacae (Dick 1973a; Sparrow 1960). These were separated into two orders by Dick (2001), and the Rhipidiales are now thought to be members of the Peronosporomycetes (Hudspeth et al. 2003; Thines et al. 2009c). The revised Leptomitales encompasses four small families, the most familiar of which are the Leptomitaceae, which are commonly known as sewage fungi. The Saprolegniomycete characteristics of *Apodachlya* and *Leptomitus* had long been been recognized (Beakes 1987) and sequence data confirms they form an early diverging clade within the class (Petersen and Rosendahl 2000). Recently the anamorphic genus *Blastulidium paedophthorum*, a parasite of freshwater cladocerans, has been confirmed to be in a clade close to *Apodachlya* and *Leptomitus* (Duffey et al. 2015), which confirms Dick's placement in the Leptomitales. To date no sequence data exists for any member of the Ducellariaceae and Letolegnielliaceae that Dick (2001) also included in the Leptomitales. These families contain a number of rarely encountered, holocarpic genera (*Aphanodictyon, Aphanomycopsis Brevilegniella, Ducellaria, Leptolegniella, and Nematophthora*) that have been mainly been documented by Karling (1981).

Order Saprolegniales E. Fisch.

The Saprolegniales is one of the largest and longest-established orders (Sparrow 1960, Dick 1973b) and forms a well-supported monophyletic clade (Dick et al. 1999; Inaba and Tokumasu 2002; Léclerc et al. 2000; Petersen and Rosendahl 2000; Riethmüller et al. 1999; Spencer et al. 2002; Steicow et al. 2014). Beakes et al. (2014a) suggested this order should be divided into three family level clades: a redefined Verrucalvaceae, the "Achlyaceae" and a re-circumscribed Saprolegniaceae sensu stricto. Dick et al. (1999) had introduced the family Leptolegniaceae which encompassed the genera *Aphanomyces, Plectospira* and *Leptolegnia*. Unfortunately, the inclusion of *Leptolegnia* with these other two genera is not well supported by most molecular studies (e.g., Arcate et al. 2006; Léclerc et al. 2000; Petersen and Rosendahl 2000; Steicow et al. 2013, 2014). Furthermore subsequent molecular studies have also shown that the grass pathogens, *Pachymetra* and *Verrucalvus*, which Dick et al. (1988) had placed in their own family, the Verrucalvaceae, also fall within the *Aphanomyces* clade (Hudspeth et al. 2003; Riethmüller et al. 2002; Telle and Thines, unpublished data). Therefore the family name Verrucalvaceae should take precedence over Leptolegniaceae. This clade is characterized by having species

with narrow hyphae and, when formed, relatively undifferentiated sporangia (Fig. 3f). Genera in this clade are predominantly soil-borne, root-infecting parasites, saprotrophs or animal parasites (Fig. 3e–g; Dick et al. 1984, 1988; Diéguez-Uribeondo et al. 2009; Johnson et al. 2002; Levenfors and Fatehi 2004; Lilley et al. 1998). The Verrucalvaceae also includes the nematode-trapping genus *Sommerstorffia* (Spies and Levesque, unpublished sequence data) as well as the recently described rotifer parasitic genus, *Aquastella* (Fig. 3d; Molloy et al. 2014). The genera *Aphanomyces* and *Plectospira* both form clusters (balls) of primary aplanospores (Fig. 6c), a feature shared with *Somerstorffia* (Johnson et al. 2002). All the genera form uni-oosporiate oogonia with more or less plerotic oospores, which in *Verrucalvus* have prominent verrucose ornamentation (similar to shown in Fig. 8n, o; Dick et al. 1988).

Although the branching order of the proposed family clades in the Saprolegniales is not well-resolved statistically, morphological and molecular evidence points to the recircumscribed Verrucalvaceae as the basal family in the Saprolegniales. A comprehensive molecular phylogenetic study of the genus *Aphanomyces* has shown that saprotrophic species, animal parasites and plant pathogens separate into three well supported sub-clades (Diéguez-Uribeondo et al. 2009). Dick et al. (1984) controversially also placed the graminicolus downy mildews in the Verrucalvaceae (Dick 2001) but this is not supported by molecular sequence data (Table 1; Hudspeth et al. 2000, 2003; Léclerc et al. 2000; Riethmüller et al. 1999, 2002; Thines et al. 2008).

The diverse genera of saprotrophic "water moulds" were traditionally all placed in a single family, the Saprolegniaceae containing a dozen or so genera (Table 1; Johnson et al. 2002; Sparrow 1960). Different genera were largely defined by their pattern of zoosporogenesis and asexual spore formation (Fig. 6d–h; Dick 2001; Johnson et al. 2002). However, it seems the best predictor of family-level relationships in the Saprolegniaceae is whether their mature oospores have centric/subcentric (as in Fig. 8k) or eccentric (as in Fig. 8l, m) organization (Léclerc et al. 2000; Spencer et al. 2002; Inaba and Tokumasu 2002). In some analyses (Inaba and Tokumasu 2002) genera with centric or subcentric oospores (*Aplanes, Aplanopsis, Calyptralegnia, Protoachlya, Newbya* and *Saprolegnia*, and possibly *Leptolegnia*) can be separated from those which produce strongly eccentric oospores (*Achlya* s. str., *Brevilegnia*, *Dictyuchus*, *Isoachlya*, and *Thraustotheca*). In the genus *Saprolegnia*, the mature ooplast often contains granules in Brownian motion as a result of the liquifaction of the matrix (Fig. 8k, g). However, even the archetypal water mould genus *Saprolegnia* is apparently not monophyletic, although molecular phylogeny is beginning to help resolve species boundaries (Diéguez-Uribeondo et al. 2007; Hulvey et al. 2007; Inaba and Tokumasu 2002; Sandoval-Sierra et al. 2014). Although we suggested a new family, the "Achlyaceae", might be warranted for the clade containing genera with strongly eccentic oospores, recent publications suggest this may be an an oversimplistic solution (Steciow et al. 2013, 2014; Sandoval-Sierra et al. 2014). Therefore we have decided not to formally split the Saprolegniaceae in this account (Table 1, Fig. 9b). Clearly further work is required before this large and complex family is formally split into well supported families.

Class: Peronosporomycetes M.W. Dick

The Peronosporomycetes are predominantly a terrestrial class. Most have a mycelial fungus-like thallus, although there are holocarpic species and many of the Rhipidiaceae have constricted thalli of determinate growth. Peronosporomycetes have been reported to have a requirement for exogenous sterols to complete oogenesis (Kerwin and Washino 1983) and the non-obligate pathogens of plants are able to utilize sulphate and variable nitrogen sources (Gleason 1976; Dick 2001), while there seems to be a tendency that non-obligate animal parasites and obligate plant parasites have defects in the pathways for the acquisition of inorganic nitrogen and sulfur (Baxter et al. 2010; Kemen et al. 2011; Sharma et al. 2015b). Peronosporomycetes produce only secondary type zoospores (Fig. 7i), which are differentiated within or transiently released into an evanescent extrasporangial vesicle in several genera (Fig. 6m). They have mono-oosporic oogonia in which the single oosphere is surrounded by a layer of periplasm (Fig. 3c, e, i; Dick 2001). Mature oospores often have complex multilayered walls (Fig. 3h, s) and a homogeneous (ooplast) vacuole (Fig. 3i).

Dick (2001) included the orders Rhipidales, Pythiales and Peronsporales within his Peronosporomycotina sub-class. Subsequent molecular studies revealed the white-blister rusts, form a separate basal order (the Albuginales) in their own right (Thines and Spring 2005). Many molecular studies suggest that the order level separation of the Pythiales and the Peronsporales along the lines proposed by Dick (2001) is not supported statistically (see discussion in Beakes et al. 2014a) and some genera, such as *Phytophthora*, were incorrectly placed (Hulvey et al. 2010; Thines et al. 2009a,). Furthermore, unpublished multigene sequencing of genera, is revealing much more diversity amongst the lagenidiaceous and pythiaceous species than has hitherto been suspected (Spies et al. 2014, 2016). However, until more statistically robust multigene sequence data are publically available, as in our previous review, we have adopted the historical position of including all these genera, into a single all-encompassing Peronosporales s. lat. and not suggested new orders and families (Fig. 16, Table 1) to account for a probably paraphyletic Pythiaceae. However, we feel that the recognition of a broad Peronosporales might be preferable over the creation of several new ill-defined orders. At least one clade, that contains the unusual recently-described lagendiaceous mycopathogen of dogs, *Paralagenidium karlingi* (de Grooters et al. 2013), appears to be located between the Rhipidiales and Albuginales and will will probably need to be placed in its own Order and Family (Table 1).

Order Rhipidiales M.W. Dick.

The Rhipidiales consists of a single family, the Rhipidiaceae, containing a small number of saprotrophic genera (Table 1), which often grow on submerged twigs and fruits. Many have determinate, often segmented, thalli with only a few genera showing typical hyphal growth (e.g., *Sapromyces*, Fig. 2p). Some genera, such as *Rhipidium,* have thalli that are anchored to their substrate by rhizoid-like structures (Dick 2001; Sparrow 1960). They typically produce uni-oosporiate oogonia with a

well differentiated periplasm (Sparrow 1960). To date only *Sapromyces elongatus* has been sequenced (Table 1). The phylogenetic placement of this species in phylogenetic trees has proven difficult and varies depending upon the gene sequenced and which other taxa are included in the analyses. Riethmüller et al. (1999) and Petersen and Rosendahl (2000) inferred a position basal to the 'saprolegnian line' in their LSU rDNA analyses, whereas Hudspeth et al. (2000) report it to form the basal clade to 'peronosporalean line'. The COII amino acid sequence derived from from the *cox*2 gene, showed that *Sapromyces* has the same signature amino acid insertion-deletion (indel) sequence (LEF/T) to that found in members of the Peronosporales s.l., and not the YTD indel sequence found in members of the Leptomitaceae (Hudspeth et al. 2000, 2003; Cook et al. 2001). It is clear that much work still needs to be done to resolve the precise relationships between families and genera that appear at the base of both main classes.

Order Albuginales Thines

Traditionally, the white blister rusts, the Albuginales (Fig. 5), were placed together with the downy mildews in the Peronosporales (Beakes 1987; Dick 2001). They are obligate pathogens of angiospermae producing small stalked globose haustoria (Coffey 1975; Mims and Richardson 2002, Soylu et al. 2003). They form blister-like lesions on the leaves (Fig. 4f, i) below the host epidermis in which the basipetal chains of deciduous conidiosporangia are borne on club-shaped sporogenous hyphae (Fig. 4g, h; Heller and Thines 2009). Molecular phylogenetic studies revealed that the white blister rusts form a well supported clade basal to the Peronosporales s. lat. (Fig. 9b; Hudspeth et al.; 2003, Riethmüller et al. 2002; Thines et al. 2009c). This clade has been given its own order designation, the Albuginales (Thines and Spring 2005), containing just one family, the Albuginaceae (Table 1). Members of this family have exceptionally thick, multilayered oospore walls (Stevens 1901; Tewari and Skoropad 1977; Beakes 1981), the outer layers of which appear to be mainly derived from the periplasm. Recent molecular studies have also revealed an unsuspected genetic diversity within this order (Choi et al. 2007, 2008, 2011; Mizaee et al. 2013; Ploch et al. 2010; Ploch and Thines 2011; Rost and Thines 2012; Thines and Voglmayr 2009; Thines et al. 2009c; Voglmayr and Riethmüller 2006) and two new genera, *Pustula* and *Wilsoniana,* have been established based upon conidiosporangium and oospore characteristics (Thines and Spring 2005). These three genera appear to be restricted to specific host orders or subclasses (Thines and Voglmayr 2009). It is also expected that more comprehensive taxonomic re-arrangement of this family will be required as more species and isolates are sequenced.

Order Peronosporales E. Fisch. s. lat

The order Peronosporales s. lat. (Waterhouse 1973) contains a large number of often diverse taxa (Table 1), presently placed in three families, the Salispiliaceae, ~Pythiaceae s. lat. and Peronosporaceae s. lat. (Beakes et al. 2014a). This classification has to be considered provisional, as many lagenidiaceous species have not yet been included in published molecular phylogenies. Within the Peronsporales s. lat.

There have been many published molecular phylogenetic studies on the important plant pathogenic genera (*Pythium*: de Cock et al. 2012; Lévesque and de Cock 2004; *Phytophthora*: Blair et al. 2008; Cooke et al. 2000; Kroon et al. 2004; Martin et al. 2014) and various downy mildew genera (Göker et al. 2003, 2004, 2007; Thines et al. 2009a, b; Voglmayr 2003; Voglmayr et al. 2004). The saprotrophic genera have been less well documented, but there have been accounts of the molecular phylogeny of *Pythiogeton* (Huang et al. 2012), *Phytopythium* (de Cock et al. 2015) and *Halophytophthora* (Nakagiri 2002), but molecular data for the "lagenidiaceaous" holocparic genera is sparse and incomplete (Beakes et al. 2006; Schroeder et al. 2012).

The Salispiliaceae is single genus family which forms a well-supported early-diverging clade in the Peronsporales s. lat. based on concatenated ITS and LSU sequences (Hulvey et al. 2010). They are saprotrophs isolated from salt marshes, with ovoid sporangia and smooth walled oogonia and oospores. However, unpublished trees based on an analysis of 16 genes do not support a basal phylogenetic position of this genus within the Peronsporales s.lat. (see Table 1; Spies et al. 2014 and personal communication). The ~Pythiaceae s. lat. as we have defined it (Beakes et al. 2014a) encompasses more than a dozen genera, including a many of holocarpic genera that were traditionally placed in the Lagenidiales (Table 1, Fig. 9b). However, a recent unpublished multigene analysis of a significant number of isolates identified as *~Lagenidium*, *~Lagena*, *~Myzocytiopsis, Pythiogeton, ~Pythium* and *Salilagenidium* has revealed at least six clades that may ultimately justify family level designation (Spies et al. 2014, 2016, and unpublished trees - summarised in Table 1). There are still a number of Pythiaceous genera, such as *Medusoides* described by Voglmayr et al. (1999) and placed by Dick (2001) in his Pythiogetonaceae, for which no sequence data are publically available. *Lagenidium,* as currently recognised, is a particularly complex paraphyletic or polyphyletic genus, with isolates occuring in several different clades. However, until detailed phylogenies become available, we have retained all of these holocarpic species in a broadly defined ~Pythiaceae s. lat. (Table 1). The genus *Pythium* contains well over a hundred species, most of which have sequence data available (Bedard et al. 2006; Briard et al. 1995; Lévesque and de Cock 2004; Martin 2000; Schurko et al. 2004; Villa et al. 2006). Lévesque and de Cock (2004) recognised 8 clades (A-K) of *Pythium*, some of which are now assigned to new genera (Bala et al., 2010; de Cock et al. 2015; Usuhashi et al. 2010). However, as the relationships of these clades have not been fully resolved, most are subsumed under *Pythium* s. lat. in this review. Species which have simple more or less filamentous sporangia now constitute the genus *Pythium* s. str. (Usuhashi et al. 2010) although some genera, including the animal pathogen *P. insidiosum* cluster with *Pythiogeton* (Huang et al. 2012).

The Peronosporaceae s. lat. family (Table 1, Fig. 9b) includes not only the hyperdiverse downy mildews, but a number of genera that had been been previously included in the Pythiaceae (Dick 2001). These include the genus *Phytopythium* (syn. *Ovatosporangium*, Usuhashi et al. 2010; formerly known as the *Pythium* K-clade, Lévesque and de Cock 2004) described by Bala et al. (2010) and which has been recently monographed by de Cock et al. (2015). A recent multigene analysis also

suggests that two other of the new pythiaceous genera introduced by Usuhashi et al. (2010), *Elongisporangium* and *Globisporangium* might also fall in the Peronosporaceae s. lat. clade (Spies et al. 2014, 2016). The polyphyletic marine genus ~*Halophytophthora* (Ho and Jong 1990; Ho et al. 1992; Nakagiri 2002) contains around 15 species many of which, including the type species, fall into a clade that sits between the *Phytopythium* and the *Phytophthora*/downy mildew assemblage. ~*Halophytophthora* spp. have ovoid to elongate sporangia, often with conspicuous papillar plugs (Nakagiri 2002, Nakagiri et al. 1994) and most show a transient vesiculate discharge of their zoospores (Fig. 6l). All have single-oospored oogonia with paragynous antheridia (Nakagiri 2002, Nakagiri et al. 1994). *Phytophthora* clades are probably paraphyletic with the hyperdiverse downy mildews, which appeared to have evolved from a clade of shoot- and leaf-infecting *Phytophthora* spp. (Cooke et al. 2000, Runge et al. 2011). Most *Phytophthora* taxa (Fig. 4a–e) have sequence data available (Blair et al. 2008; Brouwer et al. 2012; Cooke et al. 2001; Förster et al. 2000; Kroon et al. 2004; Martin and Tooley 2003a, b; Runge et al. 2011; Villa et al. 2006) and fall into 8 to 10 clades (usually referred to as groups). The clades can be broadly separated into two main evolutionary lines, encompassing those species (groups 6–8; Cooke et al. 2000) with non-papillate sporangia (e.g., *Ph. cinnamomi*; Fig. 4c) which are predominantly soil borne root or woody trunk infecting pathogens and those (Groups 1–5; Cooke et al. 2000) which have papillate sporangia (e.g., *Ph. infestans*) that often infect aerial foliage. Traditional morphological characters such as the morphology of the male antheridium and whether species are homo or heterothallic are not good markers of phylogenetic relatedness (Blair et al. 2008; Brouwer et al. 2012; Cooke et al. 2000; Kroon et al. 2004; Runge et al. 2011). In a recent phylogenetic analysis based upon whole genomes, albeit of the very restricted number of five taxa, Seidl et al. (2012) concluded that the downy mildews (represented by *Hyaloperonospora*) were sister to the *Phytophthora* clade rather than embedded within it, with the nonpapillate/semipapillate *Ph. sojae* and *Ph. ramorum* species forming a clade that was sister to the papillate *Ph. infestans* as in the analysis of Runge et al. (2011). In a recent phylogenomic analysis Sharma et al. (2015a) inferred again a sister-group relationship for *Hyaloperonospora* and *Phytophthora*, but also found that *Plasmopara halstedii* was embedded within the latter, highlighting the need for a an expanded taxon samping in future phylogenomic analyses, as the current taxon sampling is probably too low to infer robust phylogenomic trees, despite the generally high to maximum-support observed in these analyses.

The downy mildews (Fig. 4q–v) are a diverse, monophyletic, group currently encompassing 20 genera (Table 1) that are obligate parasites, predominantly of dicotyledons (Göker et al. 2007; Thines et al., 2009a, Thines 2014). Because of their importance as biotrophic plant pathogens they have been extensively studied and sequenced for phylogenetic analyses (Table 1; Göker et al. 2003, Göker et al. 2007; Riethmüller et al. 2002; Sökücü and Thines 2014; Telle and Thines 2012; Telle et al. 2011; Thines et al. 2008, 2009a; Voglmayr 2003). Downy mildews typically produce deciduous conidiosporangia (Fig. 4s) are that born on persistent conidiosporangiophores (Fig. 4u, s, v), although these may be evanescent in the

graminicolous genera *Baobabopsis*, *Eraphthora*, *Peronosclerospora*, *Sclerophthora*, and *Sclerospora* (Fig. 4n–p; Thines 2006, 2009, Telle and Thines 2012, Thines et al. 2015b). *Peronospora* and *Pseudoperonospora* have pigmented conidia and consititute the most species-rich downy mildew clade (Table 1). Features such as haustorium morphology map well onto the molecular clades (Göker et al. 2007; Thines 2006; Voglmayr et al. 2004). Downy mildews with pyriform haustoria (DMPH) form a monophyletic lineage (Fig. 9). Digit-like (hyphal) haustoria (e.g., *Peronospora viciae*; Beakes et al. 1982; Hickey and Coffey 1977, 1978) probably represent the ancestral state and are similar to those formed in *Phytophthora* (Coffey and Wilson 1983). Molecular studies have confirmed that the graminicolous downy mildew (GDM; Fig. 4n–p) genera (*Baobabopsis*, Thines et al. 2015b; *Eraphthora*, Telle and Thines 2012; *Peronosclerospora,* Hudspeth et al. 2003; Shivas et al. 2012; *Sclerophthora,* Thines et al. 2008; *Sclerospora,* Riethmüller et al. 2003) are all related to other downy mildews in the Peronosporaceae sensu *lato.* Three monotypic GDM genera, *Graminivora*, *Poakatesthia* and *Viennotia* (Göker et al. 2003, Thines et al. 2006, Thines et al. 2007) appear to exhibit characteristics intermediate between *Phytopththora* and the downy mildews sensu stricto (Thines 2009).

Maintenance and Cultivation

Saprophytic or facultative parasitic species of Oomycota can be collected very easily from soil and water, and obligate hyperparasites are sometimes found at the same time. Useful sources of information on suitable methods for isolating and culturing aquatic fungi are given by Dick (2001), Fuller and Jaworski (1987), Johnson et al. (2002) and Sparrow (1960). Obligate parasitic downy mildews and white blister rusts must be sought on their known angiosperm hosts, but the less host-specific root parasites can be isolated using various plating and baiting techniques. Reference should be made to papers cited in Karling (1981) for information on the collection of the less-known species of Oomycota. A useful source of information for collecting and maintaining hemibiotrophic species is found in Erwin and Ribeiro (1998).

Typically many species of Saprolegniaceae and a variety of *Pythium* species can be isolated from samples of soil or exposed or submerged mud by placing suitable baits (e.g., 3 or 4 autoclaved hempseeds, sesame seeds, or snakeskin scales) added to sediment slurries diluted with sterile pond water (Dick 2001; Dick and Ali-Shtayeh 1986; Fuller and Jaworski 1987; Sparrow 1960). These dishes should be left undisturbed for 1–3 days at 10°–20 °C. The baits should then be transferred to clean dishes of water and incubated at 10°–20 °C for a further 4–14 days. A wide range (about 40 species) of *Pythium* species has been isolated from soil using a dilution plate procedure (Al-Shtayeh et al. 1986; Dick and Al-Shtayeh 1986). Several species of *Phytophthora* can be isolated by dilution plate techniques using P_{10} PV hymexazol agar (for recipes see Erwin and Ribeiro 1998). Dilutions between 1:30 and 1:100 are recommended for infested soils. The same medium can be used for isolations from infected roots. Since *Mortierella* and *Pythium* are inhibited by hymexazol, the aliquots can be incorporated into the nutrient agar and the washing

stage outlined above is not needed. Incubation is at 25 °C and scanning of plates is carried out after 1–3 days of incubation. Baiting, e.g., with *Rhododendron* and other leaves is a common procedure to isolate leaf-infecting *Phytophthora* species.

For the collection of Rhipidiaceae, in situ baiting techniques are essential. A cage of plastic-coated wire mesh containing fruits (e.g., apples, oranges, tomatoes) is suspended just below the water surface or just above the bottom mud in shallow stagnant or slow-moving water for about 10 days. The fruit is then removed and the fungal pustules examined with a dissecting microscope. Filamentous oomycete saprophytes will also be found. Using selective keratin and chitin baits, species that may be parasites of nematodes and other invertebrates are often selectively isolated (Sally Glockling and Shigeki Inaba, personal communication).

A wide variety of agars is used for culturing these oomycetes, including ones based on glucose, peptone and yeast extract (GYP); glucose, soluble starch, and yeast extract; potato dextrose; potatos and carrots; V8-juice; cornmeal, and others. Agars incorporating up to 10 mg/1 of cholesterol are also used: the carrier for the sterol may be chloroform, ether, or a 1% v/v aqueous solution of Tween 80. Axenic cultures are usually achieved by using several cleansing steps, such as by growing through a Raper's ring. For more details, the reader is referred to Fuller and Jaworski (1987) and Tsoa (1970). Members of the Saprolegniaceae are often stored on infested hemp seeds in distilled water, or on infested hempseeds placed on sterilized dampened filter paper in sterile bottles (Clark and Dick 1974).

Obligate biotrophic species, like the downy mildews and the white blister rusts have so far not been grown on artificial media. There is an account of axenic cultures of graminicolous downy mildews (*Sclerophthora* and *Sclerospora*, cited in Thines 2009), which could apparently not be successfully repeated so far. Other downy mildews and white blister rusts can be maintained in the laboratory by using infected leaves to inoculate detached uninfected leaves or leaf disks of the host species with the spores from the former (e.g., by stamping onto moist leaves or spraying). After inoculation, leaves should be kept dark for 24 hours at moderate temperatures. After that, the inoculated leaves or leaf discs should be kept at 100% relative humidity and at moderate temperatures (10–20 °C depending upon the species) and light quality as close as possible to those encountered under natural field conditions and a regular day-night photoperiod cycle. White blister rusts usually have to be cultivated on whole plants and most do not tolerate high humidity during sporulation.

Evolutionary History

The Straminipila form a well-supported monophyletic clade that is sister to the alveolates (Keeling et al. 2005) within the larger SAR superkingdom (Burki et al. 2007, 2008; Burki and Keeling 2014). In analyses using multiple protein-encoding genes the Oomycota and Hyphochytiomycota appear to form a sister clade to the brown-pigmented photosynthetic algae, the Ochrophyta (Cavalier-Smith and Chao 2006; Rilsberg et al. 2009; Tsui et al. 2006). Together this monophyletic assemblage was sister to a second major heterokont clade which encompasses the fungal-like

Thraustochytrids and Labyrinthulids and the bacteriotrophic bicoecid flagellates (Beakes et al. 2014; Yubuki et al. 2010). It has been estimated that the stem origin of the Ochrophyta was around 571 million years ago (mya) although with a large margin of error (Brown and Sorhannus 2010). The Oomycota and Hyphochytiomycota probably evolved after this, which is consistent with previous molecular clock estimates had suggested the origins of the Oomycota lay somewhere between 524 and 1000 mya (Bhattacharya et al. 2009). Recent molecular clock analyses by Matari and Blair (2014) proposes that the modern pathogenic oomycetes originated around the mid-Paleozoic, approximately 430–400 mya, although they did not include data from any early diverging genera in their analyses.

From earlier single gene analyses, the marine flagellate genus *Developayella* forms the sister clade to the Oomycota (Leipe et al. 1996: Tong 1995), although they have apparently little in common. When Sekimoto (2008) included the 18S sequences derived from assorted unknown stramenopiles from diverse marine ecosytems (Diéz et al. 2001; Massana and Pedró-Alió 2008; Massana et al. 2002, 2004, 2006) in his phylogenetic analyses the heterokont tree topography was markedly altered. An unknown stramenopile clade (lineage 3), consisting of a dozen or so rather deeply branched sequences, formed the sister clade to the Oomycota, although with little statistical support. *Developayella*, clustered in a clade with the flagellate parasitoid *Pirsonia* and the Hyphochytridiomycota and formed the immediate sister clade to the Ochrophyta rather than the oomycetes. Molecular studies have also revealed that most early diverging genera are marine and many are parasites of seaweeds or marine crustaceans (Beakes and Sekimoto 2009; Beakes et al. 2011). This, together with the fact that most of their closest relatives are also marine (Tsui et al. 2006), supports the current view, contrary to that of Dick (2001), that the Oomycota are marine in origin, as saprotrophs or facultative pathogens (Beakes and Sekimoto 2009; Beakes et al. 2012, 2014a).

Molecular studies have confirmed that the Oomycota are monophyletic and have provided a sound framework for hypothesising likely evolutionary pathways within the phylum. A simplified scheme is presented in Fig. 9a. This shows that the evolutionary scheme originally proposed by Bessey (1942), in which the holocarpic Olpidiopsidaceae were evolving prior to the split of the Saprolegniaceae and Peronsporaceae, was remarkably perceptive. We now know that the earliest-diverging clades contain predominantly small, non-mycelial, holocarpic oomycete genera (Beakes et al. 2014a; Karling 1981; Sparrow 1960), none of which have been successfully cultured on artificial media. This suggests this was the likely thallus form of the ancestral Oomycota. Genera in the Haliphthorales, Atkinsiellales s.lat. (*Atkinsiella, Lagenisma*), Leptomitales s.lat. (*Apodachlya, Blastulidium, Chlamydomyzium, Leptomitus*) and Rhipidiales (*Araiospora, Rhipidium, Sapromyces*) all produce extensive, bulbous or constricted thalli (Beakes et al. 2014a), which appears to be the intermediate stage in the evolution of a more-typical branched mycelial thallus that may have occurred about the time, or shortly after, of the Saprolegniomycete-Peronosporomycete divergence. It may have been the development of long, apically extending, hyphal-like discharge tubes in genera such as *Haliphthoros* (Fig. 5j) and *Atkinsiella* that led to the hyphal thallus form, at least in the Saprolegniomycete clade.

Analysis of the host preferences in basal Oomycota also raises the possibility that these organisms might have migrated from the sea to the terrestrial/freshwater environment with their invertebrate or algal hosts. Once on land they may have switched to plant hosts, as evidenced by the morphological similiarity between nematode-infecting species of the genus *Myzocytiopsis*. (Glockling and Beakes 2006a) and the closely related (Spies, personal communication) root-infecting genus *Lagena* (Barr and Désaulniers 1987, 1990). However, it should also be borne in mind that as long as the oomycete communities in marine and estuarian detritus remain largely unexplored (Nigrelli and Thines 2013; Marano et al. 2016), other evolutionary scenarios, such as the multiple independent development of a parasitic lifestyle from saprophytic genera cannot be ruled out. The same is also true for the likelihood of the repeated transition of oomycetes from land to the sea and vice versa (Richards et al. 2012), which has occurred several times within the Peronosporomycetes (Marano et al. 2016; Thines 2014). However, on balance it seems plausible that, at least initially, oomycetes evolved in the sea from holocarpic nutritionally-versatile organisms, many of which were facultative parasites of either invertebrates and or algae.

With the possible exception of the freshwater *Olipidiopsis* spp. (Martin and Miller 1986c), all basal genera lack oogamous sexual reproduction. However, recently a sexual cycle involving conjugation of adjacent cysts or thalli has been reported in *Eurychasma,* although only on some hosts (Gachon et al. 2015), and also occurs in *Anisolpidium ectocarpi* (Johnson 1957), a species now known to be a basal oomycote (Gachon et al. 2015). The recent finding that *Lagenisma*, which also reproduces by means of conjugating meiocysts (Schnepf et al. 1977, 1978a), is a basal Saprolegniomycete (Thines et al. 2015b), could mean that oogenesis may have evolved independently in the two classes of Oomycota. This may also explain the fundamentally different morphological patterns of oosphere formation in the two classes.

A critical evaluation of the fossil evidence for ancient terrestrial oomycetes is given in a recent review by Krings et al. (2011). Stidd and Consentino (1975) describe structures that they suggested represented *Albugo* oospores in the megagametophyte seed tissue of an ancient gymnosperm, *Nucellangium glabrum,* from around 310 mya. However the structures that were described were not conclusively *Albugo* oospores (Krings et al. 2011). A more convincing, though still controversial, *Albugo*-like microfossil appears to be *Hassiella monosperma* from the 412 mya lower Devonian Rhynie chert (Taylor et al. 2006). Structures purported to be small oogonia in *Hansiella* fossils look much more like the small globose haustoria that are typical of the genus *Albugo*. If this fossil is accepted as representing an obligately biotrophic *Albugo*-like pathogen of Rhyniophyte plants, it would mean that the evolution of obligate biotrophy can be traced back nearly 400 mya, which accords with recent molecular clock deductions (Matari and Blair 2014). Obligate symbiotrophy exemplified by the Albuginales, is therefore of ancient origin and must have evolved independently at least twice in the oomycete lineage (Kemen and Jones 2012; Kemen et al. 2011; Thines and Kamoun 2010). All extant white blister rusts are obligate parasites of angiosperms and the latter only diversified from a

common ancestor about 150 mya, even though they can probably be traced back into the Permian. This implies that the white blister rusts have evolved on hosts other than those we know them on today.

Another fossil genus, *Combresomyces*, with spiny papillate oogonia with paragynus antheridia, resembling current-day *Pythium* species, has been recently described associated with the remains of a 300 mya seed fern, *Lygniopteris* (Strullu-Derrien et al. 2010). *Galteriella biscalitheceae* associated with a sporangium of a fern *Biscallitheca,* also from around ca 300 mya, has *Phytophthora*-like amphigynous and paragynous smooth-walled oogonia. Papillate multi-oospored oogonia, reminscent of those found in some present day genera in the Saprolegniaceae have also been found in Rhynie chert deposits from the same time period (Krings et al. 2010). Therefore by the early Mesozoic era, about 300 mya, fossils showing the complete range of oogonium morphologies found in present day genera in the Albuginales, Peronosporales, and Saprolegniales have all been documented and implies that most of the known oomycete diversity had already evolved by then, likely with the exception of the hyperdiverse downy mildews.

The hyperdiverse obligate parasitic downy mildews are thought to have evolved relatively recent from an ancestor belonging to one of the more derived shoot- and foliage-infecting *Phytophthora* clades with papillate sporangia (for an in depth discussion see Runge et al. 2011) and represent the pinnacle of oomycete diversity. Thines (2009) has also discussed a number of traits (indeterminate sporangiosphore development, intracellular hyphal development) in rare graminicolous downy mildew genera, such as *Viennotia* and *Poakatesthia,* that are shared with *Phytophthora* and suggests these may represent relicts of the evolution of downy mildews from *Phytophthora*-like ancestors on Poales.

Finally there appear to be a number of interesting evolutionary parallels between Fungi and Oomycota (Sharma et al. 2015b). The two earliest-diverging oomycete genera *Eurychasma* and *Haptoglossa*, have endobiotic plasmodial thalli and injecting infection mechanism, respectively. These features are mirrored in the early diverging cryptomycete *Rozella* and by microsporidia, respectively (Jones et al. 2011; Lara et al. 2009). The clade (MAST-1) of unknown marine stramenopiles that are the closest to the oomycetes (Sekimoto 2008; Yubuki et al. 2010) may be analogous to the recently described cryptofungal clade that appears to be the sister clade to the Fungi (Jones et al. 2011). This highlights that many phylogenetically critical organisms still remain to be described and we still have little idea what sort of organisms make up unknown stramenopile clades. They are probably being sampled from their zoospores, and it seems possibly that many are parasitoids or parasites. In the future, the systematic application of both genomics and multigene molecular phylogenetic studies should help resolve many of the unresolved evolutionary questions both within oomycetes and to their closest relatives.

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