

**Diatomophthoraceae** – a new family of olpidiopsis-like diatom parasitoids largely unrelated to *Ectrogella*

A.T. Buaya¹,², M. Thines¹,²*

¹Goethe-Universität Frankfurt am Main, Department of Biological Sciences, Institute of Ecology, Evolution and Diversity, Max-von-Laue Str. 13, D-60438 Frankfurt am Main, Germany
²Senckenberg Biodiversity and Climate Research Centre, Senckenberganlage 25, D-60325 Frankfurt am Main, Germany

*Corresponding author: m.thines@thines-lab.eu

**Key words:** biotrophic, *Ectrogella*, *Nitzschia*, oomycetes, pennate diatoms, phylogeny, new taxa

**Abstract:** The oomycete genus *Ectrogella* currently comprises a rather heterogeneous group of obligate endoparasitoids, mostly of diatoms and algae. Despite their widespread occurrence, little is known regarding the phylogenetic affinities of these bizarre organisms. Traditionally, the genus was included within the *Saprolegniales*, based on zoospore diplanatism and a saprolegnia/achlya-like zoospore discharge. The genus has undergone multiple re-definitions in the past, and has often been used largely indiscriminately for oomycetes forming sausage-like thalli in diatoms. While the phylogenetic affinity of the polyphyletic genus *Olpidiopsis* has recently been partially resolved, taxonomic placement of the genus *Ectrogella* remained unresolved, as no sequence data were available for species of this genus. In this study, we report the phylogenetic placement of *Ectrogella bacillariacearum* infecting the freshwater diatom *Nitzschia sigmoidea*. The phylogenetic reconstruction shows that *Ectrogella bacillariacearum* is grouped among the early diverging lineages of the *Saprolegniomycetes* with high support, and is unrelated to the monophyletic diatom-infecting olpidiopsis-like species. As these species are neither related to *Ectrogella*, nor to the early diverging lineages of *Olpidiopsis s. str.* and *Miracula*, they are placed in a new genus, *Diatomophthora*, in the present study.

**INTRODUCTION**

*Ectrogella bacillariacearum* (*Oomycetes, Saprolegniales, Ectrogellaceae, Ectrogella*) is an endobiotic, holocarpic, obligate parasite of freshwater pennate diatoms (Sparrow 1960). Described by Zopf in 1884, the parasite is the type species of its genus, and the genus is the type of the family *Ectrogellaceae*. Except for three green algal pathogens (*Ectrogella marina, E. lauderia*, and *E. dicksonii*) and one oomycete hyperparasite (*E. besseyi*), all species of the genus are obligate parasites of freshwater diatoms (*E. bacillariacearum, E. monostoma, E. gomphonematis, E. eunotiae, E. brachystoma, E. cyclotellae*) and marine diatoms (*E. liicmophorae, E. perforans, E. eurychasmioides*) (Zopf 1884, Petersen 1905, Scherfelf 1925, Sparrow & Ellison 1949, Friedmann 1952, Feldmann & Feldmann 1955, Dick 2001). The type species, *E. bacillariacearum* and other members of the genus in a strict sense have a saprolegnioid and achlyoid zoospore formation, *i.e.* they produce zoospores which exhibit diplanatism. This can be contrasted to the species with olpidiopsidoid or lagenidioid zoospore formation, *i.e.* members of the genera *Olpidiopsis* and *Lagenidiun* (Sparrow 1960). The genus *Ectrogella* has faced different interpretations in the past, and in the latest taxonomic treatment of Dick (2001), it was used as a catch-all for simple holocarpic diatom parasites, irrespective of their mode of zoospore formation. The taxonomic placement of the genus *Ectrogella* in the *Saprolegniales* has been questioned (Beakes & Thines 2017), because of the absence of oospores and the placement of *Eurychasma*, which was assumed to be related to *Ectrogella* (Scherfelf 1925, Sparrow 1960), and was found to be a very early-diverging lineage of the oomycetes (Sekimoto et al. 2008). To date, only five oomycete diatom parasitoids have been sequenced and included in the phylogeny of the *Oomycota* (Thines et al. 2015, Buaya et al. 2017, 2019a). Two of these were classified in the genus *Olpidiopsis* (*O. drebesii, O. giliii*) because of their placement within a monophyletic, yet unsupported *Olpidiopsidales* (Buaya et al. 2017). The parasite of some species of the centric diatom genus *Coscinodiscus, Lagenisma coscinodisci*, also previously speculated to represent an early-diverging lineage, was found to belong to the *Saprolegniomycetes*, a placement which is also supported by its diplanatism (Thines et al. 2015). In contrast, the olpidiopsidoid parasitoid of *Pseudo-nitzschia* spp. was initially suspected to be a member of either *Ectrogella* or *Olpidiopsis* (Hanic et al. 2009), but was found to be the earliest diverging oomycete lineage in Buaya et al. (2017) and consequently assigned to the new genus *Miracula* as *Miracula helgolandica*, to which a second, limnic species was recently added (Buaya & Thines 2019). A recent study (Buaya et al. 2019b) has shown that the genus *Olpidiopsis*, with its type species, *O. saprolegniae*, is largely unrelated to the diatom parasites currently placed in the genus, necessitating a taxonomic revision. However, the taxonomy of diatom-infecting oomycetes of the genera *Ectrogella, Olpidiopsis, Lagenidiun*, and *Aphanomyxopsis* is still uncertain, as no sequence data have been available for the type of *Ectrogella, E. bacillariacearum*. 

---

*Fungal Systematics and Evolution* is licensed under a Creative Commons Attribution-NonCommercial-ShareAlike 4.0 International License

© 2020 Westerdijk Fungal Biodiversity Institute

113
As a consequence, interpretations regarding the relatedness and taxonomy of these species have been largely based on their original descriptions made during the late 18th until the early 19th centuries (e.g. Cornu 1872, Zopf 1884, Petersen 1905, Scherffel 1925). Also, the few ultrastructural studies on *E. perforans, L. coscinodisci, and M. helgolandica* (Schnepl et al. 1978a, b, Raghu Kumar 1980, Hanic et al. 2009), are rather singular and, thus, while yielding some interesting insights into the cytology of basal oomycetes, they did not provide a basis for taxonomic revision. To clarify the taxonomy of the diatom-infecting parasitoids, which are important for understanding the evolution of holocarpic oomycetes (Beakes & Sekimoto 2009), attempts were made to sample *E. bacillariacearum*. Its presence in the river Main, a tributary to the western European stream Rhine, was monitored in Frankfurt am Main from the autumn of 2017 onward. In autumn of 2018, *E. bacillariacearum* was observed occurring in parallel to the bloom of its pennate diatom host *Nitzschia sigmoidea*, enabling the phylogenetic investigation of the parasitoid, the clarification of its relationship to the diatom-infecting species of *Olpidiopsis*. This also opened the possibility for a taxonomic revision of the diatom-infecting genus *Ectrogella*, which was the aim of the current study.

**RESULTS**

### General results and morphology

During autumn of 2018, biofilm samples containing abundant phytoplankton were collected at the river Main, Frankfurt am Main, Germany. During a careful screening for the presence of diatom-infecting oomycetes, about 5% of *Nitzschia sigmoidea* agg. were observed to be infected by *Ectrogella bacillariacearum*. Infections were also noted on a few *Sydneyma* species at very low incidence, so they could not be included in the phylogenetic analyses. Other species of pennate diatom genera (e.g. *Pinnularia*, *Meridion*, *Licmophora*, *Eunotia*), which are also reported as hosts for *E. bacillariacearum* (Karling 1942, Sparrow 1960), were co-occurring with infected individuals of *N. sigmoidea*, but none were observed to be infected during the entire sampling period. Light microscopic examination of the isolated specimens revealed that, as the thallus matures, the host chloroplasts begin to lose their normal colouration and gradually disintegrate. Usually, one thallus was present per host cell (Fig. 1C, E), but multiple infections, resulting in multiple thalli per host cell were also observed (Fig. 1A, B, D). Upon maturity, thalli normally measured 200 µm or more in length when single, with a smooth, very thin, colourless wall. The unbranched, fusiform to tubular thallus undergoes rapid development and subsequent zoosporogenesis. Mature thalli develop multiple discharge tubes predominantly at the apices of the host cell. Discharge tubes protrude at the girdle band and are short, often with a thickened base (Fig. 1F, G). The pyriform primary zoospores become briefly motile within the sporangium following zoospore cleavage. Zoospores are about 4 µm long and 2 µm broad, with two short, laterally inserted flagella. Zoospore discharge is fast, taking only a few seconds. Zoospores undergo encystment shortly after release, usually near the mouth of the discharge tube, or sometimes a few trapped spores encyst inside the sporangium. After some rest, ovoid secondary zoospores escape from the cysts, which have laterally inserted, unequal flagella, and swim with a dashing motion, frequently changing direction. No resting spores were observed.

**MATERIALS AND METHODS**

### Sampling, isolation, and microscopy

Diatom samples were collected from the River Main, Frankfurt am Main, Germany (N50°06.195', E008°40.323') as described previously (Buaya & Thines 2019). Approximately 10 mL of biofilm suspension was poured into each of several 15 mL Petri dishes, and screened for infected diatoms using a compound inverted light microscope (AE31, Motic, USA). *Ectrogella bacillariacearum* infecting *Nitzschia sigmoidea* was observed and collected between Sep. and Nov. 2018. Parasitised diatoms were individually picked using a 10 µL micropipette (Braun, Germany), and rinsed by transfer through a series of droplets of sterile distilled water to remove attached debris from the frustule and subsequent immersion in 250 µL of *RNAload* (Invitrogen, Thermo Fisher, Lithuania) for DNA extraction or into 5 µL molecular grade water (Life Technologies, USA) for direct PCR. Approximately 30 infected cells were collected per 2 mL tube (Sarstedt, Germany) for extraction, and 10 cells per 200 µL PCR tube (Sarstedt, Germany) for direct PCR. For morphological characterisation and DIC micrographs of life cycle stages, infected cells were also mounted on glass slides using sterile distilled water. Microscopy was done using a compound light microscope (Imager2, Carl Zeiss, Göttlingen, Germany) equipped with a Zeiss Axiocam MRC5 (Carl Zeiss, Göttlingen, Germany). Infected cells preserved in 70% ethanol were deposited in the herbarium collection of the Senckenberg Museum of Natural History, Frankfurt am Main (accession number: FR-0046108).

### DNA extraction, PCR and molecular phylogeny

Infected diatom samples were centrifuged at 19 000 g for 1 min to pellet the cells. Subsequently, *RNAload* was carefully removed by pipetting and 400 µL SLS buffer of the innuPREP Plant DNA Kit (Analytik Jena AG, Germany) was added. Samples mixed with 100 mg of sterile 0.1 mm silica glass beads (Carl Roth GmbH, Germany) were homogenised at 25 Hz for 25 min in a Retsch Mixer Mill MM 200 (Retsch GmbH, Germany). Extraction of DNA was carried using the innuPREP Plant DNA Kit, as described in the protocol provided in the kit. PCR for the amplification of partial nuclear ribosomal small subunit (18S) and sequencing was performed as described in Buaya et al. (2017). PCR amplicons were sent for sequencing to the laboratory centre of the Senckenberg Biodiversity and Climate Research Centre (Frankfurt am Main, Germany), with the primers used in PCR. The partial 18S (nrSSU) sequence obtained in this study was deposited in GenBank (accession number: MK253531). Alignments based on the dataset of Buaya et al. (2019b) with the addition of the newly obtained sequence were done using the Qi-INS-i algorithm of MAFFT (Katoh & Stadley 2013) on the TrEase webserver (http://thines-lab.senckenberg.de/trease/). Minimum Evolution phylogenetic inference was done using MEGA v. 6.0 (Tamura et al. 2013) as described in Buaya et al. (2017), and Maximum Likelihood inference using RAxML version 8, (Stamatakis 2014) with the GTRGAMMA model and running 1 000 bootstrap replicates.
Diatomophthoraceae fam. nov.

Editor-in-Chief
Prof. dr P.W. Crous, Westerdijk Fungal Biodiversity Institute, P.O. Box 85167, 3508 AD Utrecht, The Netherlands.
E-mail: p.crous@westerdijkinstitute.nl

Molecular phylogeny

In phylogenetic reconstructions inferred from partial 18S sequences of *Ectrogella bacillariacearum* on *Nitzschia sigmoidea* (Fig. 2), the parasitoid clustered in a well-supported clade with two marine parasites, *Atkinsella dubia* (crustacean parasite) and *Lagenisma coscinodisci* (*Coscinodiscus* parasite), the freshwater oomycetes, *Apodachiya brachynema* (saprophyte) and *Chlamydomyzium* sp. (rhabditid nematode parasite), as well as two environmental sequences. Other sequenced oomycete diatom parasitoids, classified in the genus *Olpidiopsis* (*O.* drebesii, *O.* gillii) and genus *Miracula* (*M.* helgolandica, *M.* moenusica) were forming earlier-diverging lineages, diverging before the split of the two major oomycete lineages, the *Peronosporomycetes* and the *Saprolegniomycetes*.

Taxonomy

*Diatomophthoraceae* A.T. Buaya & Thines, fam. nov. MycoBank MB831325.

Obligate parasitic in diatoms, thallus endobiotic, holocarpic, thin-walled at maturity; discharge tube usually single, without basal thickening or with a slightly thickened base; zoospores numerous, without clear-cut diplanism; resting spores not known.

Type genus: *Diatomophthora* A.T. Buaya & Thines

*Etymology:* *Diatomophthora* refers to the known host range of the genus and its destructive effect on host populations.

Obligate parasitic in diatoms; thallus endobiotic, holocarpic, broadly tubular, fusiform, ellipsoidal or spherical, colourless, thin-walled at maturity, often pushing apart the host valves, sometimes with equatorial swelling; discharge tubes often single, mostly elongating, tubular to slightly tapering, without a strongly thickened base; zoospores escaping after the dissolution of the tip of the discharge tube, numerous, moving or swarming within the thallus prior to release, without clear-cut diplanism; resting spores not observed.

Type species: *Diatomophthora drebesii* (A.T. Buaya & Thines) A.T. Buaya & Thines

*Diatomophthora drebesii* (A.T. Buaya & Thines) A.T. Buaya & Thines, *comb. nov.* MycoBank MB831327.
Basionym: *Olpidiopsis drebesii* A.T. Buaya & Thines, *Mycol. Prog.* 16: 1048. 2017.

Typus: Germany. Helgoland Roads, 29 Jun. 2017, A.T. Buaya (holotype FR-0247058). Ex-type partial nrSSU sequence MF926410.

*Diatomophthora gillii* (de Wild.) A.T. Buaya & Thines, *comb. nov.* MycoBank MB831328.
Basionym: *Olpidium gillii* De Wild., *Ann. Soc. Belge Microscop.* 20: 41. 1896.
Typus: J. Royal. Microsc. Soc. (London) 1893, part 1, plate I, fig. 3, H. Gill (lectotype designated here from the figures cited in the description of the species by De Wildeman, MBT388917).

Epitype: Germany, Hessen, Frankfurt am Main, river Main, A.T. Buaya, 2017, deposited in 70 % ethanol in the Herbarium Senckenbergianum (FR-0046005, epitype designated here, MBT387362). GenBank MH971238 (ex-epitype, partial nrSSU).

DISCUSSION

Despite their widespread occurrence and recent efforts by researchers, holocarpic parasitoids of diatoms are poorly studied compared to other biotrophic oomycetes (Thines et al. 2015, Schoz et al. 2016, Buaya et al. 2017, 2019c, Buaya & Thines 2019). In fact, the present understanding of these inconspicuous parasites is still fundamentally based on descriptions made almost a century ago, and several species have only been observed once or a few times since their discovery. Also, the taxonomic affinity of several species and genera is still unresolved because most have not yet been included in molecular phylogenies (Beakes & Thines 2017, Buaya et al. 2019a). To date, the majority of the diatom-parasitic oomycetes included in molecular phylogenetic investigations or studied for cellular ultrastructure are from marine environments (Schnepl et al. 1978a, b, Chakravarty 1978, Raghu Kumar 1980, Hanic et al. 2009, Thines et al. 2015, Buaya et al. 2017). So far, only two diatom infecting species from freshwater, Diatomophthora gillii and Miracula moenusa, have been investigated for their molecular phylogenetic affinities (Buaya & Thines 2019, Buaya et al. 2019a). Scherffel (1925), Karling (1942), Sparrow (1960), and Dick (2001) all agree with the placement of Ectrogella in the Saprolegniales (Ectrogellaceae), in line with the current study. However, because of heterogeneity in zoospore size, shape and formation, assessment of the delimitation of Ectrogella was variable, leading to several taxonomic revisions over time and several attempts have been made to restructure the holocarpic oomycetes, sometimes by describing new genera (Karling 1942, Cejp 1959, Sparrow 1960, Dick 2001). However, zoospore formation and thallus development might differ, depending on phyiochemical properties, similar to the situation found in some terrestrial pathogens (Runge et al. 2012).

According to Dick (2001), the genus Ectrogella contains 13 species (E. bacillariacearum, E. besseyi, E. brachystoma, E. cyclotellae, E. dicksonii, E. eunotiae, E. eurymachoides, E. gomphonematis, E. lauderia, E. licmophorae, E. marina, E. monostoma, E. perforans), all forming single-celled, unbranched, endobiotic thalli, mostly producing zoospores with diplanetism, which we assume as the key diagnostic feature of the genus (Zopf 1884, Petersen 1905, Scherffel 1925, Sparrow & Ellis 1949, Friedmann 1952, Feldmann & Feldmann 1955, Dick 2001). The majority of the species in the genus sensu Dick (2001) are parasitoids of diatoms (E. bacillariacearum, E. monostoma, E. gomphonematis, E. eunotiae, E. brachystoma, E. cyclotellae, E. licmophorae, E. perforans, E. eurymachoides), others parasitise algae (E. marina, E. lauderia, E. dicksonii) and one is an endobiotic oomycete hyperparasite (E. besseyi). Within the group, zoospore morphology, development and movement, as well as discharge pattern, differ. For example, in E. perforans zoospores swarm within the sporangia prior to discharge (Petersen 1905), while in e.g. E. monostoma, non-motile spores are discharged. A similar situation was described for E. besseyi, which, unlike E. bacillariacearum, also produces non-flagellated primary aplanospores, encysting at the orifice of the discharge tube and forming a cluster of spores similar to Achlya. After encystment, they germinate, producing secondary zoospores (Scherffel 1925). Also, the normal number of exit tubes varies for several species within the genus. For example, E. bacillariacearum, E. licmophorae and E. perforans have multiple exit tubes, while E. monostoma, E. gomphonematis, E. eunotiae, E. marina, E. besseyi and E. eurymachoides produce only one or two (Zopf 1884, Petersen 1905, Scherffel 1925, Friedmann 1952, Feldmann & Feldmann 1955). Additional species were added to the genus, some with incomplete life-cycle descriptions and unclear zoospore diplanetism, e.g. E. brachystoma, E. cyclotellae, E. dicksonii, E. eunotiae, E. eurymachoides, E. lauderia, and E. marina, E. perforans (Sparrow 1960, Dick 2001). It has been speculated that Ectrogella belongs to the basal oomycetes (Garvetto et al. 2018), but the phylogenetic reconstructions of this study places Ectrogella among the early-diverging Saprolegniomycetes to which also another diatom parasitoid, Lagenisma coscinodisci, belongs. Therefore, Ectrogella is unrelated to the diatom parasites previously in Olpidiopsis, which are placed in a new genus, Diatomophthora, in this study. The inclusion of the Ectrogellaceae into the deep-branching Saprolegniales is in line with the formation of zoospores with diplanetism, and confirms earlier treatments of Ectrogella in the Saprolegniales (Scherffel 1925, Coker & Mathews 1937, Karling 1942, Sparrow 1960, Dick 2001). As this phylogenetic and morphological study further confirms the importance of zoospore development for evaluating the taxonomy of oomycetes, only those species with a clear-cut diplanetism should be attributed to the Saprolegniomycetes, while the species that produce monomorphic and monoplanetic zoospores are unlikely to belong to Ectrogella or even to the Saprolegniomycetes, and should be carefully scrutinised to infer their phylogenetic position. Whether the sole endobiotic hyperparasite in the genus Ectrogella, E. besseyi, is a bona fide member of the genus remains to be shown, but it also has an achlya-like pattern of zoospores discharge similar to other diatom infecting species (Sparrow & Ellis 1949). Until more data become available for these elusive pathogens, it remains unclear, if the different modes of zoospore discharge by Ectrogella species (i.e. saprolegnia-like vs. achlya-like) have phylogenetic significance.

ACKNOWLEDGEMENTS

The Katholischer Akademischer Ausländer-Dienst (KAAD) is gratefully acknowledged for a graduate scholarship to AB. The authors also thank Sebastian Ploch for laboratory support. This study has been supported by LOEWE in the framework of the LOEWE Centre for Translational Biodiversity Genomics (TBG), funded by the Ministry of Science of the Government of Hessen.

Fig. 2. Molecular phylogeny using minimum evolution analyses inferred from partial 18S sequences. Numbers on branches denote bootstrap values from maximum likelihood and minimum evolution analyses, in respective order. A dash “-” indicates less than 50 % bootstrap support for the presented or a conflicting topology.
References

Beakes GW, Thines M (2017). Hypodochtiomyctea and Oomycota. In: Handbook of the Protists (Archibald JM, Simpson, AGB, Slamovits CH, eds). Springer, Germany: 435–505.

Beakes GW, Sekimoto S (2009). The evolutionary phylogeny of oomycetes—insights gained from studies of holocarpic parasites of algae and invertebrates. In: Oomycete Genetics and Genomics: Diversity, Interactions, and Research Tools (Lamour K, Kamoun S, eds) Wiley-Blackwell, New York, USA: 1–24.

Buaya AT, Ploch S, Hanic L, et al. (2017). Phylogeny of Miracula helgolandica gen. et sp. nov. and Olpidiopsis drebesii sp. nov., two basal oomycete parasitoids of marine diatoms, with notes on the taxonomy of Ectrogella-like species. Mycological Progress 16: 1041–1050.

Buaya AT, Ploch S, Thines M (2019a). Rediscovery and phylogenetic placement of Olpidiopsis gillii (de Wild.) Friedmann, a holocarpic oomycete parasitoid of freshwater diatoms. Mycoscience 60: 141–146.

Buaya AT, Ploch S, Inaba S, et al. (2019b). Holocarpic oomycete parasitoids of red algae are not Olpidiopsis. Fungal Systematics and Evolution 4: 21–31.

Buaya AT, Kraberg A, Thines M (2019c). Dual culture of the oomycete Lagenisima coscinodisci Drebes and Coscinodiscus diatoms as a model for plankton/parasite interactions. Helgoland Marine Research 73: 2.

Buaya AT, Thines M (2019). Miracula moenusica, a new member of the holocarpic parasitoid genus from the invasive freshwater diatom Pleurosigma laevis. Fungal Systematics and Evolution 3: 35–40.

Cejp K (1959). Flora CSR - Oomycetes. Nakladatelství Ceskoslovenské Akademie Ved, Praha.

Chakravarty DK (1978). Electron microscopic study of the zoospores of Lagenisima coscinodisci. Cytologia 43: 197–201

Coker WC, Matthews VC (1937). Blastocladiaceae, Monoblepharidales, Saprolegniales. North American Flora 2: 1–76.

Cornu M (1872). Monographie des saprolegnesie; etude physiologique et systematique. Annales des Sciences Naturelles Botanique 15: 1–198.

Dick MW (2001). Straminipilous Fungi. Springer, Netherlands.

Feldmann J, Feldmann G (1955). Observations sur quelques Phycomycetes marins nouveaux ou peu connus. Revue Mycologique 20: 231–251.

Friedmann I (1952). Über neue und wenig bekannte auf Diatomeen parasitierende Phycomyzeten. Österreichische Botanische Zeitschrift 99: 173–219.

Garovete A, Nezan E, Badis Y, et al. (2018). Novel widespread marine Oomycetes parasitising diatoms, including the toxic genus Pseudo-nitzschia: Genetic, Morphological, and Ecological Characterization. Frontiers in Microbiology 9: 2918.

Hanic LA, Sekimoto SS, Bates SS (2009). Oomycete and chytrid infections of the marine diatom Pseudo-nitzschia pungens (Bacillariophyceae) from Prince Edward Island, Canada. Botany 87: 1096–1105.

Karling JS (1942). The simple holocarpic biflagellate Phycomycetes. Published by Karling JS, New York.

Katoh K, Standley DM (2013). MAFFT multiple sequence alignment software version 7: improvements in performance and usability. Molecular Biology and Evolution 30: 772–780.

Petersen HE (1905). Contributions a la connaissance des Phycymycetes marins (Chytridinae Fischer). Oversigt over det Kongelige Danske videnskabernes selskabs forhandlinger 5: 439–188.

Raghu Kumar C (1980). An ultrastructural study of the marine diatom Lichmophora hyalina and its parasite Ectrogella perforans. II. Development of the fungus in its host. Canadian Journal of Botany 58: 2557–2574.

Runge F, Ndambi B, Thines M (2012). Which morphological characteristics are most influenced by the host matrix in downy mildews? A case study in Pseudoperonospora cubensis. PLoS One 7: e44863.

Scherffel A (1925). Endophytic Phycymyceten-Parasiten der Bacillariaecen und einige neue Monadinen. Ein Beitrag zur Phylogenie der Oomyceten (Schröter). Archiv für Protistenkunde 52: 1–141.

Schnepf E, Deichgräber G, Drebes G (1978a). Development and ultrastructure of the marine parasitic oomycete Lagenisima coscinodisci Drebes (Lagenidiales). Archiv für Mikrobiologie 116: 141–150.

Schnepf E, Deichgräber G, Drebes G (1978b). Development and ultrastructure of the marine parasitic oomycete Lagenisima coscinodisci Drebes (Lagenidiales): formation of the primary zoospores and their release. Protoplasma 94: 236–280.

Scolz B, Guillou L, Marano AV, et al. (2015). Zoospore parasites infecting marine diatoms-A black box that needs to be opened. Fungal Ecology 19: 59–76.

Sparrwo FK (1960). Aquatic Phycymycetes. The University of Michigan Press, Ann Arbor USA.

Sparrwo FK, Ellisson B (1949). Olpidiopsis schenkiana and its hyper-parasite Ectrogella besseyi n. sp. Mycologia 41: 28–35.

Sekimoto S, Beakes GW, Gachon CMM, et al. (2008). The development, ultrastructural cytology, and molecular phylogeny of the basal oomycete Eurychasm a dicksonii, infecting the filamentous phaeophyce algae Ectocarpus siliculosus and Pyelia littoralis. Protis 159: 299–318.

Stamatakis A (2014). RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics 30: 1312–1313.

Tamura K, Stecher G, Peterson D, et al. (2013). MEGA6: Molecular Evolutionary Genetics Analysis version 6.0. Molecular Biology and Evolution 30: 2725–2729.

Thines M, Nam B, Nigrelli L, et al. (2015). The diatom parasite Lagenisima coscinodisci (Lagenimatales, Oomyctae) is an early diverging lineage of the Saprolegniomycetes. Mycological Progress 14: 75.

Zopf W (1884). Zur Kenntniss der Phycymyceten. I. Zur Morphologie und Biologie der Ankyliesten und Chytridiaceen. Nova acta Academiae Caesareae Leopoldino-Carolitinae Germanicacae Naturre Curiosorum 47: 143–236.