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Miracula blauvikensis: a new species of *Miracula* from Iceland, and report of a co-cultivation system for studying oomycete-diatom interactions

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Abstract: The genus *Miracula* represents an early-diverging lineage of diatom-parasitic *Oomycota*, straminipilous eukaryotes that have evolved fungal features independent from the opisthokont *Fungi*. Recent studies have revealed that diatom parasitoids are much more species-rich than previously thought and may play an important role in limnic and marine ecosystems. Of the different diatom-parasitic lineages, the genus *Miracula* is one of the most abundant in marine ecosystems. Here a species of *Miracula* parasitising *Fragilaria capucina s.l.* from Iceland is described as *Miracula blauvikensis*. In addition, its phylogenetic position is clarified and its life-cycle documented. The species has been brought into co-cultivation with its host, and due to the ease of cultivation and the convenient microscopy of the diatom threads, this co-culture might be a useful tool to study oomycete-diatom interactions in the future.

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INTRODUCTION

Primary production in marine ecosystems largely depends on diatom photosynthesis, especially in temperate and arctic environments (Miettinen 2018, Gilbertson *et al*. 2022). There is accumulating evidence that oomycetes might be important players in regulating diatom blooms (Garvetto *et al*. 2018, Chambouvet *et al*. 2019), so for an in-depth understanding of diatom communities it is vital to elucidate the diversity and interactions of oomycetes with their diatom hosts (Scholz *et al*. 2016, Illicic & Grossart 2022). While previously almost all diatom parasitoids had been attributed to a single genus, *Ectrogella* (Dick 2001), recent research has shown that diatom parasitism has evolved multiple times and that species parasitising diatoms can be found throughout the oomycete tree of life (Buaya & Thines 2020c). So far, there is one confirmed diatom-infecting genus in *Peronosporales*, the genus *Lagena* (Thines & Buaya 2022), one diatom-infecting lineage in the *Saprolegniales*, the genus *Aphanomycopsis* (Buaya & Thines 2021a), and two diatom-infecting genera in the *Leptomitales*, namely *Ectrogella* (Buaya & Thines 2020b) and *Lagenisma* (Thines *et al*. 2015). However, the largest diversity of diatom parasitoids is apparently among the early-diverging oomycete lineages, *i.e*. those that diverge before the split of the two "crown" groups, the *Peronosporomycetes* and the *Saprolegniomycetes*, which contain more than 95 % of the oomycete species described to date (Beakes & Thines 2017).

The first members of these early-diverging oomycete diatom parasites for which sequence data could be obtained were *Miracula helgolandica* (Hanic *et al*. 2009, Buaya *et al*. 2017), and *Diatomophthora drebesii* (Buaya *et al*. 2017, Buaya & Thines 2020b). The latter species was initially described as a member of *Olpidiopsis*, a catch-all genus for holocarpic oomycetes (*i.e.* oomycetes that convert the entire cytoplasm into zoospores upon asexual sporulation) not producing morphologically divergent primary and secondary zoospores. This was because sequence data for the type species of *Olpidiopsis*, *O. saprolegniae*, a parasite of animal-parasitic oomycetes, was lacking. Once sequence data became available for *O. saprolegniae*, it was apparent that it was largely unrelated to the olpidiopsis-like oomycetes infecting diatoms. Thus, the formerly named *Olpidiopsis drebesii* became the type species of *Diatomophthora*, into which genus also *Olpidiopsis gillii* and *Ectrogella perforans* were transferred (Buaya *et al.* 2019a, c, 2020a).

In subsequent studies, additional species of *Miracula* were discovered, both in freshwater (Buaya *et al*. 2019d, Thines & Buaya 2022) and in marine (Buaya *et al.* 2021c) environments. In addition to these physically recovered species, the sequencing of uncultivated diatom parasites (Garvetto *et al*. 2019) as well as environmental sequencing (Hassett *et al*. 2019), have revealed the presence of several additional species-level clades in both *Diatomophthora* and *Miracula*.

Iceland has a rich diatom flora (Hansen 2006, Furey *et al*. 2020) and is, thus, a promising region for the discovery of new

species, especially those that were previously found without preserved specimens in northern Europe (Garvetto *et al*. 2018) or the arctic ocean (Hassett *et al*. 2019). It was the aim of this study to search for diatom parasites previously known only from sequence data, focussing on members of the genus *Miracula*.

MATERIALS AND METHODS

Blávík research station

The Blávík research station is located in east Iceland, on Fáskrúðsfjörður, a fjord around 15 km long and 2 km wide at the location of the station. The station offers direct access to a beach with large pebbles, onto which detached algae strand during low tide, and rocks in the intertidal zone, overgrown with various brown and red algae. The macroalgae present are predominantly *Fucus*, *Ectocarpus*, *Capsosiphon* and *Porphyra* species. In the lower littoral and sublittoral, *Laminaria* species are dominant, especially *L. digitata* and *L. hyperborea*. In addition, a steep cliff allows direct access to deeper fjord waters for plankton net tows. The research infrastructure at the station features a Nikon Eclipse 1000T inverted compound light microscope, a dissecting microscope, and facilities for DNA extraction and PCR.

Host and pathogen samples

Host and pathogen samples were collected daily from the 26th of July to the 8th of August 2022 by plankton net tows from a cliff. The plankton net had a mesh size of 20 µm (Hydro-Bios, Kiel, Germany) and was towed vertically through the water-column several times, from a depth of about 2.5 m to the surface. Plankton concentrates were poured into 500 mL plastic bottles and directly brought to the station for further examination. In the station, samples were poured onto 12-cm-diam Petri dishes (Sarstedt, Nümbrecht, Germany) (except for the 8th of August) and investigated using a Nikon Eclipse 1000T inverted microscope (Nikon, Japan). Thereby, threads of *Fragilaria capucina s.l*. infected with an oomycete parasite were found on the 1st up to 6th of August. Infected diatom threads were individually picked up for DNA extraction using a micropipette (10 µL, Brandt, Germany), and transferred through plain seawater until only infected filaments were seen. These filaments were collected in 2 mL vials for DNA extraction. DNA was extracted using an *innuPREP* plant DNA extraction kit from AnalytikJena (Analytik Jena, Jena, Germany) according to the instructions of the manufacturer. PCR for amplification was done as described previously (Buaya *et al*. 2017), and amplification products were visualised after agarose gel electrophoresis using a blue light transilluminator (TW26, VWR, Leuven, Belgium), and gel bands were visualised using the ROTI®GelStain (Carl Roth GmbH, Germany) with Safe Imager™ Blue-Light Transilluminator (Thermo Fisher, Germany) googles.

In addition, samples collected on the 8th of August were transferred directly into 50 mL tubes (Sarstedt, Nümbrecht, Germany) and transported to the Senckenberg Biodiversity and Climate Research centre at ambient temperature and poured into 12-cm-diam Petri dishes approximately 10 h after collection. These Petri dishes were then placed into a climate chamber set to continuously 10 °C and a 14 h light / 10 h dark cycle (CMP 6010, Conviron, Canada). During the following days, additional infected filaments were collected. Also for these samples, PCR was done as described in Buaya *et al*. (2017). However, for cleaning infected filaments not plain but sterile seawater was used. After visually inspecting amplification products as outlined in Buaya *et al*. (2017), they were bidirectionally sequenced at the laboratory centre of the Biodiversity and Climate Research Centre. In addition, amplicons were cloned and sequenced as described previously (Buaya *et al*. 2019a). Consensus sequences were obtained by assembly and editing of the reads using Geneious v. 5.6 (Biomatters INC., New Zealand). Sequences of the parasitoid infecting *Fragilaria capucina s.l.* were deposited in GenBank (OP918674 for *cox2*, OP908040 for nrSSU).

As sequences were identical for all samples, only one representative sequence was added to the dataset of Thines & Buaya (2022). In addition, a sequence of *Miracula einbuarlaekurica* was included. Phylogenetic inference was done using the TrEase webserver (www.thines-lab.senckenberg.de/trease) with default settings, for both Minimum Evolution and Bayesian inference.

Morphological characterisation

Morphological characterisation was done using a Zeiss Imager M2 compound light microscope (Carl Zeiss, Göttingen, Germany), equipped with DIC. Measurements were done on calibrated images taken with a Zeiss Axiocam MRc5 camera using the software AxioVision (Carl Zeiss, Göttingen, Germany).

Establishment of dual cultures

Dual cultures were established in Petri dishes incubated as described above by first propagating clean host filaments in f/2 (Sigma-Aldrich, UK) marine water enrichment medium (Guillard & Ryther 1962, Schnepf & Drebes 1977), which were obtained by serial transfer through sterile seawater. During this period of time, diatom growth in plankton samples was supported by adding f/2 medium, to ensure that host diatoms would not perish as previously described in Buaya *et al*. (2019b, 2020a). After clean host cultures were established, infected filaments with one pathogen thallus and cleaned as described above were added to healthy host samples.

RESULTS

Establishment of dual cultures

In total, 10 strains of the pathogen were established, which were transferred to new hosts once per week. The strains were similar in virulence, and after three weeks, almost all host cells were parasitised and killed.

Life cycle observation and morphological characterisation

The life cycle of the pathogen started when a zoospore encysted at the girdle zone of the host (Fig. 1A) and developed a very thin infection tube that finally reached the host cytoplasm. The unwalled parasitoid moved towards the nucleus and enlarged, gradually degrading the host cytoplasm, until only bright orange to chestnut-coloured phaeoplast residues were visible at the poles of the host cell. Thalli usually one per cell, but occasionally, up to five thalli were observed in a single host cell. Thalli were usually broadly elongate, following the outline of the host cell when single,

or roundish when multiple infections were present and measured 12–22 by 8–12 µm. While thalli matured, they developed a thin, colourless wall, and their cytoplasm became coarser. At this stage, the thalli did not grow further, but developed one to several short discharge tubes (5–9 µm long and 3–6 µm diam, Fig. 1B), which were slightly thickened at the base. Zoospores cleaved simultaneously in the periphery of a large central vacuole and assumed motility within the sporangium. After the tip of the discharge tube dissolved, zoospores 3–4 µm long and 2–3 µm broad escaped from the sporangium. Some of the zoospores encysted directly at the orifice of the discharge tube, leaving behind empty clusters of spores (Fig. 1C), while others swam in an irregular pattern in random directions before coming to rest. The germination of resting cysts was not observed, and no oospores or any other evidence of a sexual cycle were seen.

Phylogenetic reconstruction

The phylogenetic reconstruction based on partial small ribosomal subunit (18S) sequences (Fig. 2) revealed a high level of sequence identity to a parasitoid from *Fragilaria capucina s.l.* and *Licmophora* sp. found by Garvetto *et al.* (2019), with which it was grouped together with maximum support in both analyses. While the crown oomycete group of *Peronosporomycetes* and *Saprolegniomycetes* and most genera of early-diverging oomycetes received high to maximum support in all analyses, higher-level relationships remained mostly unresolved. For the early-diverging genera support for the observed monophyly of *Pontisma* and *Diatomophthora* was low.

The phylogenetic reconstruction using partial cytochrome oxidase 2 (*cox*2) sequences (Fig. 3) revealed a topology congruent with the 18S-based reconstruction. However, the sequences of the parasitoid of *Fragilaria capucina s.l.* differed slightly from those reported earlier by Garvetto *et al*. (2019), with which they form a monophyletic group with maximum support in all analyses. Similar to the phylogenetic reconstruction based on partial 18S sequences, most higher-level relationships could not be resolved.

Taxonomy

Based on the host parasitised and the large genetic distance to other species of *Miracula*, the parasitoid of *Fragilaria capucina s.l.* is herewith introduced as a new species of the genus.

Miracula blauvikensis Buaya & Thines, ***sp. nov.*** MycoBank MB 846741. Fig. 1A–C.

Etymology: Named after the locality in Iceland, Blávík, from where the type specimen was isolated.

Typus: **Iceland**, Fáskúðsfjörður, Blávík, 6 Aug. 2022, coll. *A. Buaya*, isol. 22 Aug. 2022 (**holotype** Herb. Senckenbergianum (FR), FR-0046158), ex-type sequences deposited in GenBank (OP918674 for *cox2*, OP908040 for nrSSU).

Diagnosis: Differs from all know species of *Miracula* by parasitising the diatom genus *Fragilaria*.

Description: Thallus endobiotic in diatoms of the genus *Fragilaria*, 12–22 µm long, 8–12 µm broad, usually one per host cell, sometimes up to five. Thallus naked at first, later thin-walled, producing one to usually two to three, sometimes up to five discharge tubes. Zoospores usually 4 µm long and 3 µm broad, starting to move inside the sporangial thallus, and either encysting directly at the orifice of the discharge tube, or swimming in the surrounding media for some time before coming to rest. Resting cyst germination and sexual reproduction not observed.

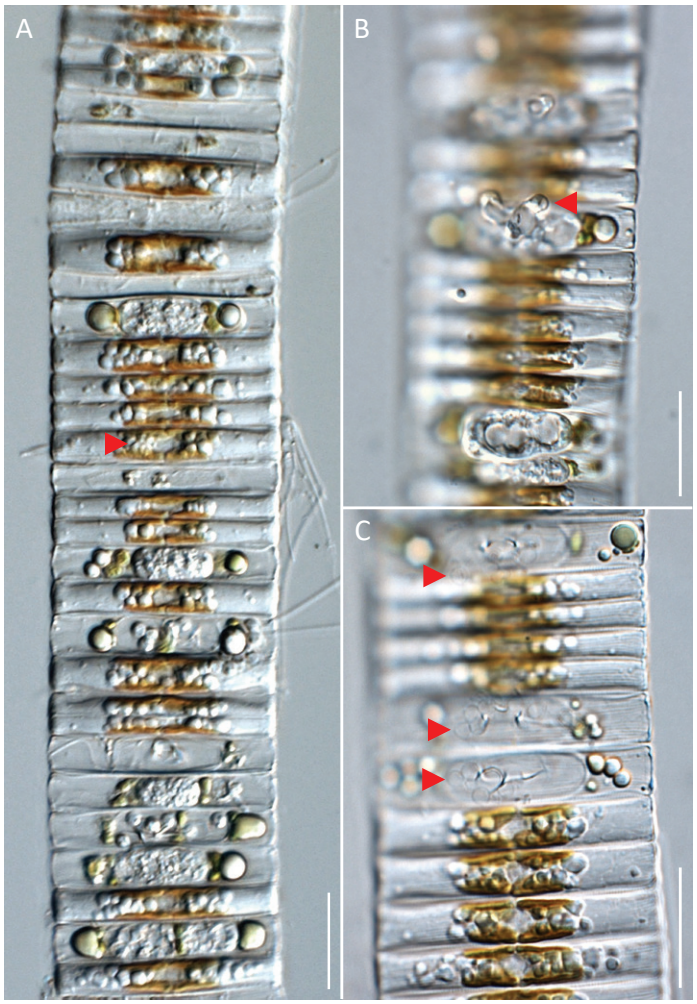

Fig. 1. DIC micrographs of various infection stages. **A.** Various infection stages of *Miracula blauvikensis* in a filament of *Fragillaria capucina s.l.*, the red arrowhead pointing to a thallus in an early stage, closely attached to the host nucleus. **B.** Discharge tubes of *Miracula blauvikensis* (near the tip of the red arrowheads). **C.** Empty thalli after spore discharge, the red arrowheads pointing to empty cysts near the orifices of discharge tubes. Scale bar = 25 µm.

Habitat: Marine, living cells of *Fragilaria* species.

Known distribution: Iceland.

DISCUSSION

Oomycetes that act as parasitoids of diatoms can have major impacts, especially on marine ecosystems (Scholz *et al*. 2016, Klawonn *et al*. 2021), as they can lead to the decline of diatom blooms, which form an important component of the base of the pelagic food web. Considering this, research into the diversity, ecology, physiology, and host-parasitoid interaction of these organisms seems highly warranted (Scholz *et al*. 2016, Chambouvet *et al*. 2019, Buaya & Thines 2020c). However,

Fig. 2. Phylogenetic reconstruction in Minimum Evolution on the basis of partial nrSSU sequences. The first and the second number on the branches denote bootstrap support equal or greater to 60 % in Minimum Evolution and Maximum Likelihood, respectively. The third number refers to posterior probabilities equal to or greater than 0.95 from the Bayesian phylogenetic inference. A minus sign denotes lack of support for the presented or an alternate topology. A blue arrowhead denotes the position of the novel species.

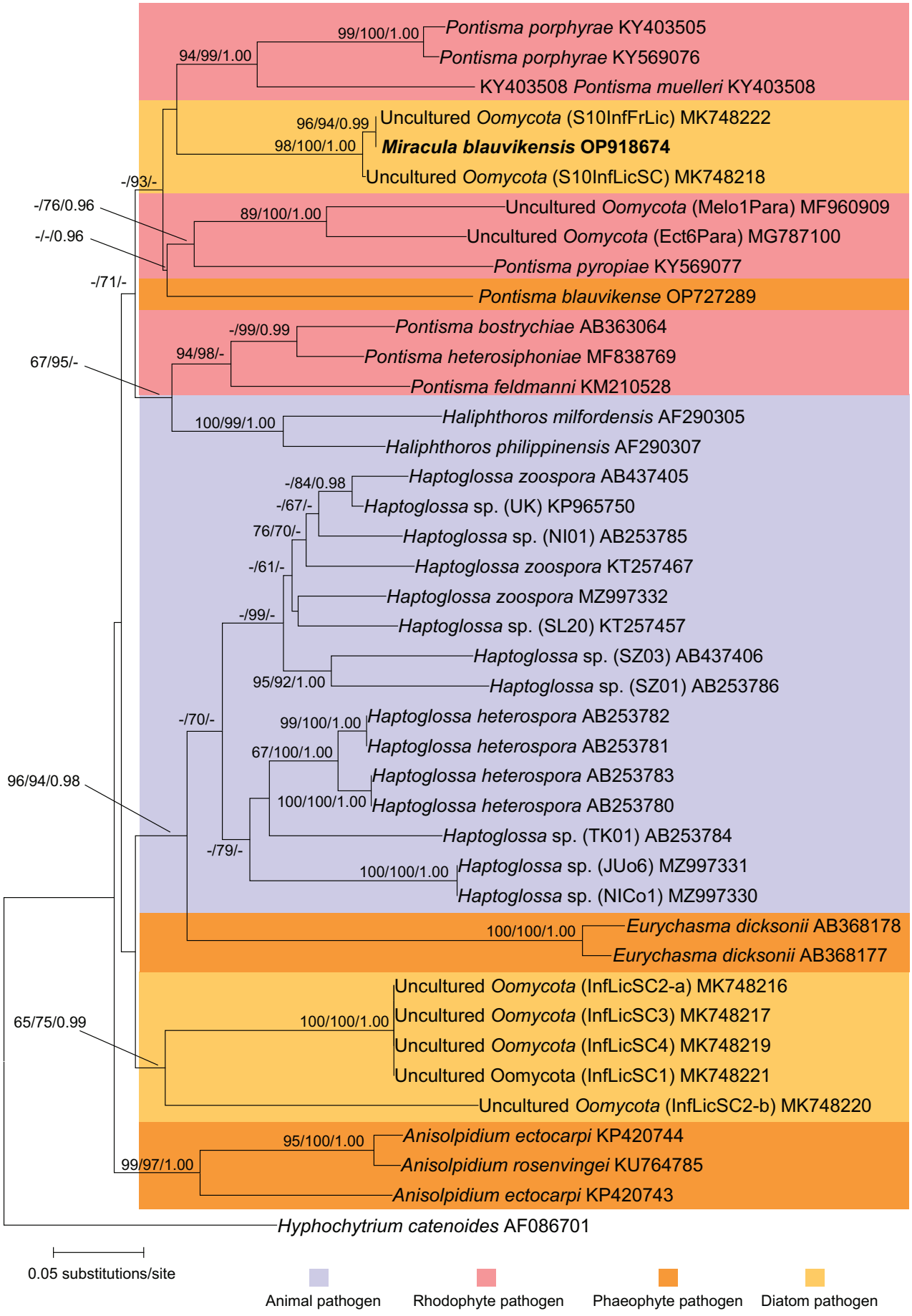

Fig. 3. Phylogenetic reconstruction in Minimum Evolution on the basis of partial *cox*2 sequences. The first and the second number on the branches denote bootstrap support equal or greater to 60 % in Minimum Evolution and Maximum Likelihood, respectively. The third number refers to posterior probabilities equal to or greater than 0.95 from the Bayesian phylogenetic inference. A minus sign denotes lack of support for the presented or an alternate topology.

there are only few studies that have evaluated the host range of oomycetes infecting algae (Müller *et al*. 1999, Gachon *et al*. 2009, Strittmatter *et al*. 2009) or diatoms (Drebes 1966, Buaya *et al*. 2019b, 2020a), or that have started to investigate the molecular and chemical interaction of holocarpic oomycetes and their hosts (Beakes & Glocking 1998, Gachon *et al*. 2009, Beakes *et al*. 2012, Vallet *et al*. 2019, Murúa *et al*. 2020). Apart from this, the biodiversity of holocarpic oomycetes remains obscure on all levels, despite some recent progress (Buaya *et al*. 2017, Garvetto *et al*. 2018, Buaya & Thines 2020c). Recent studies focussing on environmental sequencing have revealed a tremendous diversity of oomycete lineages in the marine realm (Garvetto *et al*. 2018, Chambouvet *et al*. 2019, Hassett *et al*. 2019), which is contrasted by the relatively few species described so far. The species described in this study, *Miracula blauvikensis*, or a closely related species, has been observed both by environmental sequencing (Hassett *et al*. 2019), and single cell sequencing (Garvetto *et al*. 2019). This suggests that the species, similar to *M. helgolandica*, is widespread throughout the northern hemisphere.

The host-parasite co-culture reported in this study represents the fourth oomycete genus parasitising marine diatoms that could be brought into co-cultivation with its host, after *Lagenisma* (Buaya *et al*. 2019b), *Diatomophthora* (Buaya *et al*. 2020a), *Miracula* (Buaya & Thines 2021b), and *Lagena* (Thines & Buaya 2022). However, it is the first oomycete-diatom system featuring a diatom host with relatively small cells. As host cell volume and genome size are strongly correlated in diatoms (Vardi *et al*. 2009, Nakayama 2022), this system could thus be useful for investigating the genetic basis of diatom-oomycete interaction. For this, host and parasite strains are freely available from the authors upon request. We hope that this resource will help to shed light on the poorly understood parasitic interactions that form an important cornerstone of the global food web.

Conflict of interest: The authors declare that there is no conflict of interest.

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