



Introducing a new pathosystem for marine pathogens – the green alga *Urospora neglecta* and its pathogen *Sirolopidium litorale* sp. nov.

Anthony T. Buaya^{1,2} · Ichen Tsai^{1,2} · Tatyana A. Klochkova³ · Marco Thines^{1,2}

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Abstract

Holocarpic oomycetes, which had fallen into relative scientific obscurity for quite some time, recently regained scientific interest. Among these organisms, some stand out for infecting commercially valuable red algae, such as the nori algae of the genus *Pyropia*, rendering them economically significant. After having observed simple holocarpic pathogens of green algae in previous sampling trips, most of which we could not fully characterise due to their scarcity, we now discovered a parasite of the widespread littoral green algae *Urospora neglecta*. This previously unnoticed parasite turned out to be distinct from another green algae-infesting species, *Sirolopidium bryopsidis*. This finding led us to formally describe it as *Sirolopidium litorale*, marking the first new species of holocarpic oomycetes of green algae to be found on the shores of Blávík, East Iceland. The ease of cultivation of *U. neglecta* offers a unique opportunity to establish a genetically tractable system for studying how *Sirolopidium* interacts with algae. This could help uncover the underlying mechanisms behind the pathogenicity of the species of this genus and provide valuable insights into their ecological roles and evolutionary history.

Keywords Algae · Blávík research station · Holocarpic oomycetes · Iceland · Parasitism · Pathogenicity · Phylogenetics · *Pontisma*

Introduction

Holocarpic oomycetes are a diverse yet relatively obscure group of fungus-like protists within the kingdom *Straminipila* (Dick 2001). This group of oomycetes have increasingly gained attention due to molecular phylogenetic studies indicating their high diversity and ubiquitous presence (Cook

et al. 2001; Küpper et al. 2006; Sekimoto et al. 2008; Thines et al. 2015; Buaya et al. 2017, 2021a; Gachon et al. 2017; Badis et al. 2019; Buaya and Thines 2023). Many holocarpic oomycetes fall outside the crown group of the *Peronosporomycetes* and *Saprolegniomycetes* (Buaya and Thines 2020a). Notably, the genus *Olpidiopsis*, previously a catch-all for holocarpic oomycetes with simple unbranched thalli, has been confined to holocarpic parasites of oomycetes, prompting the transfer of diatom parasitoids previously categorized in *Olpidiopsis* to *Diatomophthora* and parasites of algae to *Pontisma* (Buaya et al. 2019a; Buaya and Thines 2020b; Buaya et al. 2020). Recent research has shown that *Sirolopidium* and *Pontisma* are congeneric, broadening the host range of a single genus from green algae (*Chlorophyceae*) to red algae (*Rhodophyceae*) (Buaya et al. 2021b). To this, a species parasitising brown algae (*Phaeophyceae*) was recently added (Buaya et al. 2023). However, Karling (1942) had combined *Pontisma lagenidioides* into *Sirolopidium*, hence establishing priority for the latter genus, so these parasites should be considered as members of *Sirolopidium*. This genus has been widely documented across the Holarctic, infecting economically important species from the genera *Pyropia* and *Porphyra* (Klochkova et al. 2016; Badis et al. 2019). As algal

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✉ Anthony T. Buaya
anthony.buaya@senckenberg.de

✉ Marco Thines
m.thines@thines-lab.eu

¹ Senckenberg Biodiversity and Climate Research Centre (SBiK-F), Senckenberganlage 25, 60325 Frankfurt am Main, Germany

² Department of Biological Sciences, Institute of Ecology, Evolution and Diversity, Goethe University Frankfurt am Main, Max-von-Laue-Str. 13, 60438 Frankfurt am Main, Germany

³ Chair of Ecology and Nature Management, Kamchatka State Technical University, 683003 Petropavlovsk-Kamchatsky, Russia

farming expands, the economic influence of *Sirolopidium* is expected to grow.

Using environmental sequencing Hassett et al. (2019) have revealed that in the Arctic Ocean, there are numerous additional lineages of the genus representing undescribed species. Iceland, with its rich diversity of seaweeds and microalgae has the potential for the discovery of some of those lineages, prompting a continued survey of algae at the Blávík research station in the East Fjords of Iceland in search of new species of holocarpic oomycetes infecting algae. During this investigation, an unusual holocarpic parasite was discovered on the green alga *Urospora neglecta*. This study aimed to characterise it and lay the foundation for a pathosystem for studying the interactions of algae and holocarpic oomycetes.

Materials and methods

Sampling, isolation, and characterization

Infected threads of the filamentous marine green alga *Urospora neglecta* were collected throughout July and August 2023, in Blávík, Southeast Iceland (Fig. 1A, 64°53'37.0" N; 13°50'26.9" W). Samples were collected from the coastal intertidal area by scraping the algal threads directly from their rocky substrate during low tide (Fig. 1B) and transferring those to sterile 50 mL plastic tubes filled with fresh seawater. These samples were transferred into Ø 150 mm Petri dishes filled with fresh seawater and examined for oomycete parasites using an inverted compound light microscope (Eclipse T1000, Nikon, Tokyo, Japan). Samples with infected algal filament segments were transferred to the Senckenberg Biodiversity and Climate Research Centre in Frankfurt am Main, Germany, where they were screened for infected filaments, which were carefully dissected on an inverted microscope (AE31, Motic, Xiamen, PRC), transferred several times through autoclaved seawater, and isolated segments were transferred into 2 ml tubes with 70% ethanol for subsequent DNA extraction. A specimen derived from the collection on 13 August 2023 was preserved in 70% ethanol and deposited in the herbarium collection of the Senckenberg Museum of Natural History, Cryptogams Section, Frankfurt am Main (accession FR-0046167). Some infected algal filaments were also mounted on microscopic slides using seawater for life-cycle observations, morphological characterisation, and DIC micrographs using a DIC light microscope (Imager M2, Carl Zeiss, Göttingen, Germany) and pictures were taken with a Zeiss Axiocam MRc5 (Carl Zeiss, Göttingen, Germany). Pathogen and green algal host identity were determined by light microscopy and 18S sequence barcoding. Host and pathogen cultures are available from the authors upon request.

DNA extraction, PCR amplification, and phylogenetic analyses

DNA extraction from infected filament sections of *Urospora neglecta* was done with an innuPREP Plant DNA Extraction Kit (Analytik Jena, Jena, Germany) following the protocol provided by the manufacturer. Before extraction, the 70% ethanol was aspirated out, and SLS buffer from the extraction kit was added. The sample was homogenized using silica glass beads and metal beads in 2 mL tubes as described in Buaya et al. (2023). Subsequently, PCR amplification of partial nuclear ribosomal small subunit (nrSSU) sequences was done following the protocol outlined in Buaya et al. (2019a), using Mango-Taq DNA Polymerase (Meridian Biosciences, London, UK) and 18S primers Euk422-445 and Euk1422-1440 (Wang et al. 2014). Dideoxy sequencing of the PCR amplicons was done by the sequencing facility of the Senckenberg Biodiversity and Climate Research Centre in Frankfurt am Main, using the same primers as in PCR. The obtained sequences were assembled using Geneious (version 5.6) and aligned using the Q-INS-I algorithm in MAFFT version 7, available on the MAFFT web server (Katoh and Standley 2013; Katoh et al. 2019). Subsequently, after the removal of leading and trailing gaps, phylogenetic analyses were done on the TrEase webserver (Mishra et al. 2023) employing FastTree2 (Price et al. 2010) for Minimum Evolution and RAxML (Stamatakis 2014) for Maximum Likelihood inference, with 1000 bootstrap repeats for each analysis. The partial nrSSU sequence acquired in this study has been deposited in GenBank (OR660115). The alignment used in this study can be accessed at <https://doi.org/10.6084/m9.figshare.24497467>.

Results

Morphology and life-cycle traits

The morphology and life cycle development of the oomycete pathogen of *Urospora neglecta* found in the present study was documented using several infected filaments of the host. The life cycle of the parasite starts with the germination of an encysted spore on the outer surface of its algal host, developing a very fine penetration tube that pierces into the thick cellulosic wall of the host until reaching the cytoplasm. Once established, the parasite thallus undergoes rapid growth, initially pushing the host chloroplast into the periphery of the cell (Fig. 1C), and subsequently degrading it into dark green or golden green residues (Fig. 1D). The thallus is naked at the early stages,

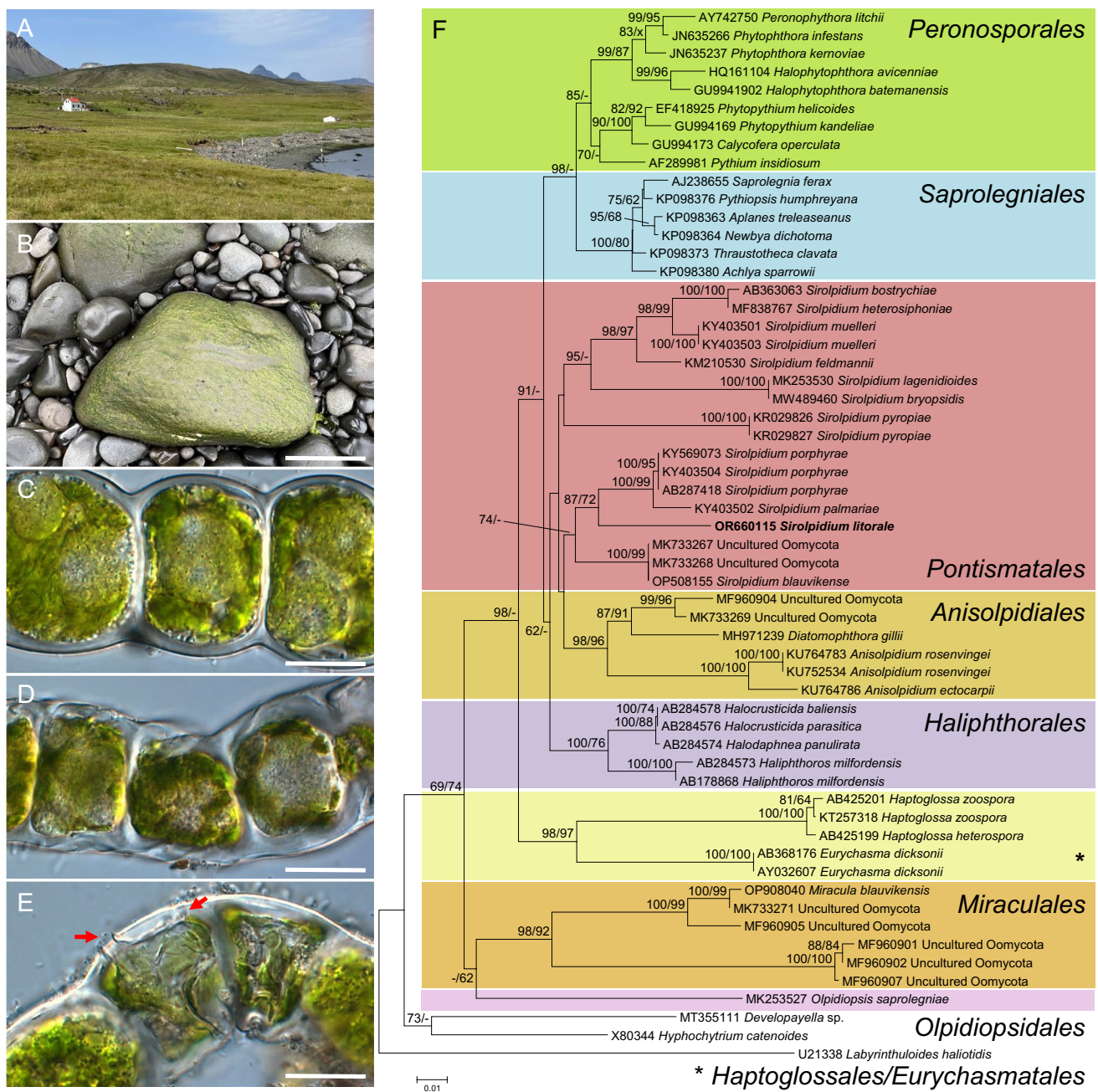


Fig. 1 **A, B** Habitat of *Urospora neglecta* infected with *Sirolopidium littorale*. **A** The research station at Blávík, with the littoral of the rocky beach on the right side (north) having a green colour due to colonization of stones with *U. neglecta*. **B** Close-up of a stone covered with *U. neglecta* filaments. **C–E** Life cycle stages of *S. littorale*. **C** Early infection with thalli in their biotrophic phase. **D** Late infection stages, with the host cytoplasm and chloroplasts showing signs of degradation. **E** Empty thallus after zoospore release with

red arrows pointing to the broadly cylindrical discharge tubes. The scale bar equals about 10 cm in **B** and 20 µm in **C–E**. **F** Phylogenetic reconstruction in Minimum Evolution based on partial nrSSU sequences. Numbers on branches denote bootstrap support in Minimum Evolution and Maximum Likelihood, in the respective order. A minus sign denotes support for the presented or an alternate topology lower than 60%, an x denotes a conflicting topology with a support value higher than 60%

but gradually forms very thin colourless wall containing the hyaline thallus with scattered tiny droplets of lipid, completely filling a segment of infected filaments, causing slight hypertrophy. Multiple infections are common

in young cells, but a single segment of infected host cell often contains one to three spherical, subspherical, to oblong thallus (15–60 µm long, 10–30 µm in diameter), which are compacted within the host cell and do not invade

into adjacent healthy cells. Once the thallus becomes fully mature, each thallus develops one to two short, broadly cylindrical discharge tubes that are 5–18 µm long and 5–10 µm in diameter (Fig. 1E). As soon as the thallus matured, the protoplasmic contents became coarser and differentiated into narrowly pyriform shaped biflagellate zoospores (4–8 µm long by 5–7 µm broad). The zoospores matured within the thallus before emerging through the discharge tube and swimming away from the orifice in vortical motion for a short distance in random directions for a few minutes, before settling and becoming immotile. The parasite was aggressively infecting young filaments of the host algae rather than older or moribund portions. About 60% of the *U. neglecta* filaments collected during the summer of 2023 from the intertidal zone of the coast at Blávík, southeast Iceland, were observed to be parasitized by *Pontisma*. Field samples further incubated for 3–4 weeks at controlled conditions as previously reported (Buaya et al. 2021b) led to a further increase of the pathogen density. The infections could be maintained on young *U. neglecta* filaments to which infected filaments were added. Other marine algae of the genera *Pylaiella*, *Capsosiphon*, *Bryopsis*, *Palmaria*, *Porphyra*, and *Polysiphonia* were also co-occurring with infected *U. neglecta*, but did not show infection.

Molecular phylogeny

Phylogenetic reconstructions using partial small nuclear ribosomal subunit (18S) sequences showed that the parasite found in *Urospora neglecta* belonged to the genus *Sirolopidium*, grouping with *Sirolopidium porphyrae* with moderate to high support (Fig. 1F). Most of the main groups of holocarpic oomycetes were resolved as monophyletic. However, no support for the monophyly or polyphyly of *Pontismatales* was obtained, similar to previous studies (e.g. Buaya et al. 2023). Also, higher-level relationships above the order level could mostly not be resolved with confidence, except for a sister-group relationship of *Eurychasmatales* and *Haptoglossales*, which received high support in both analyses.

Taxonomy

The oomycete species discovered in this study in *Urospora neglecta* on the shore of Blávík, Iceland, is described here as a new species of the genus *Sirolopidium*.

Sirolopidium litorale Buaya & Thines, **sp. nov.**, MycoBank MB 850852.

Etymology: Derived from *litora*, the Latin word for shore, relating to the upper littoral habitat of host and pathogen.

Description: *Straminipila*, *Oomycota*, *Pontismatales*. *Thallus* endobiotic in cells of *Urospora neglecta*, unwallied shortly after infection, bounded by a thin wall at maturity, 15–60 µm long, 10–30 µm in diameter in case of single infections, smaller in case of multiple infections per host cell, which usually remains in its original shape or becomes hypertrophic, while chloroplasts are gradually degraded into greenish residues. *Exit tubes* short, broad cylindrical, 5–18 µm long and 5–10 µm in diam. *Zoospores* assuming motility within the mature thallus, swimming away in a vortical movement after discharge before coming to a rest and encysting, 4–8 µm long by 5–7 µm broad, heterokont and biflagellate. *Resting spores* not observed.

Type: Iceland, Fáskrúðsfjörður, Blávík, 64°53'37.0"N 13°50'26.9"W, collected by I. Tsai and M. Thines on the 13th of August 2023, deposited in the Herbarium Senckenbergianum (FR) under the accession number FR-0046167, ex-type partial nrSSU sequence OR660115.

In an earlier publication by Buaya et al. (2019a, b), several holocarpic species infecting red algae were combined into *Pontisma* in the absence of molecular data for *Sirolopidium bryopsidis*. As *Pontisma* and *Sirolopidium* are now considered the same genus (Buaya et al. 2021b), these are now transferred to *Sirolopidium*, as by combining *Pontisma lagenidioides* into *Sirolopidium* Karling (1942) established the priority of *Sirolopidium* over *Pontisma*. Also the recently-described species *Pontisma blauvikense* (Buaya et al. (2023) should have already been described in *Sirolopidium*. Herewith we have rectified this by listing the necessary new combinations.

Sirolopidium blauvikense (Buaya & Thines) Buaya & Thines, **comb. nov.**, MycoBank MB 850853. Basionym: *Pontisma blauvikense* Buaya & Thines, Journal of Eukaryotic Microbiology 70:e12957, p. 5 (2023), MB 844447. ***Sirolopidium bostrychiae*** (Sekimoto, T.A. Klochkova, J.A. West, Beakes & D. Honda) Buaya & Thines, **comb. nov.**, MycoBank MB 850854. Basionym: *Olpidiopsis bostrychiae* Sekimoto, T.A. Klochkova, J.A. West, Beakes & D. Honda, Phycologia 48: 463 (2009), MB 830684. ***Sirolopidium heterosiphoniae*** (G.H. Kim & T.A. Klochkova) Buaya, T.A. Klochkova & Thines, **comb. nov.**, MycoBank MB 850855. Basionym: *Olpidiopsis heterosiphoniae* G.H. Kim & T.A. Klochkova, Fungal Systematics and Evolution 4: 27 (2019) MB830685. ***Sirolopidium muelleri*** (Y. Badis & C.M.M. Gachon) Buaya & Thines, **comb. nov.**, MycoBank MB 850856. Basionym: *Olpidiopsis muelleri* Y. Badis & C.M.M. Gachon, Fungal Systematics and Evolution 4: 27 (2019), MB830686. ***Sirolopidium palmariae*** (Y. Badis & C.M.M. Gachon) Buaya & Thines, **comb. nov.**, MycoBank MB 850857. Basionym: *Olpidiopsis palmariae* Y. Badis & C.M.M. Gachon, Fungal Systematics and

Evolution 4: 29 (2019), MB830687. *Sirolpidium porphyrae* (Sekimoto, Yokoo, Y. Kawam. & D. Honda) Buaya & Thines, **comb. nov.**, MycoBank MB 850858. Basionym: *Olpidiopsis porphyrae* Sekimoto, Yokoo, Y. Kawam. & D. Honda, Mycological Research 112: 369 (2008), MB511288. *Sirolpidium pyropiae* (G.H. Kim & T.A. Klochkova) Buaya, T.A. Klochkova & Thines, **comb. nov.**, MycoBank MB 850859. Basionym: *Olpidiopsis pyropiae* G.H. Kim & T.A. Klochkova, Fungal Systematics and Evolution 4: 29 (2019) MB830688.

Discussion

Holocarpic oomycetes are characterised by converting their entire cytoplasm into zoospores. While this is likely to be an ancestral trait for oomycetes (Beakes and Thines 2017), this mode of sporulation has re-evolved in *Lagena*, which likely originates from eucarpic, pythium-like oomycetes (Thines and Buaya 2022). Since cultivation apart from the host could not be achieved for most genera, so far, research in these organisms is sparse in comparison to the eucarpic oomycetes (Beakes and Thines 2017). However, two model systems have been already established, for diatoms namely *Lagenisma coscinodisci* (Buaya et al. 2019b; Vallet et al. 2019) and *Miracula blauvikensis* (Buaya and Thines 2022), and parasites of brown algae, two species of *Anisolpidium* (Gachon et al. 2017; Murúa et al. 2020; Küpper et al. 2021) and *Eurychasma dicksonii* (Gachon et al. 2009; Klinger et al. 2019) have been suggested as model systems. A stable dual host-parasite culture, which can be used as an experimental system is currently lacking for *Sirolpidium*. One factor contributing to this phenomenon is the decline in the infectivity of the parasites over time when cultured under laboratory conditions. This was the case after 10 years in *S. heterosiphoniae* (Klochkova et al. 2017) or already after some months (*S. bostrychiae*, West et al. 2006; and *P. pyropiae*, Klochkova et al. 2016).

Species of the widespread genus *Sirolpidium* infect a variety of hosts, including red algae (Sekimoto et al. 2008; Klochkova et al. 2012, 2016; Buaya et al. 2019a), green algae (Buaya et al. 2021b; this study), as well as diatoms and brown algae (Buaya et al. 2023). This wide host spectrum is remarkable, and considering that its hosts are largely unrelated, has likely been expanding by a series of host jumps (Thines 2019).

In this study, the new species *Sirolpidium litorale* was found as a parasite of the widespread green alga *Urospora neglecta* in the upper intertidal zone near the research station Blávik in the East Fjords of Iceland. The extensive occurrence of the genus *Sirolpidium* (Hassett et al. 2019), along with its broad spectrum of host species (Buaya et al. 2023), makes it a pertinent candidate for studying the interaction between

holocarpic oomycetes and their host organisms. *Sirolpidium litorale* seems especially suited for this, as its host, *U. neglecta* can be easily cultivated and has the advantage that genetically homogenous single spore cultures can be obtained from zoospores. This not only renders experimentation easier but could also facilitate establishing genetic tools for the host. In conjunction with the fact that *S. litorale* efficiently infects young stages of its host, the *Sirolpidium/Urospora* pathosystem could be well-suited for gaining deeper insights into pathogenicity mechanisms and resistance in marine algae and their holocarpic oomycete parasites.

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Authors' contributions ATB and MT conceived the study. IT and MT did the fieldwork and provided materials. ATB conducted the laboratory experiments and performed the microscopic characterisation. MT performed the phylogenetic analyses. MT and ATB wrote the manuscript, with the contributions of IT and TAK. All authors agreed with the submission of the manuscript.

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Data availability Sequence Data have been deposited in GenBank.

Declarations

Ethics approval and consent to participate Not applicable.

Consent for publication Not applicable.

Competing interests MT is the Editor-in-Chief of Mycological Progress, but was not involved in the editorial processes associated with handling this manuscript.

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