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New records of the marine diatom parasites *Lagenisma coscinodisci* (Lagenismatales, Oomycetes) and *Paulsenella kornmannii* (Thoracosphaerales, Dinophyceae) in Korea

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This study presented the first record of two marine diatom parasites, *Lagenisma coscinodisci* (Oomycetes) and *Paulsenella kornmannii* (Dinophyceae), in Korea. Plankton samples were collected from Yongho Harbor, Busan, in March 2022, and diatoms infected by these parasites, *Coscinodiscus wailesii* by *L. coscinodisci* and *Eucampia zodiacus* by *P. kornmannii*, were isolated for morphological and molecular analyses. Both parasites exhibited developmental characteristics consistent with previous descriptions. The 18S rRNA gene sequences of *L. coscinodisci* (1,430 bp) and *P. kornmannii* (1,331 bp) were successfully obtained, with the latter being reported for the first time. Phylogenetic analysis placed *L. coscinodisci* within Oomycetes, clustering with *Thraustotheca clavata*, while *P. kornmannii* was positioned within Dinophyceae, closely related to *P. vonstoschii*. This study provides new insights into the biodiversity of parasitic protists in Korean waters and contributes the first molecular data for *P. kornmannii*.

Keywords: 18S rRNA, *Coscinodiscus wailesii*, *Eucampia zodiacus*, molecular phylogeny, morphology, parasitism

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Introduction

Diatoms are susceptible to infection by broad taxonomic groups of parasitic protists, including Aphelidiomycetes, Bigyromonadea, Chytridiomycetes, Dinophyceae, Ellobiopsea, Labyrinthulomycetes, Oomycetes, Phytomyxea, and Thecofilosea (Drebes and Schnepf, 1988; Schnepf *et al*., 1990; Cavalier-Smith, 1993; 2018; Kühn, 1997; Schweikert and Schnepf, 1996; Scholz *et al*., 2016; Dumack *et al*., 2017; Danz and Quandt, 2023; Cho and Kim, 2024). Among these, Oomycetes represent a diverse lineage of fungus-like protists that infect animals, plants, and algae in marine and freshwater ecosystems (Lee *et al*., 2015; Larousse and Galiana, 2017; Buaya and Thines, 2020; Buaya *et al*., 2021). *Lagenisma coscinodisci* Drebes, 1968 (Lagenismatales, Oomycetes) is a parasite of centric diatoms of the genus *Coscinodiscus* and is one of the few studies marine holocarpic pathogenic Oomycetes (Beakes *et al*., 2014). The species was initially reported as a fungal parasite, *Lagenidium* sp. infecting the marine diatom *Coscinodiscus centralis* from Hecate Strait, British Columbia (Parsons, 1962). Although Parsons illustrated the organism, he failed to describe sexual apparatus and sporangia using formalin-preserved plankton samples and only tentatively assigned it to *Lagenidium* sp. Later, in 1966, Drebes (1966) collected a very similar parasite to Parson's fungus from Helgoland (Germany). He clearly documented its morphology, asexual reproduction, and infection cycle through photomicroscopy, maintained the infection in laboratory-grown *Coscinodiscus* cultures. In 1968, Drebes formally

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named the fungus *Lagenisma coscinodisci*. Since then, the parasite has been observed in the North Sea (Drebes, 1966; 1968; 1974), along the west coast of the USA (Gotelli, 1971), and near Jamaica (Grahame, 1976).

The genus *Paulsenella* Chatton, 1920 (Dinophyceae) is an ectoparasitic dinoflagellate parasitizing marine diatoms. In 1911, Paulsen described an ectoparasite from the coastal waters of eastern Greenland, feeding on the diatoms *Chaetoceros borealis* and *Chaetoceros decipiens*, and named it tentatively *Apodinium chaetoceratis* Paulsen, 1911. Chatton (1920) later transferred it to a new genus, *Paulsenella* in his literature on parasitic dinoflagellates. Later, Drebes and Schnepf (1988) isolated three *Paulsenella* strains infecting *C. decipiens*, *Eucampia zodiacus*, and *Streptotheca thamesis*, respectively, from the Wadden Sea near List/Sylt (North Sea, Germany). They then compared their morphology, development, host range, and feeding mode using host-parasite cultures and described two new species, *Paulsenella kornmannii* Drebes & Schnepf, 1988 on *Eucampia zodiacus* and *Paulsenella vonstoschii* Drebes & Schnepf, 1988 on *Streptotheca thamesis*, based on their developmental processes and biological traits, including the timing of peduncle formation, the number of food vacuoles, and variation in cyst production (Drebes and Schnepf, 1988). The two *Paulsenella* species, *P. kornmannii* and *P. vonstoschii*, showed similar morphological characteristics, but they differed in host range and specificity. *P. kornmannii* exhibited high host specificity, infecting only the diatom *Eucampia zodiacus*, while *P. vonstoschii* showed a wide host range, infecting several diatom genera including *Streptotheca*, *Neostreptotheca*, *Lithodesmium*, and *Bellerochea* (Paulsen, 1911; Drebes and Schnepf, 1988; Konovalova, 2008; Purushothaman *et al*., 2023). To date, the molecular phylogenetic position has been reported only for *P. vonstoschii* (Kühn and Medlin, 2005). Therefore, molecular sequence data for other *Paulsenella* species are needed to elucidate the phylogenetic relationships within the genus.

In this study, the marine diatoms *Coscinodiscus wailesii* and *Eucampia zodiacus* were observed to be infected by the parasites *L. coscinodisci* and *P. kornmannii*, respectively, in Yongho Harbor, Busan, Korea in March 2022. We established parasite and host culture systems to examine their morphological and developmental characteristics as well as their 18S rRNA gene sequences. This study is the first to report the molecular phylogenetic position of *P. kornmannii* based on 18S rRNA gene sequences. Additionally, it presented the first record of these two parasitic species infecting marine diatoms in Korea.

Materials and Methods

Sample collection and cultivation

Plankton samples were collected using a 20 μm mesh net from the surface seawater at the Yongho Harbor of Busan in Korea (35°08′00″N, 129°06′55″E) in March 2022. Net samples were immediately transported to the laboratory within 15 min. The samples were stored at room temperature until further microscopic examination. Surface seawater temperature and salinity were measured *in situ* using a YSI Pro30 (YSI Inc. OH, USA).

Infected diatom cells were isolated using a capillary pipette, washed in serial drops of 0.2 μm syringe-filtered sterile seawater and put into a 24-well plate containing sterile seawater with naive host cells under an inverted microscope (Axio Imager A1, Carl Zeiss Inc., Oberkochen, Germany) (Yoo and Kim, 2020). Additionally, uninfected host diatom cells were isolated as describe above and placed into 24 well plate. Host cultures were maintained by weekly transfers with f/2 + Si medium (Guillard and Ryther, 1962). All cultures were incubated with a 14 : 10 light-dark cycle at 130 μmol photons m^{-2} s^{-1} at 20°C. The parasite cultures were transferred to naive host cultures twice a week.

For the specimen slide preparation, the culture of the diatom *C. wailesii* cells infected by the parasite *L. coscinodisci* strain MPL-CwLc01 and the net-tow sample of the diatom *Eucampia zodiacus* cells infected by the parasite *P. kornmannii* collected from the Yongho Harbor on March 14, 2022, were fixed with glutaraldehyde at a final concentration of 2%. Infected cells were individually isolated from the fixed samples and rinsed repeatedly with serial drops of distilled water. Glycerol gelatine was melted on a water bath at 60°C and dropped to a slide. The washed cells were mounted on the slide by mixing with glycerol gelatin and covered with a coverslip. The slides were deposited to the Honam National Institute of Biological Resources and the Nakdonggang National Institute of Biological Resources.

Light microscopy

Specimens were observed using an Axio Imager A2 (Carl Zeiss Inc., Oberkochen, Germany) and recorded at ×400 and ×630 magnifications using a digital cinema camera (Canon EOS R5C, Canon Inc., Tokyo, Japan) mounted on the microscope. Cell size was measured using Zen software (Carl Zeiss Inc.) based on still images extracted from video recordings. To examine the thecal plates of parasites, cells were fixed with glutaraldehyde (1% final concentration), stained with Calcofluor White (40 μg mL^{-1} final concentration), and observed under ultraviolet light (excitation at 360 nm and emission at 460 nm) using an Axio Imager A2 (Fritz and Triemer, 1985).

DNA extraction, PCR, and sequencing

Newly generated parasite zoospores were isolated, washed in serial drops of sterile filtered seawater, and put into a polymerase chain reaction (PCR) tube. DNA was extracted using the Chelex extraction method (Kim and

Park, 2014). The 18S rRNA gene regions were amplified using primer sets EUKA (5′-AAC CTG GTT GAT CCT GCC AGT-3′)/1209R (5′-GGG CAT CAC AGA CCT G-3′) or 328F (5′-ACC TGG TTG ATC CTG CCA G-3′)/329R (5′-TGA TCC TTC YGC AGG TTC AC-3′) (Giovannoni *et al*., 1988; Moon-van der Staay *et al*., 2000). PCR was performed by adding 2 μL of template DNA, 2 μL of each forward and reverse primer, and 14 μL of deionized sterile water to an AccuPower PCR premix (Bioneer, Daejeon, Korea). The reactions were performed using a C1000 Touch thermal cycler (Bio-Rad, Hercules, CA, USA) under the following conditions: an initial denaturation at 95°C for 3 min, followed by 40 cycles of denaturation at 95°C for 45 s, annealing at 50°C for 45 s, and extension at 72°C for 45 s, with final extension at 72°C for 7 min (Cho and Kim, 2024). PCR products were visualized on 1% TAE agarose gels stained with Eco Dye (SolGent Co., Daejeon, Korea) and run at 110 V for 15 min. Purification was performed using Exo SAP-IT (Thermofisher Scientific). The purified products were then sequenced using the EUKA/1209R or 328F/329R primer sets with a Big-Dye Terminator v3.1 Cycle Sequencing kit (Applied Biosystem) and an ABI model 3730xl DNA Analyzer (Applied Biosystems: Foster City, CA, USA). Low-quality regions were trimmed, and sequence reads were assembled using ContigExpress (Vector NTI v. 10.1: Invitrogen, Grand Island, NY, USA). The resulting sequences were verified through a BLASTN search in NCBI.

Alignment and phylogenetic analyses

A total of 57 18S rRNA gene sequences, including three sequences of parasites generated from this study, along with 28 taxa of stramenopiles and 26 taxa of alveolata downloaded from GenBank (http://www. ncbi.nlm.nih.gov), were aligned using MAFFT v7.10 (Katoh and Standley, 2013; Katoh *et al*., 2019). The aligned dataset was trimmed the ambiguous site using MEGA11 (Tamura *et al*., 2021), and the resulting 1968 informative sites were applied for further phylogenetic analyses. Maximum likelihood analysis was performed using RAxML 8.0.0 (Stamatakis, 2014) based on the GTRGAMMA evolution model with 2,000 bootstrap replicates.

Results and Discussion

Taxonomic summary

Phylum Gyrista Cavalier-Smith, 1998 stat. n. 2018
Class Oomycetes Winter, 1880
Order Lagenismatales Dick, 2001
Family Lagenismataceae Dick, 2001
Genus *Lagenisma* Drebes, 1968

***Lagenisma coscinodisci* Drebes, 1968 (Fig. 1)**
Reference: Buaya *et al*. (2019).

Material examined. Marine water (salinity 32.2, temperature 12.1°C) collected from Yongho Harbor of Busan, Republic of Korea (35°08′00″N, 129°06′55″E) on March 02, 2022.
Accession number. PV110864.
Description. Zoospores are kidney-shaped and laterally biflagellate, measuring approximately 10.0 μm in length (range: 8.8–11.1 μm) and about 6.5 μm in width (range: 5.0–7.9 μm) *in vivo*. They attach to the exterior of the host frustule and subsequently penetrate into the host cell. Inside the host, the thallus initially develops as a small, undifferentiated structure that gradually expands. The thallus becomes visible within 12 hours following zoospore attachment. It spreads throughout the host cytoplasm, eventually occupying the entire host cavity. Approximately 18 hours after attachment, the thallus matures and differentiates into a zoosporangium, in which new zoospores are formed. The zoosporangium becomes densely packed with developing zoospores that gradually acquire motility. Around 22 hours after attachment, a discharge tube extends outside the host, within an hour, zoospores are released through the discharge tube. These motile zoospores actively exit the host, resume their free-swimming stage, and disperse to locate new hosts.
Host. *Coscinodiscus wailesii* Gran & Angst, 1931.
Distribution. Puget Sound, USA (Gotelli, 1971), Kingston Harbour, Jamaica (Grahame, 1976), Wadden Sea near List/Sylt, Germany (Schnepf and Drebes, 1977), Oosterschelde, Netherlands (Wetsteyn and Peperzak, 1991), and Helgoland Roads, Germany (Buaya *et al*., 2019)
Remark. The Korean strain of *Lagenisma coscinodisci* exhibited developmental characteristics identical to those reported by Gotelli in 1971 (Fig. 1). While the previously reported strain has a zoospore size of 7 × 8 μm, the Korean strain measured 6.5 × 10 μm, showing a similar width but a slightly greater length. The surface water temperature range for *L. coscinodisci* has been reported as 8.2–20.2°C (Wetsteyn and Peperzak, 1991); however, the Korean strain was observed within a narrower range of 12.1–13.5 °C. Similarly, while the documented salinity for *L. coscinodisci* is 29.8–32.4, the Korean strain was found within a range of 31.2–32.2. Previous studies have reported *L. coscinodisci* infecting various diatom species, including *Coscinodiscus concinnus*, *C. granii*, *C. wailesii*, and other *Coscinodiscus* species (Drebes, 1966; Chakravarty, 1974). However, in Korean field samples, despite the presence of various *Coscinodiscus* species, parasite infections were observed only in *C. wailesii*.
Voucher slide. Slide with glutaraldehyde-fixed specimens was deposited at the Honam National Institute of Biological Resources (HNIBRPR41).

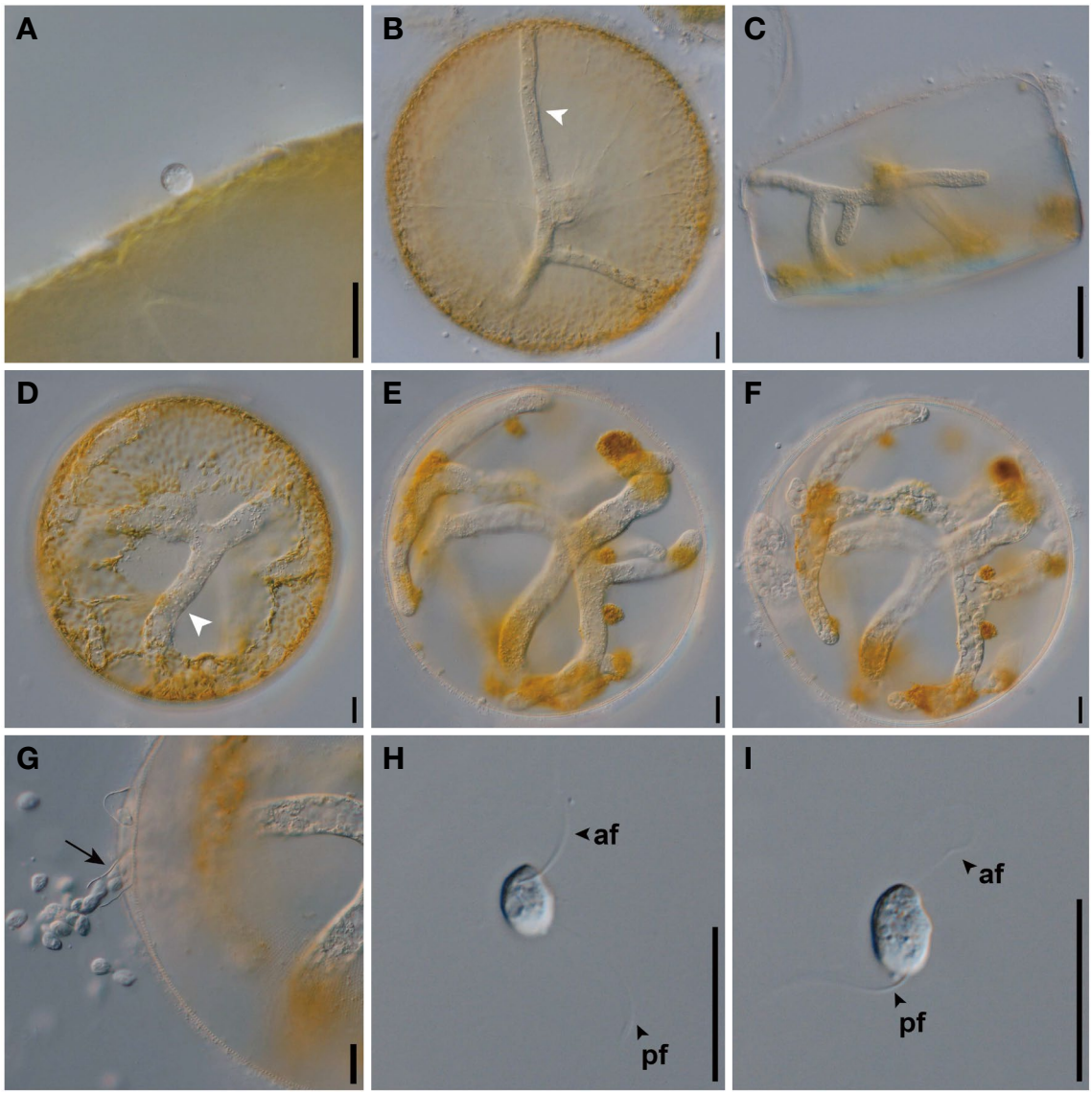

Fig. 1. Light micrographs showing *Lagenisma coscinodisci* infecting the marine diatom *Coscinodiscus wailesii*. (A) A zoospore attached to the host frustule. (B) Valve view of the diatom host showing the holocarpic formation of the parasite zoosporangium (white arrowhead) inside the host. (C) Lateral view of the diatom possessing a zoosporangium. (D) The growth stage of the thallus which splits into branches. (E) The thallus becomes more voluminous. (F) The thallus transforms into a zoosporangium inside *C. wailesii*. (G) Formation of zoospores and protrusion of a discharge tube (black arrow) from the host cell. (H) Flagella (black arrowhead) are laterally inserted. (I) Kidney-shaped zoospore. af; anterior flagellum, pf; posterior flagellum. Scale bars represent 20 μm.

Phylum Miozoa Cavalier-Smith, 1987 stat. n. 1999
Class Dinophyceae Pascher, 1914
Order Thoracosphaerales Tangen, 1982
Family Thoracosphaeraceae Schiller, 1930 emend. Tangen, 1982
Genus *Paulsenella* Chatton, 1920

***Paulsenella kornmannii* Drebes & Schnepf, 1988 (Fig. 2)**
Reference: Drebes and Schnepf (1988).

Material examined. Marine water (salinity 31.2, temperature 13.5°C) collected from Yongho Harbor of Busan, Republic of Korea (35°08′00″N, 129°06′55″E) on March 14, 2022.
Accession number. PV110865.
Description. The dinospore has a hemispherical or conical epitheca and a hemispherical hypotheca, measuring approximately 16.2 μm in length (range: 14.5–17.6 μm) and 12.8 μm in width (range: 11.8–14.5 μm) *in vivo*. It penetrates the host through an intercingular slit located in the host's girdle and forms a peduncle inside the host approximately 30 minutes after attachment. Using the peduncle,

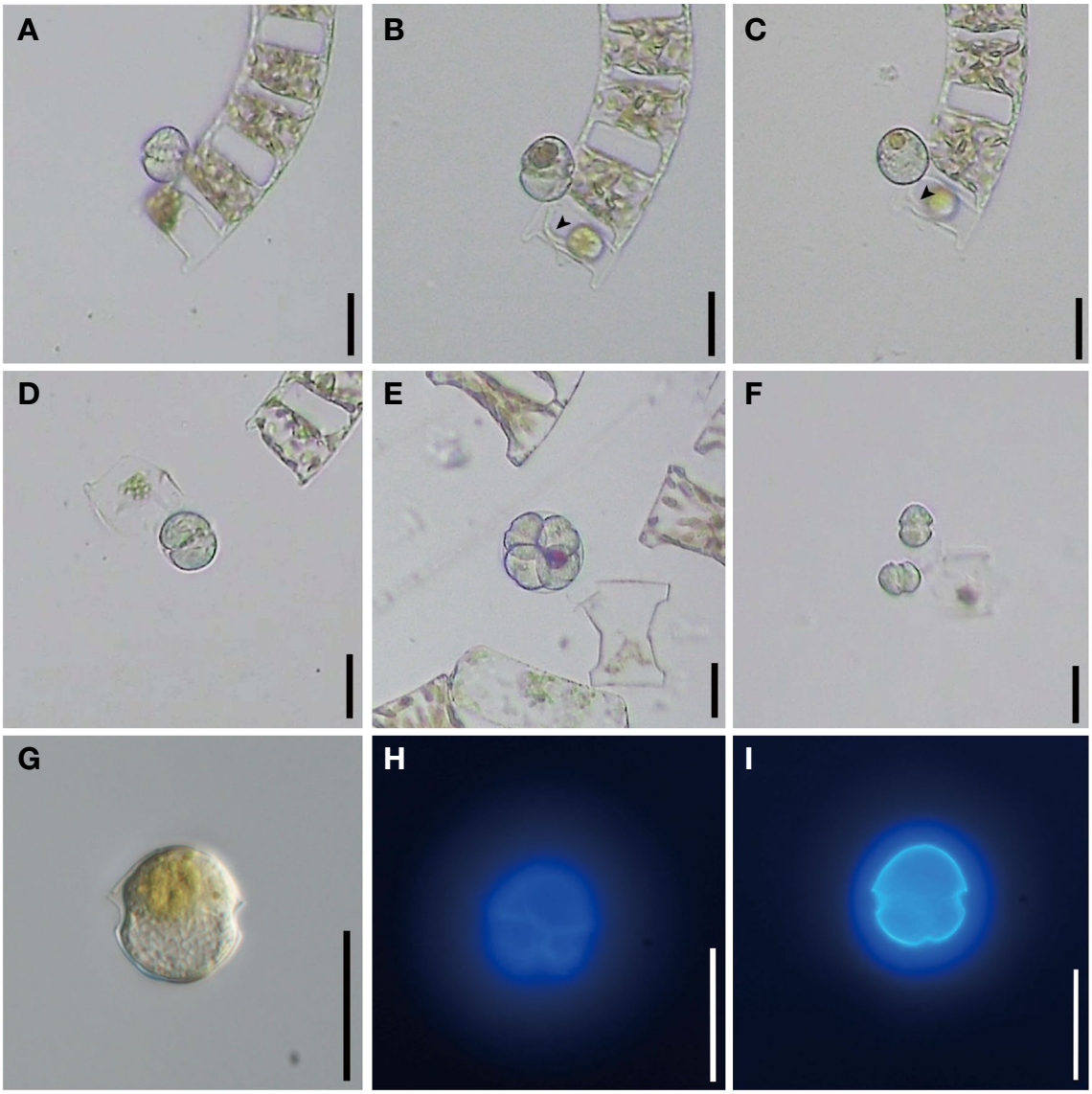

Fig. 2. Light micrographs showing *Paulsenella kornmannii* infecting the marine diatom *Eucampia zodiacus*. (A) A dinospore attached to the host frustule. (B) The parasite feeding on the host material using a peduncle (arrowhead). (C) The parasite transforming into an encysted trophont. (D) The first division of the encysted trophont. (E) The second division of the encysted trophont. (F) Newly produced dinospores being released from the cyst. (G–I) Dinospore with thecal plates. (H, I) Calcofluor-stained thecal plates of the dinospore. Scale bars represent 20 μm.

the dinospore absorbs the host materials and develops a single large vacuole. Within four hours after the peduncle is formed, the entire host cytoplasm is consumed. After feeding, it changes into a round shaped and transforms into an encysted trophont. During the trophont stage, it lacks both cingulum and sulcus. Approximately 19 hours after attachment, the first cell division occurs. The encysted trophont subsequently undergoes a series of divisions, ultimately producing two to four dinospores. Division is complete approximately 28 hours after attachment, after which the newly formed dinospores are released to locate new hosts.

Host. *Eucampia zodiacus* Ehrenberg, 1839.
Distribution. Wadden Sea near List/Sylt, Germany (Drebes and Schnepf, 1988).
Remark. The Korean strain of *Paulsenella kornmannii* exhibits morphological and developmental characteristics consistent with those described by Drebes and Schnepf (1988). Similar to the strain from the German Bight, the Korean strain has a hemispherical or conical epitheca and a hemispherical hypotheca. The Korean strain measures 14.5–17.6 μm in length and 11.8–14.5 μm in width, closely aligning with the size range reported for the German strain (15–19 μm in length, 12–15 μm in width). Both strains

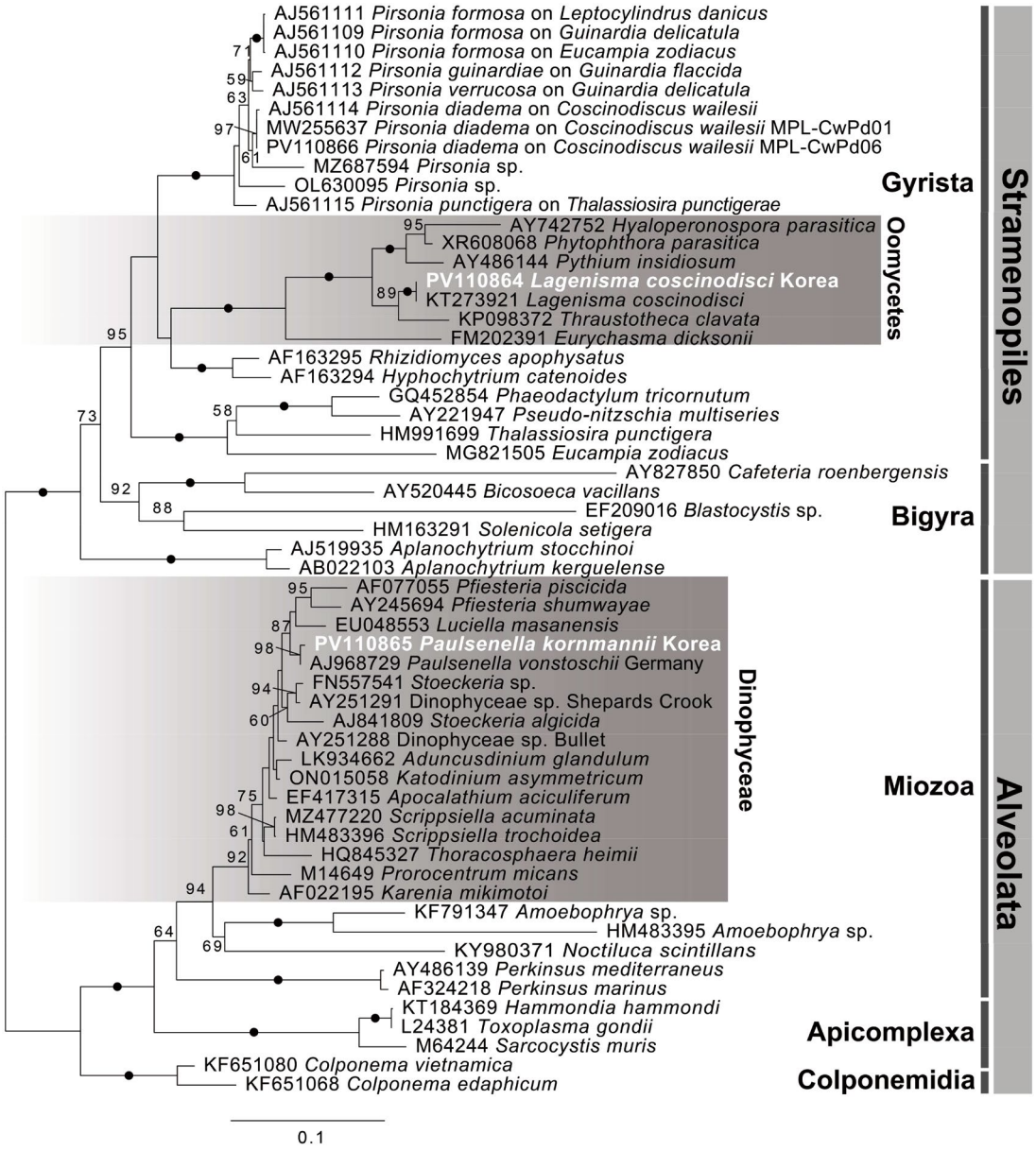

Fig. 3. Maximum likelihood phylogeny inferred from 18S rRNA gene sequences. Sequences generated from this study are presented in white. Bootstrap values (over 50%) are shown above nodes. Closed circles indicate robust support with 100% bootstrap values.

share key developmental traits, including penetration through the intercingular slit in the host's girdle region and formation of a peduncle upon attachment. Additionally, both develop a single large food vacuole and exhibit similar division patterns, producing two to four dinospores. Several developmental differences have been reported between the morphologically similar species *P. kornmannii* and *P. vonstoschii*. Among these developmental differences, *P. kornmannii* lacks the refractive granules and loses its flagella more rapidly than *P. vonstoschii*. In addition, *P. kornmannii* often extrudes the residual body of the food vacuole during the final cell division, whereas in *P. vonstoschii*, the residual body is typically retained within the dinospore (Drebes and Schnepf, 1988). The Korean strain of *P. kornmannii* was observed at temperatures ranging from 13.5 to 14.5°C and at a salinity of 31.2–31.8. However, environmental conditions for the German strain were not specified in the original description. Host specificity also remains consistent, as both strains infect *Eucampia zodiacus*.

Voucher slide. Slide with glutaraldehyde-fixed specimens was deposited at the Nakdonggang National Institute of Biological Resources (NNIBRDN2210).

rRNA gene sequences and molecular phylogeny

The 18S rRNA gene sequences of the two parasites, *L. coscinodisci* and *P. kornmannii*, were successfully obtained, with sequence lengths of 1,430 bp and 1,331 bp, respectively. Notably, this study represents the first publication of the molecular sequence of *P. kornmannii*. A BLASTN search revealed that the sequence of *P. kornmannii*, which infects the diatom *E. zodiacus*, exhibited 99.47% similarity to *P. vonstoschii* (AJ968729), a parasite infecting the diatom *Streptotheca thamesis*, isolated from the Wadden Sea near List/Sylt, Germany (Kühn and Medlin, 2005). The 18S rRNA gene sequence of the Korean strain of *L. coscinodisci* partially matched the Helgoland strain (KT273921) with 100% identity, but with relatively low query coverage (66%, 943 bp). Additionally, it showed 98.9% identity and 100% query coverage with *Crypticola clavulifera* (MF066365), an Oomycetes pathogen of mosquito larvae (Frances *et al*., 1989; Mendoza *et al*., 2018).

A maximum likelihood (ML) phylogenetic tree inferred from the 18S rRNA sequences demonstrated that the two parasitic species infecting marine diatoms belong to two distinct phyla, Miozoa and Gyrista (Fig. 3). The Korean and Helgoland (KT273921) strains of *L. coscinodisci* clustered together with *Thraustotheca clavata* (KP098372) with high bootstrap support (89%) and formed a sister lineage to a clade containing *Hyaloperonospora parasitica*, *Phytophthora parasitica*, and *Pythium insidiosum* within the class Oomycetes (Fig. 3). The Korean strain of *P. kornmannii* grouped closely with *P. vonstoschii* with strong bootstrap support (98%) and formed a sister lineage to a clade containing *Pfiesteria* and *Luciella* species, which received moderate bootstrap support (87%), within the class Dinophyceae (Fig. 3).

Conflicts of Interest

The authors of this paper have no affiliation with any interests and are solely responsible for the paper.

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