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Cyst-Motile Stage Relationship and Phylogenetic Study of Levanderina fissa, a Bloom-Forming Dinoflagellate from Chabahar Bay in the Coasts of the Sea of Oman

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Abstract

Levanderina fissa is a cosmopolitan, unarmored marine dinoflagellate capable of forming harmful algal blooms (HABs), which adversely impact marine ecosystems and coastal economies. Despite its ecological significance, knowledge of its life cycle, particularly the role of benthic cysts in bloom dynamics, remains limited, particularly in the Sea of Oman. This study presents the first isolation and characterization of *L. fissa* resting cysts from sediments collected using a Van Veen grab sampler in the Konarak region along the southeastern coasts of Iran. Single cysts were isolated and germinated in the f/2 medium at 25°C under a 12:12 light photoperiod with an irradiance of 60 µmol photons m^{-2} s^{-1}. Morphological examination of the cysts revealed a spherical to ovoidal shape with a thick, unornamented wall. Following germination, the morphology of the resulting motile cells was examined using light microscopy, revealing key diagnostic features, including an unusual and distinctly formed sulcus, consistent with the description of *L. fissa*. For molecular confirmation and phylogenetic placement, the Internal Transcribed Spacer (ITS) region was amplified and sequenced. Phylogenetic analysis using Maximum Likelihood (ML) placed the Iranian strain firmly within a monophyletic clade containing other *L. fissa* strains, supported by a 98–100% bootstrap value. This combined morphological and molecular approach unequivocally confirms the species identity. This research underscores the critical importance of integrating cyst studies into HAB monitoring programs, as understanding the distribution and germination dynamics of benthic resting stages is essential for predicting bloom timing, magnitude, and spatial extent in vulnerable coastal ecosystems such as the Sea of Oman.

Keywords: Cyst, Motile stage, Dinoflagellate, Phylogeny, Sediment, Southeastern Coasts of Iran

Introduction

A significant proportion of extant marine dinoflagellate species, estimated at over 13–16%, undergo a critical life cycle that incor-

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porates a dormant cyst stage (Mertens et al., 2015). This stage is indispensable for their survival during adverse environmental conditions such as senescence, nutrient limitation, and temperature fluctuations. The formation of these cysts, a characteristic ability of marine dinoflagellates, typically involves a migratory descent towards the seafloor (Liu et al., 2012). This cyst-forming capability facilitates protection, dispersal, and genetic recombination, with excystment often initiating harmful algal blooms (HABs). *Levanderina fissa* (Levander) Moestrup, Hakanen, Gert Hansen, Daugbjerg & M.Ellegaard 2014 (formerly *Gyrodinium instriatum* Freudenthal & J.J.Lee) is a well-documented bloom-forming dinoflagellate that frequently causes red tides, which can severely impact coastal fisheries (Chen et al., 2024; Caroppo et al., 2025) and forms cysts in sediment.

Studying dinoflagellate cysts is crucial for understanding the ecology and biogeography of these algae. While the motile stage can be relatively short-lived and challenging to identify, particularly for unarmored or morphologically ambiguous species, examining cysts from a specific aquatic region provides a robust method to uncover species not detected during plankton surveys (e.g., Baula et al., 2011; Attaran-Fariman, 2012; Yedema et al., 2023; Attaran-Fariman et al., 2025). This approach significantly expands species inventories and refines the biogeographical understanding of specific dinoflagellates. Most planktonic dinoflagellates produce cysts, enabling populations to survive unfavorable conditions until environmental improvements, with excystment frequently initiating algal blooms (Hallegraeff et al., 2004; Kremp and Parrow, 2006; Bravo and Figueroa, 2014).

Molecular studies, particularly targeting the Internal Transcribed Spacer (ITS) region, offer a valuable alternative to microscopic identification. The ITS sequence serves as a robust identifier for phylogenetic and taxonomic analyses among highly diverse species. Globally, extensive research investigates the intricate cyst-motile stage relationships and phylogenetic positions of diverse dinoflagellates, which is crucial for understanding their life cycles and ecological impact. Studies on genera such as *Protoperidinium* (Matsuoka et al., 2006; Ribeiro et al., 2010; Attaran-Fariman, 2011; Mertens et al., 2013), *Scrippsiella* (Gu et al., 2008; Attaran-Fariman et al., 2012; Gu et al., 2013), and *Gymnodinium* (Attaran-Fariman et al., 2007; Gu et al., 2015) have successfully combined morphological assessments with molecular analyses. These integrated approaches are consistently emphasized as necessary for accurate classification and provide valuable context for understanding bloom-forming species globally, including *Levanderina fissa*.

In Iran, comprehensive studies focusing on the phylogeny and relationships between the cyst and motile stages of phytoplankton remain limited, primarily confined to contributions by Attaran-Fariman et al. (2007, 2011, 2012) and Attaran-Fariman and Bolch (2014). However, investigations into the diversity, distribution, and morphological identification of phytoplankton cysts have been more frequently conducted (Attaran Fariman et al., 2012; Attaran Fariman et

al., 2017; Attaran Fariman et al., 2018a; Attaran Fariman et al., 2018b; Dolatabadi et al., 2021; Raisi et al., 2023; Attaran Fariman et al., 2025). While these regional studies have largely focused on identifying various cyst species and their distribution patterns in coastal sediments, they seldom delve into the intricate phylogenetic connections or the complete life cycle dynamics. Addressing this knowledge gap, this study provides the first morphological and molecular identification of *Levanderina fissa* from Iranian waters, specifically focusing on the isolation and cultivation of its cysts under laboratory conditions to thoroughly examine its cyst-motile stage relationship and phylogenetic position.

Material and methods

Sediment sampling

Chabahar Bay, the largest bay in Iran, is situated on the margin of the Oman Sea and represents the closest waterway to the Indian Ocean (Figure 1). This bay experiences a tropical climate, with distinct winter (NE) and summer (SW) monsoon winds. Annually, phytoplankton blooms have been reported in this region during and after the Northeast Monsoon (Ershadifar et al., 2020; Anjaneyan et al., 2023). In this study, sediment samples were collected from the Konarak region within Chabahar bay (Figure 1) using a Van Veen Grab with a sampling area of 0.025 m². Sediment samples were transferred to plastic bottles and stored at 20°C until further processing.

Cyst germination analysis

Cysts were isolated from sediment samples using a sieving and culturing method. Initially, 2 to 3 grams of sediment were suspended in filtered seawater and homogenized for two minutes using a D1900Sc homogenizer to achieve complete disaggregation of sediment particles. The resulting slurry was sequentially passed through 125 µm and 20 µm mesh sieves, as described by Bolch and Hallegraeff (1990). Sediment retained on the 20 µm sieve was thoroughly rinsed with filtered seawater and transferred to a sterile Petri dish.

Individual cysts were then manually isolated under a stereomicroscope and transferred to separate Petri dishes, each containing 20 mL of sterile f/2 culture medium (Guillard and Ryther, 1962). Cultures were incubated under controlled conditions at 25°C. Illumination was provided by white fluorescent lamps at an irradiance of 60 µmol photons m^{-2} s^{-1}, measured with an MS6612 light meter, under a 12-hour light:12-hour dark photoperiod. Petri dishes were monitored weekly to observe cyst germination. Upon successful excystment, unialgal cultures were established from individual excysted cells, yielding two strains for subsequent analysis. Morphological characteristics of both cysts and excysted cells were documented using a Nikon ECLIPSE-TS100 inverted microscope and a Nikon ECLIPSE 50i inverted microscope, with photographic records taken for detailed analysis.

Phylogenetic analysis

Genomic DNA was extracted from excysted cells using the cetyltrimethylammonium bromide CTAB method (Wylezich et al., 2010; Zadehabbas Shahabadi, 2010). DNA quality was assessed by electrophoresis on a

1% agarose gel, and visualization and image capture performed using a gel doc system (E-BOX-VX2/20M). DNA concentration was determined using an RS232C spectrophotometer, and the extracted DNA was stored at −20°C until further analysis.

Partial sequences of the ribosomal RNA gene, including approximately 750 bp of the internal transcribed spacer (ITS) regions,encompassing ITS1, ITS2, and the complete 5.8S rDNA gene, were amplified using ITSA and ITSB primers (Adachi et al., 1996). Polymerase Chain Reaction (PCR) for the two Iranian strains was conducted in a final reaction of 25 µL containing 2.5 µL of PCR buffer, 200 µM dNTPs, 1.5 µM $MgCl_2$, 10 pM of each forward and reverse ITS1-ITS2 primer, 1 U of Taq polymerase, 10 ng of template DNA, and nuclease-free water to the final volume. Amplification was performed in a Thermal Cycler (TC25 Convergys Peltier-Thermal Cycle) under the following thermal program: initial denaturation at 95 °C for 5 min; 35 cycles of denaturation at 94°C for 1 min, annealing at 45 °C for 1 min, and extension at 72 °C for 1 min; and a final extension at 72°C for 10 min.

PCR products were verified by gel electrophoresis and submitted to Pishgam Company for Sanger sequencing. Resulting sequences were edited and manually verified in BioEdit v7.2 (Hall, 1999). Multiple sequence alignment was performed using ClustalW (Thompson et al., 1994) with default gap opening (10.0) and extension (0.2) penalties. Alignment quality was visually inspected and manually curated; all positions containing gaps or missing data were excluded from the final dataset, yielding a trimmed alignment of approximately 636–645 bp.

Phylogenetic analysis was performed using the Maximum Likelihood (ML) method implemented in MEGA6 (Tamura et al., 2013). The best-fit nucleotide substitution model was selected under the Akaike Information

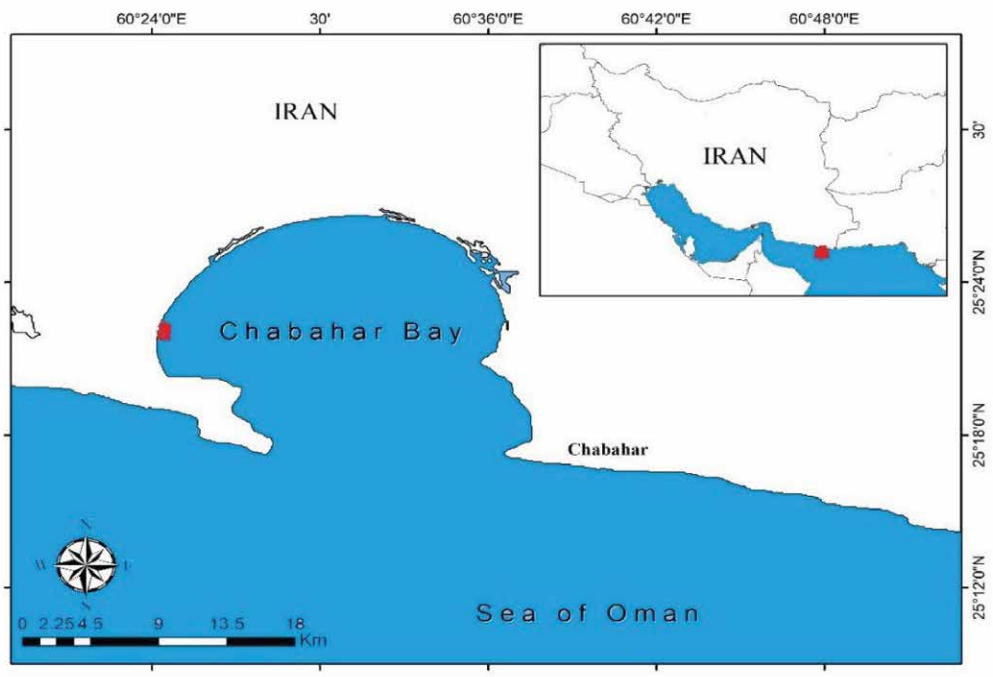

Fig. 1. Location of sediment sampling area in the Konarak, Chabahar Bay

Criterion (AIC) using the Model Selection tool in MEGA6. The Kimura 2-parameter model with gamma-distributed rate variation (K2+G) was identified as the optimal model and applied to all ML analyses. Bootstrap support values were estimated from 1,000 replicates using the same settings. The dataset included 19 reference sequences of Gymnodiniales retrieved from GenBank, with *Prorocentrum minimum* designated as the outgroup. The two Iranian sequences were deposited in GenBank under accession numbers MN604388 (CHcLf1) and MN604387 (CHcGi3).

Results

Morphological characterization of resting cysts and excysted vegetative cells.

The isolated cysts from the sediment were spherical to ovoid, characterized by a thick, unornamented wall. Live cysts contained numerous colorless to orange-brown granules, mostly concentrated in the center. The cysts measured 25–35 µm in width and 35–45 µm in length (n = 30; including speciemens collected fromboth filed sampls and laboratory culture (Figures 2a–b).

After 6 to 7 weeks of single-cyst cultivation, motile, golden-brown cells were observed in both culture plates, leading to the establishment of two unialgal cultures. These motile, flagellated cells were morphologically similar and pyriform (Figures 3h, i). Morphometric measurements were taken from n = 50 motile cells, measuring 30–35 µm in width and 45–50 µm in length. The epitheca of the cell was dome-shaped and slightly narrower than the hypotheca. The hypotheca was cup-shaped with slightly rounded or flattened margins and was divided into two asymmetrical parts, with the left side being larger than the right side (Figures 3h- l). A large, spherical nucleus was located in the epitheca (Figures 3j, k). The cells were yellowish-brown and exhibited elongate chloroplasts radiating from the cell center (Figures 3j, l). The cell possessed two grooves: a transverse groove (cingulum) from which the transverse flagellum extended, and a longitudinal groove (sulcus) from which the longitudinal flagellum emerged. The cingulum was equatorial, sharply displaced downwards on the right ventral side by approximately one-third of the cell's length (Figure 3h). The longitudinal groove divided the lower part of the cell into two unequal sections (Figures 3 g–l). Red accumulation bodies were present in some cells within the hypocone, particularly in older samples (Figures 3a, b). Morphological examination of the excysted cells revealed their similarity to *Levanderina fissa*, classifying it within the group Miozoa, Dinophyceae, Gymnodiniales, Gyrodiniaceae. The Iranian strains were designated as CHcLf1 and CHcGi3.

Phylogenetic analysis

Partial ITS sequences (ITS1–5.8S rDNA–ITS2), approximately 636–645 bp after trimming, were successfully amplified from both Iranian strains (CHcLf1 and CHcGi3) and deposited in GenBank (MN604388 and MN604387, respectively).

The analysis included 19 similar Gymnodiniales sequences retrieved from GenBank. The resulting ML phylogenetic tree (Figure 4) placed both Iranian strains within a well-supported clade containing *Levanderina fissa*. Independent phylogenetic anal-

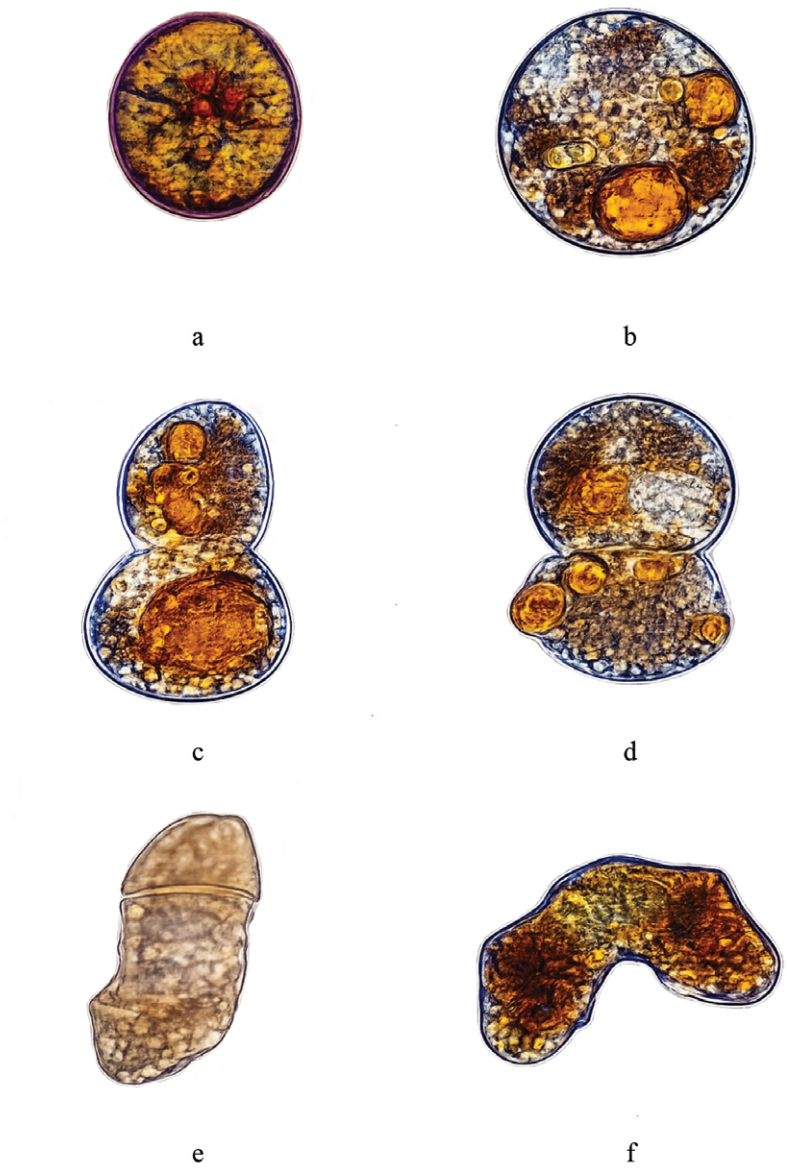

Fig. 2a–f: L.M. *Levanderina fissa* cyst isolated from Konarak region sediments (a); cyst produced under laboratory conditions (b); Excysted cells in culture undergoing division (c–d); motile cells undergoing division (e–f). All scale bars = 10 µm, except (a) = 5 µm

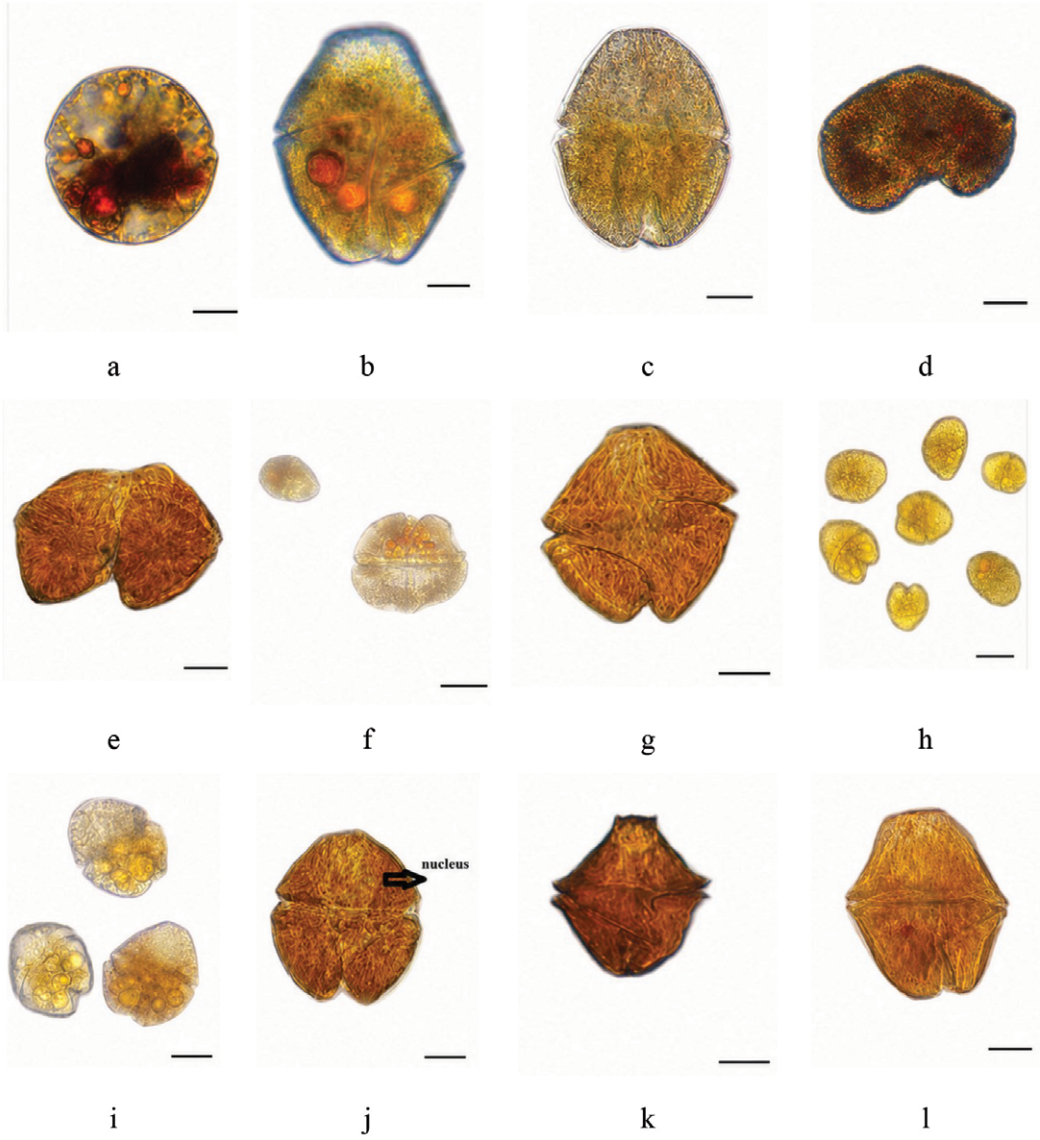

Fig. 3 a–l: L.M. *Levanderina fissa* motile cells in culture medium. Apical view (a); ventral view, showing cingulum displacement and red accumulation body (b); dorsal view showing deeply sulcus grove where longitudinal flagellum emerged (c); cell division (d–f); indicating chloroplast (g); motile cells showing cup shape hypotheca (h and i); showing spherical nucleus in epicone (j–l). All scale bars = 10 µm

yses conducted for each strain separately (data not shown) consistently recovered this placement with 100% bootstrap support. The combined analysis of both isolates yielded the same topology, with 98% bootstrap support (Figure 4), confirming their identification as *Levanderina fissa*.

Discussion

Ecological significance of Levanderina fissa

The present study reports the first isolation and morpho-molecular characterization of *Levanderina fissa* from Iranian coastal waters, representing a significant geographic range extension for this species in the Sea

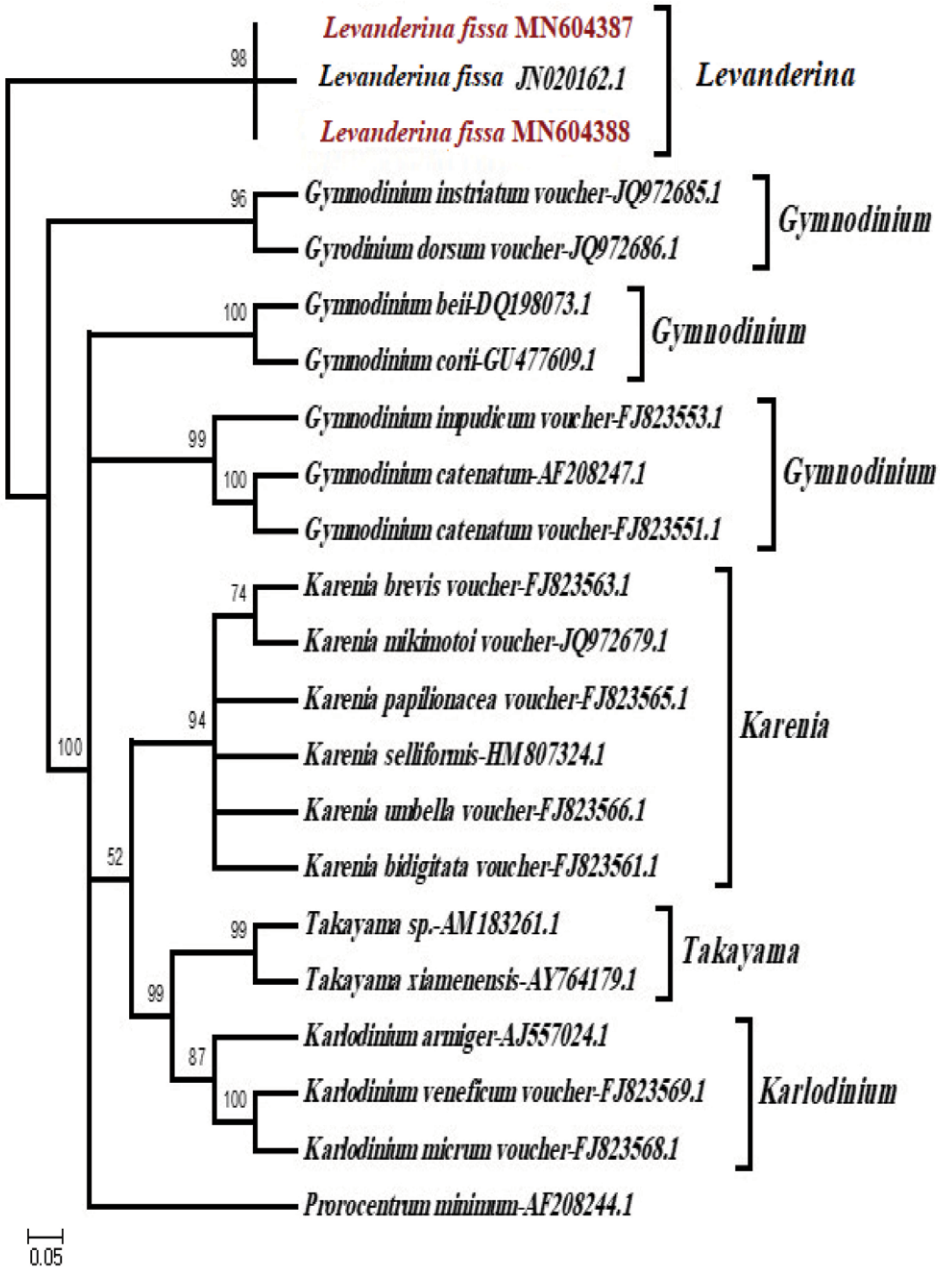

Fig. 4. Phylogeny of *Levanderina fissa* (MN604388 and MN604387) isolated from the Chabahar bay located in Sea of Oman based on gene sequence of ITS region using ML method and Bootstrap confidence with 1000 replication. *Prorocentrum minimum* is outgroup taxon

of Oman. Examination of cysts from marine sediments provides a robust method to uncover dinoflagellate species not detected during plankton surveys (Dale, 1983; Marret and Zonneveld, 2003), particularly for unarmored or morphologically cryptic taxa whose motile stages are short-lived and difficult to identify. As most planktonic dinoflagellates produce cysts to survive unfavorable conditions, their excystment frequently initiates algal blooms (Hallegraeff et al., 2004; Kremp and Parrow, 2006), and ap-

proximately 200 marine dinoflagellate species possess this cyst-forming ability (Liu et al., 2012).

Levanderina fissa (formerly *Gyrodinium instriatum*; Moestrup et al., 2014) is a widely recognized cyst-forming dinoflagellate frequently implicated in red tides and documented to cause harm to aquatic organisms (Gárate-Lizárraga, 2014; Borbor-Cordova et al., 2019). Its ecological success is underpinned by a broad tolerance of temperature and salinity, including salinities below 5 PSU (Nagasoe et al., 2006), and its cysts can dominate sediments, accounting for over 53% of total dinoflagellate cyst counts near Yokohama Port (Matsuoka, 1999).

The successful recovery of viable *L. fissa* cysts from Konarak sediments suggests that this species is well-established along the Iranian Sea of Oman coast and may contribute to HAB events that have previously gone undetected or unidentified at the species level. Given that this coastline supports economically important fisheries, aquaculture activities, and port infrastructure in the Chabahar–Konarak area, these findings highlight the need to incorporate *L. fissa* as a target species in routine HAB monitoring and early warning programs.

Morphological and molecular phylogeny

The Iranian *L. fissa* cysts exhibited a spherical morphology with a thick, unornamented wall and brown/orange internal contents, measuring 25–35 µm in width and 35–45 µm in length. This size range is notably smaller than those reported in previous studies: Moestrup et al. (2014) described dimensions of 41–54 × 31–48 µm; Orlova et al. (2003) reported pear-shaped cysts of 51–55 µm length and 39–42 µm width; and Kojima and Kobayashi (1992) documented larger pear-shaped to ovoid cysts of 50–75 µm length and 37.5–57.5 µm width. This size reduction most likely reflects ecophenotypic plasticity in response to local environmental parameters such as temperature, salinity, and nutrient availability (Lewis and Hallett, 1997), rather than a taxonomically meaningful distinction, as the overall morphological traits, wall structure, absence of ornamentation, and brown/orange granular internal contents remain fully consistent with established descriptions of *L. fissa*.

The excysted motile cells were pyriform and flagellated, measuring 30–35 µm in width and 45–50 µm in length. Despite being smaller than the dimensions reported by Orlova et al. (2003) and Kojima and Kobayashi (1992), all key taxonomically diagnostic features were conserved, including a deep cingulum displaced approximately one-third of the cell length, a deep sulcus extending toward the epicone, absence of distinct surface ornamentation, and a prominent nucleus situated within the epitheca. The consistent expression of these diagnostic characters across both Iranian strains strongly supports their identification as *L. fissa* and is consistent with the known intraspecific morphological variability reported for this taxon across geographically distant populations.

The taxonomic ambiguity of unarmored dinoflagellates, such as *Gymnodinium* and *Gyrodinium* species, presents a significant challenge, largely due to the rapid degradation of essential cellular structures during microscopic observation (Partensky et al.,

1988; Huang and Dong, 2000). Consequently, ITS-based rDNA analysis has become the standard approach for robust species identification and phylogenetic reconstruction in this group (Moestrup et al., 2014). The ITS region was selected as the primary molecular marker because it evolves at an appropriate rate for resolving species-level relationships within morphologically cryptic Gymnodiniales. In addition, a comprehensive ITS reference dataset is available in GenBank, and amplification was reproducible for both Iranian isolates. Although LSU and SSU rDNA provide complementary resolution at higher taxonomic levels, ITS has been specifically validated for species delimitation within the *Gyrodinium–Levanderina* complex (Moestrup et al., 2014; Kim and Kim, 2007) and therefore considered the most appropriate marker for the present study.

Gyrodinium instriatum was historically misclassified under *Gymnodinium* due to similarities in its epithecal groove (Coats and Park, 2002); however, molecular phylogenetic studies demonstrated that *G. instriatum* and *G. uncatenum* form a robust monophyletic clade distinct from the type species *Gyrodinium spirale* (Moestrup et al., 2014; Kim and Kim, 2007). Our ML phylogenetic analysis based on the ITS region is fully consistent with this consensus: both Iranian strains cluster with *Levanderina fissa* with 98–100% bootstrap support, providing the formal molecular basis for their designation as *L. fissa*.

The ITS sequences of strains CHcLf1 and CHcGi3 (636–645 bp) are notably longer than previously reported values for related taxa (576–615 bp for *Gymnodinium* species; 604–605 bp for *Gyrodinium instriatum*; Shao et al., 2004). Intra-strain ITS length variability is a recognized phenomenon in dinoflagellates, arising from multiple rDNA operon copies within a single genome (Alpermann et al., 2010; John et al., 2014). However, replicate sequencing of both Iranian strains consistently yielded sequences within the 636–645 bp range with no evidence of co-amplified variants in the chromatograms, strongly suggesting that the observed length difference reflects genuine interspecific or interpopulation genetic divergence rather than intra-strain polymorphism or sequencing artifact. Future studies employing clonal sequencing, amplicon-based next-generation sequencing, and broader geographic sampling of *L. fissa* populations would provide a more comprehensive picture of ITS diversity within this taxon.

Conclusion

This investigation successfully isolated, cultivated, and genetically validated *Levanderina fissa* cysts from marine sediments collected off the Konarak coast (southeastern Iran). Subsequent molecular and morphological analyses of the excysted motile cells confirmed their identity and phylogenetic placement within the family Gyrodiniaceae. To our knowledge, this represents the first confirmed record of *L. fissa* from Iranian coastal waters, contributing a significant geographic data point to the known global distribution of this species in the Sea of Oman region.

The definitive identification of *L. fissa* is ecologically relevant, as this species has been documented as a causative agent of

Harmful Algal Blooms (HABs) in various regions worldwide (Gárate-Lizárraga, 2014; Borbor-Cordova et al., 2019). While the presence of *L. fissa* cysts in Konarak coastal sediments raises legitimate concern regarding its bloom potential in Iranian waters, we emphasize that no environmental, nutrient, or pollution data were collected in the present study. Consequently, any causal link between anthropogenic nutrient loading or industrial wastewater discharge and bloom initiation by this species remains speculative and is not supported by the experimental evidence presented here. Overall, this research provides crucial molecular and life-cycle data, elucidating the phylogenetic position of *L. fissa* in Iranian coastal waters and contributing significant insight into the species' morphology and size variability compared to global strains. These findings are essential for developing region-specific monitoring strategies and contribute fundamentally to the broader global understanding of *L. fissa* biogeography and HAB dynamics in the Sea of Oman and adjacent regions.

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