



A remarkable new monothalamid (Rhizaria, Foraminifera) from the shoreline of Livingston Island, Antarctica

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ABSTRACT

In this study, we describe a novel monothalamous Foraminifera, discovered in shoreline sediment samples from the Southern Ocean. The individuals, approximately 75 µm in diameter, are relatively small for Foraminifera, mostly spherical, with an organic-walled test. Notably, these Foraminifera exhibit a unique behavior in culture: they surround themselves in planktonic diatoms, enabling them to float in the water column. This floating behavior is unusual for Foraminifera, which are often larger and possess a thick test made of calcite or agglutinated particles. We hypothesize that the small size of the organism, its lightweight organic test, and the habit of surrounding itself with centric diatoms may enable the floating behavior observed in culture and potentially aid dispersal in nature. Phylogenetic analysis of the 18S rDNA barcoding fragment places this undescribed organism as an independent lineage among monothalamid Foraminifera. We erect the novel genus *Pensilisphaera* with its type species *Pensilisphaera antarcticaensis*.

1. Introduction

Foraminifera are protists branching as a sister group to radiolarians, both being part of Rhizaria (Sierra et al., 2022). These organisms produce either single-chambered (monothalamous) or multi-chambered (polythalamous) tests, with wall compositions that can be organic, agglutinated, or calcareous (Loeblich and Tappan, 1987; Pawlowski et al., 2013). Most research has focused on multichambered Foraminifera with rigid, calcareous tests, while organic-walled and agglutinated monothalamids have received much less attention.

In recent decades, molecular and morphological techniques have been used to characterize monothalamous Foraminifera. This combined approach has led to the discovery of numerous new species and genera (Gooday et al., 2020; Gooday et al., 2004; Gooday et al., 2022b; Holzmann et al., 2022). Studies of these organisms have also contributed to understanding the evolutionary history of Foraminifera. Molecular phylogenetic analyses suggest that monothalamids form a paraphyletic group at the base of the foraminiferal evolutionary tree, with some clades comprising both organic-walled and agglutinated species (Pawlowski et al., 2013).

Monothalamids are benthic organisms found in marine environments worldwide, ranging from estuaries to deep-sea trenches (Gooday,

2002; Henderson, 2023), with some lineages also inhabiting terrestrial and freshwater habitats (Holzmann et al., 2021; Meisterfeld et al., 2001; Siemensma and Holzmann, 2023). They are an important meiofaunal taxon in many marine settings, particularly the deep sea, where they can also make a major contribution to the macro- and megafauna (Gooday et al., 2017, 2020). Monothalamids are also common in high latitudinal regions with several genera occurring in Arctic and Antarctic settings (Gooday et al., 2022a; Holzmann et al., 2022; Pawlowski et al., 2008).

The present study describes a new genus and species of monothalamid Foraminifera, *Pensilisphaera antarcticaensis*, from shallow marine water environments of Livingston Island in the South Shetland Islands of Antarctica. An unusual floating behavior has been observed in cultures of this species that has not been reported yet for Foraminifera.

2. Material and methods

2.1. Isolation and cultivation

Marine sediment samples including seawater were collected on the shoreline of the Byers Peninsula (Livingston Island, Antarctica, −62.666946, −61.095524, Fig. 1) in January 2023 (Antarctic summer). The upper layer (approximately the top 1 cm) of the muddy sediment

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was manually collected with a custom grab sampler near the shore at a water depth of approximately 1 m. The water temperature was not determined at the time of sampling. However, the annual maximum surface temperatures in the Antarctic/Southern Ocean range from -1.9°C to $+5^{\circ}\text{C}$ (measured at 10–20 m depth) (Barnes et al., 2006; Morley et al., 2010), and air temperatures around the Antarctic Peninsula typically range from 0°C to 5°C during Antarctic summer but can occasionally exceed 15°C (Gorodetskaya et al., 2023). Thus, it is reasonable to assume that the water temperature at the time of sampling was well above 0°C . In the laboratory, the samples were stored at 4°C , distributed into 24-well plates, and screened regularly with a Nikon Eclipse TS100 inverted light microscope (up to $400\times$ magnification, phase contrast). In one of the wells, organic-walled monothalamids were observed. Individuals were repeatedly picked with a glass micropipette and transferred into new wells containing F/8 medium (Guillard, 1975). Various diatoms (isolated from the same samples) were added as a food source. The foraminiferal cultures were re-transferred to fresh F/8 medium approximately every 2 weeks and stored in a climate chamber at 15°C with a light/dark cycle of 16 h/8 h to promote diatom growth. This way, the cultures could be maintained for approximately 10 months, but were ultimately lost.

2.2. Light microscopy

Specimens were observed and photographed either directly from the 24-well plates with a Nikon Eclipse TE2000-E inverse microscope (10, 20, and $40\times$ objectives, phase contrast) with a Nikon digital sight DS-U2

camera (program: NIS-Elements V4.13.04), or observed and isolated from Petri dishes using a Nikon Diaphot inverted microscope with dark field illumination ($4\times$ objective) and phase contrast (10, 20, and $40\times$ objectives).

Living specimens of each strain were transferred to slides and compressed by pressing a needle on the cover slip until the cytoplasm flowed out of the aperture or the ruptured test, by which means nuclei became visible and could be counted and measured, using an Olympus BX51 microscope with phase contrast and differential interference contrast (DIC). Specimens were filmed and photographed with a Touptek E3ISPM 20 MP camera on the BX51 and a Canon 5D Mark II on the Diaphot microscope. Adobe Photoshop was used for image processing. Cellular features (test size, nucleus size) were measured in ImageJ ver. 1.53k (Schneider et al., 2012) and ToupView software.

2.3. DNA extraction, sequencing

Two foraminiferal individuals were picked with a sterilized glass micropipette, repeatedly washed in fresh F/8 medium to remove diatoms and other contaminants, and then transferred to $50\text{ }\mu\text{l}$ of guanidine lysis buffer each. DNA was extracted as described by Pawlowski (2000). Amplification of the 18S (SSU) rRNA gene was performed using the Foraminifera-specific primer s14F3 (Pawlowski et al., 2014) and the general eukaryotic primer EukB (Medlin et al., 1988).

$1\text{ }\mu\text{l}$ of extracted DNA was added to $17\text{ }\mu\text{l}$ PCR mixture. The mixture contained $1.7\text{ }\mu\text{l}$ of $10\text{ }\mu\text{M}$ forward primer s14F3, $1.7\text{ }\mu\text{l}$ of $10\text{ }\mu\text{M}$ reverse primer EukB, $0.34\text{ }\mu\text{l}$ of 10 mM dNTPs, $1.7\text{ }\mu\text{l}$ of Dream Taq Green Buffer,

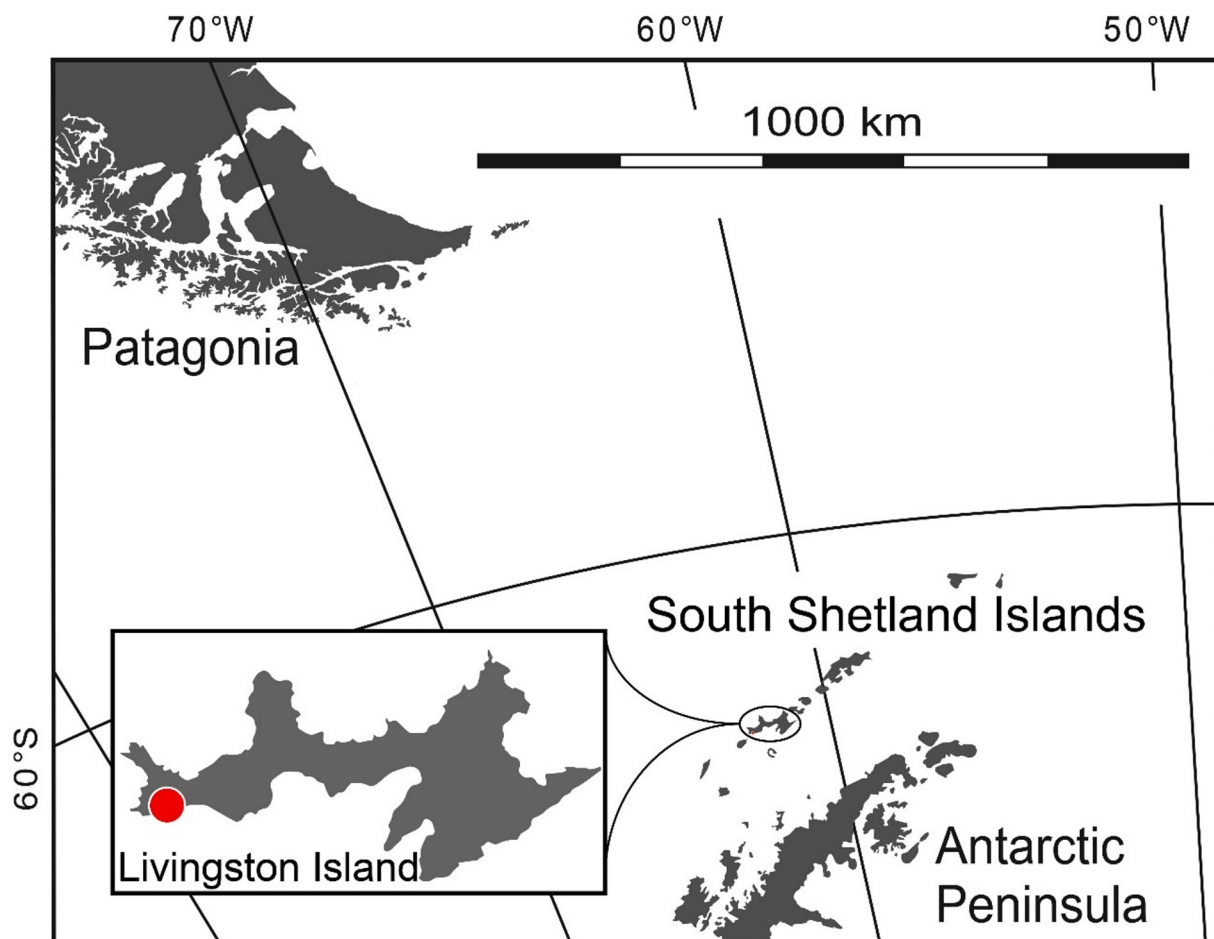


Fig. 1. Map of sampling location. Livingston Island is enlarged, and the approximate sampling spot is marked in red. Figure adapted and modified from Holzmann et al. (2022) (license: CC BY 4.0), original map data obtained from FreeVectorMaps.com (<https://freevectormaps.com>). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

0.17 μ l of DreamTaq polymerase (Thermo Fisher Scientific, Dreieich, Germany), and 11.4 μ l of water. The following PCR conditions were used: initial denaturation at 95 °C for 5 min, 35 cycles (denaturation at 95 °C for 30 s, annealing at 50 °C for 30 s, elongation at 72 °C for 2 min), terminal extension at 72 °C for 7 min, and cooling at 10 °C. 8 μ l of the PCR products were purified by adding 0.15 μ l of Exonuclease I, 0.9 μ l of FastAP, and 1.95 μ l of water, heating at 37 °C for 30 min, and consecutively at 85 °C for 20 min. Sanger sequencing was performed with the BigDye Terminator Cycle Sequencing Kit (Thermo Fisher Scientific, Dreieich, Germany) and an ABI PRISM automatic sequencer at the Cologne Center for Genomics (CCG) with the abovementioned primers. The chromatograms were manually checked in Chromas ver. 2.6.6 (Technelysium Pty. Ltd., Australia), and the partial sequences were assembled into sequence contigs.

2.4. Phylogenetic analysis

The two obtained sequences were compared to the publicly available 18S database of Foraminifera (NCBI/Nucleotide; <https://www.ncbi.nlm.nih.gov/nucleotide/>) and aligned to a set of 38 sequences representing members of all described marine monothalamid clades and monospecific lineages. The alignment contained 40 sequences (Supplementary Table 1), and 1764 sites were used for analysis. Sequences were aligned using the default parameters of the Muscle automatic alignment option as implemented in SeaView ver. 4.3.3 (Gouy et al., 2010).

The phylogenetic tree was constructed using maximum likelihood phylogeny implemented in PhyML ver. 3.0 (Guindon et al., 2010) from the ATGC Montpellier Bioinformatics Platform. An automatic model selection by Smart Model Selection/SMS (Lefort et al., 2017) based on the Akaike Information Criterion (AIC) was used, resulting in a GTR

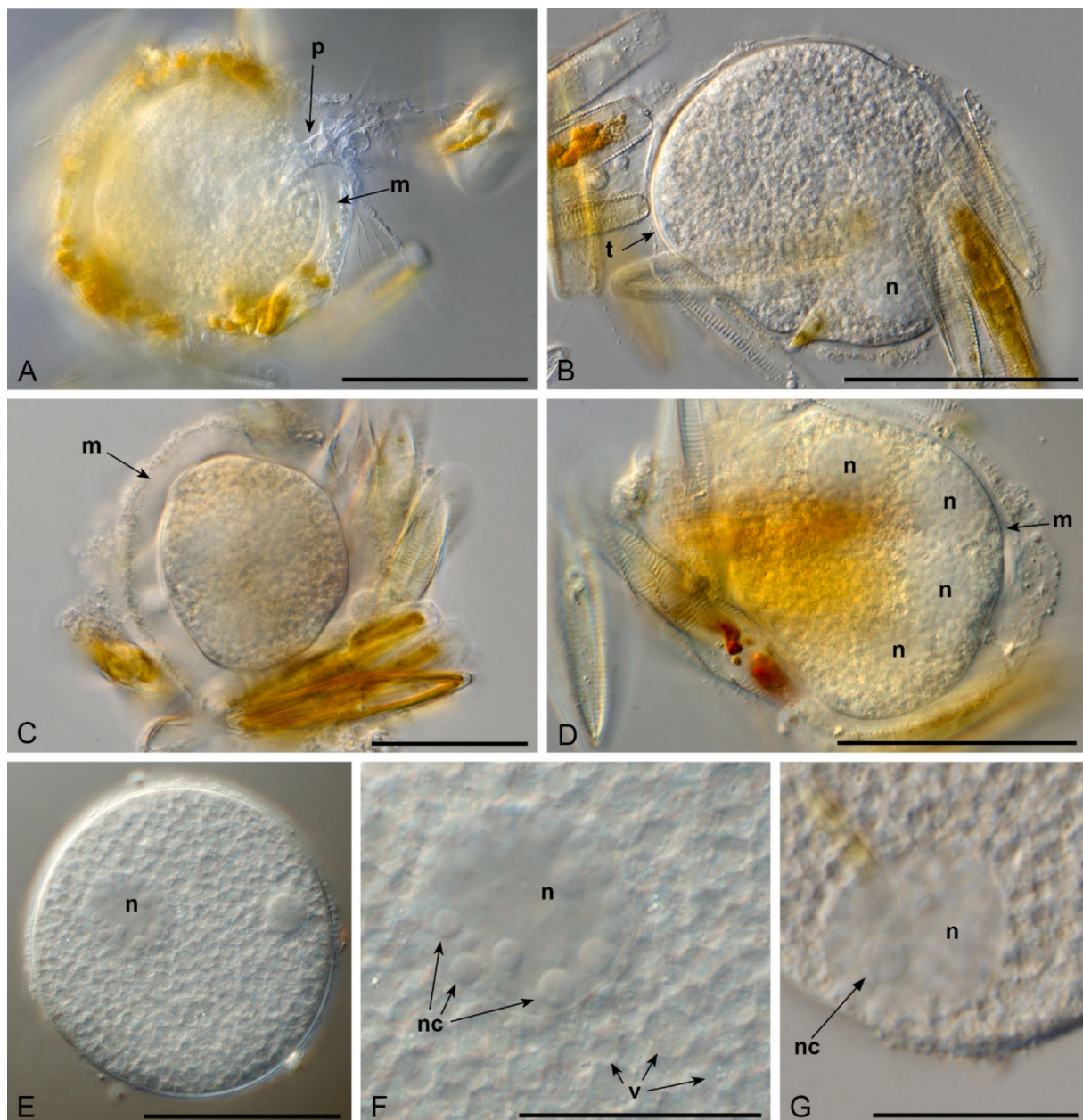


Fig. 2. *Pensilisphaera antarcticaensis* gen. nov., sp. nov. (A) Holotype specimen. (B) Slightly compressed cell, showing the organic membranous test. (C) Cell with thick mucus layer. (D) Cell with five nuclei, one not visible. (E) Compressed cell, showing numerous vacuoles and a single nucleus. (F) Detail of a cell, with nucleus, nucleoli, and vacuoles with granules. (G) Nucleus with one large and some smaller nucleoli. m, mucous layer; n, nucleus; nc, nucleolus; p, peduncle; t, test wall; v, vacuole. Scale bars: 20 μ m (F–G) and 50 μ m (A–E).

substitution model being selected for the analysis. The initial tree was based on the BIONJ algorithm (Gascuel, 1997). Bootstrap values (BV) were based on 100 replicates.

3. Results

3.1. Taxonomic description

Rhizaria Cavalier-Smith, 2002

Retaria Cavalier-Smith, 1999

Foraminifera d'Orbigny, 1826

Monothalamids Pawlowski et al., 2013

ZooBank registration number of the present work. Urn:lsid:zoobank.org:pub:9898E928-C330-4640-AFE8-321B08BE1855.

ZooBank registration number of the new genus. Urn:lsid:zoobank.org:act:84EC4362-8425-41B7-947E-88ADCFB71033.

ZooBank registration number of the new species. Urn:lsid:zoobank.org:act:9F39683A-F799-4C30-8E5C-F269618E6B9E.

Pensilisphaera gen. nov.

Diagnosis. Individuals more or less spherical with a hyaline, flexible, organic-walled test, often surrounded by a mucous layer. Peduncle relatively short. One or more nuclei present. Nuclei spherical, ovular, with several spherical nucleoli. Cytoplasm with many small vacuoles, containing one or up to five small granules. No crystals observed.

Type species. *Pensilisphaera antarcticaensis* sp. nov.

Etymology. A composite of the Latin adjective *pēsil-is*, *-is*, *-e* [m, f, n] (hanging, floating) and the Latin noun *sphaera* [f] (sphere). The genus

name *Pensilisphaera* refers to the mostly spherical morphology of the shell and the peculiar floating behavior of the cells when surrounded with planktonic diatoms. *Pensilisphaera* is considered feminine.

***Pensilisphaera antarcticaensis* sp. nov.** (Figs. 2–4, Supplementary Figs. 1 and 2)

Examined material. 25 specimens with LM.

Diagnosis. As for the genus. *Pensilisphaera* is currently monotypic.

Etymology. A composite of the Neolatin noun *Antarctica* [f] (Antarctica) and the Latin feminine suffix *-ensis* (of or from a place). The species name refers to the origin of the isolates from the Antarctic/Southern Ocean.

Type locality. Marine sediments, shoreline of Byers Peninsula (Livingston Island, South Shetland Islands, Antarctica, –62.666946, –61.095524).

Type material. The specimen depicted in Fig. 2A constitutes the holotype under Article 73.1.4 of the International Code of Zoological Nomenclature (ICZN, 1999) and Recommendation 73G in Declaration 45 (ICZN, 2017). The holotype is no longer available because it was destroyed during microscopic examination with a compound microscope. Its DNA was not extracted.

Description. Observed individuals of *Pensilisphaera antarcticaensis* had a mostly spherical or slightly oblong organic-walled test with a diameter of approximately 75 μm ($74.9 \mu\text{m} \pm 14.4 \mu\text{m}$, $n = 24$). There were up to five nuclei per cell, varying in size between 17.7 and 20.8 μm ($n = 7$). Nuclei had one to more than 15 spherical nucleoli, varying in size from 1.7 to 3.4 μm , within clear nucleoplasm. The cytoplasm contained numerous small vacuoles, about 2.3–3.9 μm in diameter, each containing 1 to 4 small granules, about 0.4–0.6 μm . The tests were

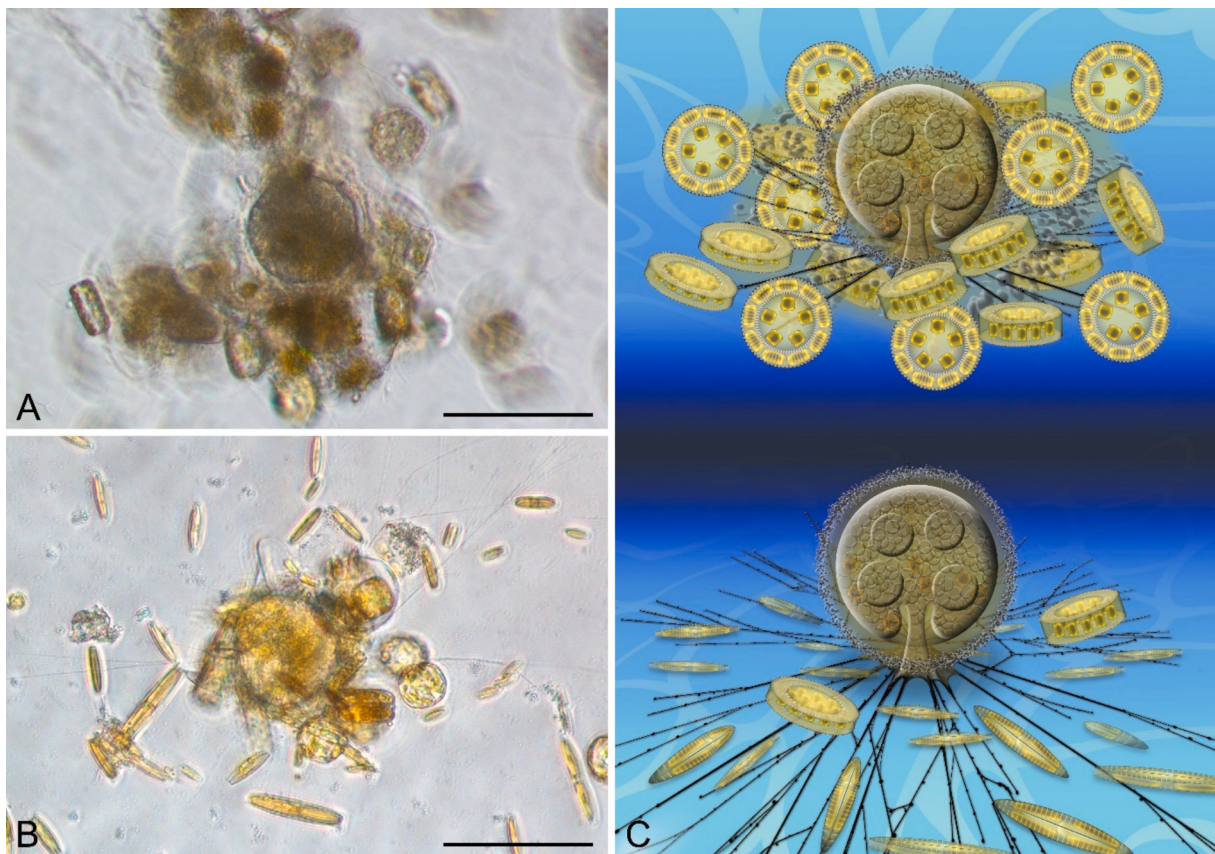


Fig. 3. Floating and attached cells of *Pensilisphaera antarcticaensis*. (A) Floating cell surrounded by planktonic centric diatoms, mucus, and debris particles. In this stage, the granuloreticulopodia were often retracted. (B) Cell attached to the bottom of the well with extended granuloreticulopodia. (C) Illustration of *Pensilisphaera antarcticaensis* in both stages. Scale bars: 100 μm .

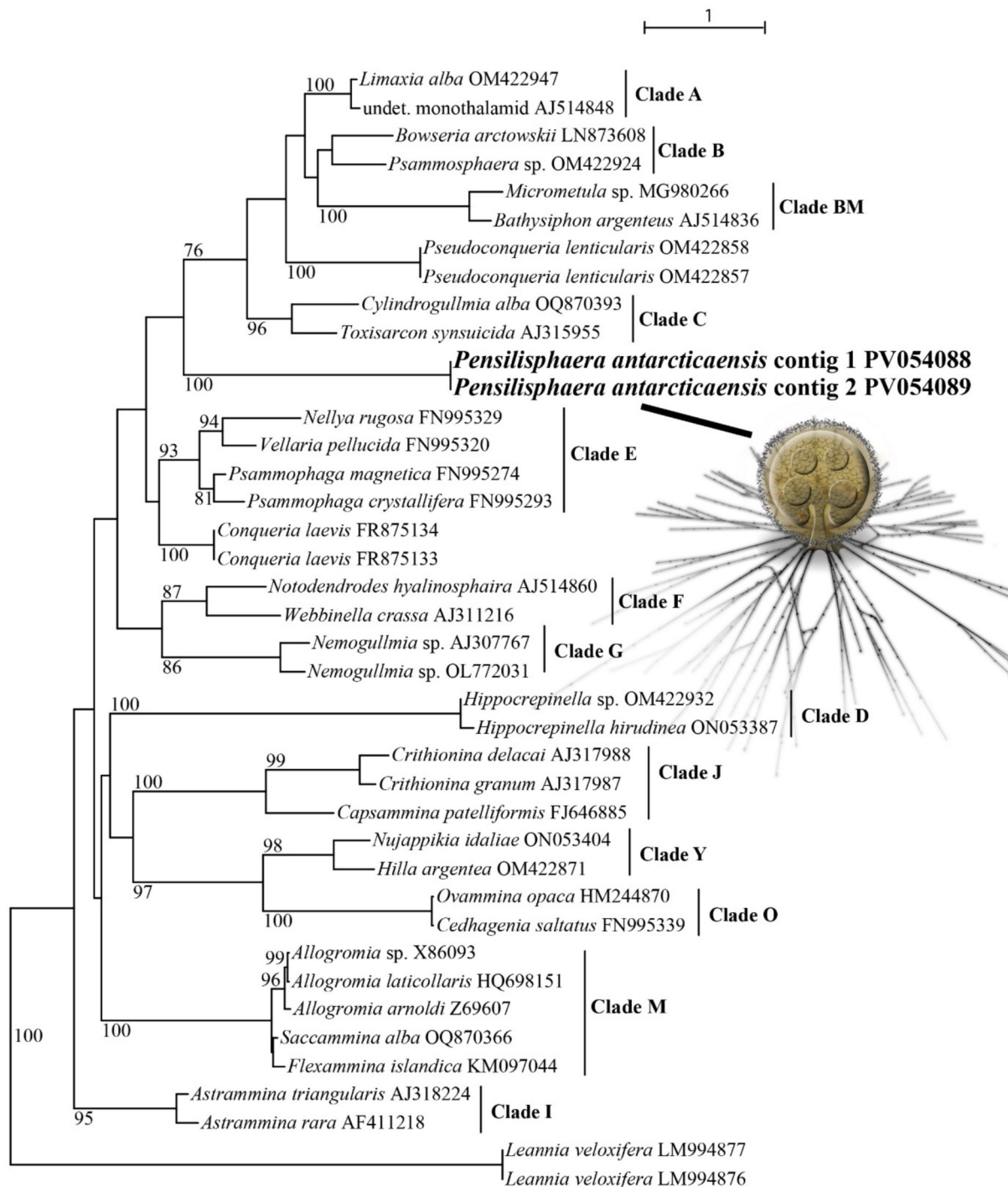


Fig. 4. PhyML phylogenetic tree based on the 3' end fragment of the 18S (SSU) rRNA gene, showing the evolutionary relationships of 40 monothalamid foraminiferal sequences. Sequences of *Pensilisphaera antarcticaensis* acquired for the present study are marked in bold. The tree is unrooted. Specimens are identified by their accession numbers. Numbers at nodes indicate bootstrap values (BV). Only BV > 70 % are shown.

usually surrounded by a mucus layer that was up to 8.0 μm thick, covered by numerous granules of unknown origin, food particles and digestion residues, mainly empty diatom frustules, which made it often difficult to recognize the specimens.

Individuals consumed various diatoms (pennate and centric) as well as small flagellates (Figs. 2 and 3, Supplementary Figs. 1A and 2). In our cultures, specimens were often observed to surround themselves with planktonic, centric diatoms (*Cyclotella* spp.) and found floating in the water column (Fig. 3A). The centric, planktonic diatoms were actively collected, sometimes over distances of more than 1 mm, even when

plenty of pennate diatoms were present in the cultures (Supplementary Fig. 3). In absence or depletion of those planktonic diatoms, specimens of *P. antarcticaensis* were attached to the bottom of the wells and often displayed a wide network of granuloreticulate pseudopodia (Figs. 2A, 3B, Supplementary Fig. 1A).

Molecular characteristics. The sequence length of *P. antarcticaensis* amounts to 857 (individual 1) and 887 (individual 2) nucleotides, the GC content is 43 %. The sequences of both individuals were identical, differing only in the presence of additional bases at the respective sequence termini due to sequence quality. *Pensilisphaera antarcticaensis*

(100 % BV) branches at the base of Clades A, B, BM, C and the monospecific lineage *Pseudoconqueria lenticularis*. The branching is not supported by bootstrap values.

3.2. Molecular phylogeny

The two sequences obtained from *Pensilisphaera antarcticaensis* (100 % BV) cluster in a new monothalamid lineage (Fig. 4). The phylogenetic tree contains thirteen Clades (A–Y) previously described by Pawlowski et al. (2002) and three monospecific lineages branching independently: *Pseudoconqueria lenticularis* (Holzmann et al., 2022), *Conqueria laevis* (Gooday and Pawlowski, 2004), and *Leannia veloxifera* (Apotheloz-Perret-Gentil and Pawlowski, 2015). The tree can be divided into two groups. One group contains Clades A, B, BM, *P. lenticularis* and Clade C, with *P. antarcticaensis* branching at their base. Clade E and *C. laevis* branch as sister to the former assembly with Clades F and G branching at the base of the group. The second group contains Clade D, Clade J, Clade Y and Clade O with Clade M branching at their base. Clade I and *L. veloxifera* branch at the base of the two groups. Clades and lineages are strongly supported (86–100 % BV), except for Clade B that has a BV of 58 % (not shown). Relationships between Clades and lineages are not supported except for Clades A, B, BM, C and *P. lenticularis* (76 % BV).

3.3. Differential diagnosis

The thin, organic and flexible test of *Pensilisphaera antarcticaensis*, along with its rounded shape, resembles that of *Allogromia laticollaris*, which also occurs in the coastal zone (Arnold, 1948). However, with a diameter of approximately 75 µm, *P. antarcticaensis* is significantly smaller. In contrast, the average size of *A. laticollaris* is around 160 µm, with mature individuals ranging from 100 µm to 450 µm. Daughter cells produced through asexual reproduction measure between 20 µm and 40 µm (Arnold, 1948). Additionally, *A. laticollaris* has a distinct collar surrounding its aperture, which is absent in *Pensilisphaera*.

Allogromia arnoldi (Goldstein et al., 2022) can be differentiated from *Pensilisphaera* by its larger size (up to 1 mm) and its often bright orange protoplasm. In some *A. arnoldi* specimens, more than one aperture has been observed. Unlike *Pensilisphaera*, a mucous layer surrounding the test has not been noted in *Allogromia*.

Pensilisphaera shows some resemblance to the Astroperuliidae, a family of small monothalamids containing two described species, *Astroperula dumacki* and *A. parvipila* (Siemensma and Holzmann, 2023). Astroperuliidae are organic-walled, multinucleate Foraminifera with a flexible test and an eccentrically located peduncle that is almost half the length of the cell. In *Pensilisphaera* the peduncle is centered and short (Fig. 2A). *Astroperula dumacki* measures 122 µm, while *A. parvipila* is smaller (65 µm). Both species contain numerous yellow, birefringent rod-shaped crystalline inclusions in the cell body that are absent in *Pensilisphaera*. Astroperuliidae are further distinguished by the fact that they are a family of freshwater Foraminifera with no known representatives in marine settings.

4. Discussion

With its round shape, flexible organic membrane and single aperture, *Pensilisphaera* resembles the typical allogromiid morphotype. A peduncle has also been described for *Allogromia laticollaris* as well as a preference for diatoms as a food source (Arnold, 1948). Different allogromiid species are united in Clade M, with organic (*Allogromia*) and agglutinated (*Saccammina*, *Flexammina*) tests. The results of our molecular analyses, however, show that *Pensilisphaera* is not a close relative to *Allogromia* but branches as an independent monothalamid lineage. We could not observe the complete life cycle of *Pensilisphaera* but found specimens containing up to five nuclei that may indicate the first stage of reproduction by division of the cell body into several daughter cells (schizogony). A dividing specimen was noticed in the culture

(Supplementary Fig. 1B). The test was elongated with a constriction in the middle part and had two opposed apertures. We did not observe the beginning and the end of the division and can therefore not conclude how much time the cell separation takes. Similar cell divisions were observed in two freshwater species, *Limnogromia leanneae* and *Astroperula parvipila* (Siemensma and Holzmann, 2023), where it took several hours up to three days for the cells to separate.

The observed floating behavior of *Pensilisphaera antarcticaensis* is particularly intriguing. Floating specimens in laboratory cultures were surrounded by planktonic diatoms. Floating behavior of Foraminifera has been reported for other species, such as *Ammonia* spp. (Cedhagen, 2024). One of the authors (M.H.) has observed floating behavior in benthic Foraminifera with calcareous tests, including *Ammonia*, *Rosalina*, *Sorites*, *Amphisorus*, *Heterostegina*, and *Operculina*, under laboratory conditions. In these cases, Foraminifera floated on the surface of Petri dishes by extending their granuloreticulopodia, creating a net-like structure around their tests. Before floating, none of these Foraminifera had ever collected or surrounded their tests with planktonic diatoms.

We hypothesize that this unusual floating behavior may serve as a dispersal mechanism in *Pensilisphaera*, differing from the typical dispersal strategies of benthic Foraminifera. The active dispersal mechanism of benthic Foraminifera is locomotion by use of their granuloreticulopodes, which is limited to short distances. Several passive dispersal methods have been described of which the most important are probably the transport of propagules (embryonic juveniles) and passive suspension and transport of different growth stages of benthic Foraminifera (Alve, 1999; Alve and Goldstein, 2002, 2010; Cedhagen, 2024). Passive suspension into the water column is caused by physical and biological factors (Alve, 1999) such as currents and turbulence created by strong winds but also feeding activities or movements of benthic macrofauna that stir up the sediment surface.

Another passive transport mechanism is provided by suspended organic matter aggregates to which even relatively large adult benthic Foraminifera measuring several hundred µm can adhere. This has been observed in coastal areas of the Japanese Islands (Nomura et al., 2010; Takata et al., 2019). The aggregates are formed by *Prorocentrum minimum*, a neritic dinoflagellate that produces blooms. After the blooms develop, the dinoflagellates sink to the seafloor, where they are eventually resuspended (Takata et al., 2019). The Foraminifera observed on these aggregates include *Ammonia*, *Trochammina* and *Saccammina* (Takata et al., 2019), which are generally larger with robust calcite or agglutinated tests.

In contrast, *Pensilisphaera* is relatively small-sized (~75 µm), with a lightweight organic-walled test and a tendency in culture to enmesh itself actively with live planktonic diatoms. These features seem to serve as mechanisms to create buoyancy and suggest a possible adaptation to a meroplanktic lifestyle. Such a temporary planktonic stage has been documented for some benthic Foraminifera with calcareous tests, which construct a float chamber before undergoing sexual reproduction (Alve, 1999; Cedhagen, 2024; Jorissen, 2014). If replicated in nature, the floating behavior of *Pensilisphaera* may provide several ecological advantages, such as enhanced dispersal capabilities by passive transport over long distances, and access to planktonic food sources, particularly diatoms, which appear to be a primary food source for this species. This way, *P. antarcticaensis* can potentially exploit a niche that is relatively inaccessible to solely benthic Foraminifera. Our conclusions are thus far based only on laboratory observations, and the presence of *P. antarcticaensis* in the natural plankton of the Southern Ocean requires confirmation through sampling with plankton tows or environmental sequencing of pelagic zone samples.

CRedit authorship contribution statement

Marcel Dominik Solbach: Writing – review & editing, Writing – original draft, Visualization, Resources, Investigation,

Conceptualization. **Ferry Siemensma:** Writing – review & editing, Writing – original draft, Visualization, Investigation, Conceptualization. **Maria Holzmann:** Writing – review & editing, Writing – original draft, Visualization, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ejop.2025.126148>.

Data availability

The sequences were submitted to NCBI GenBank under the following accession numbers: PV054088, PV054089.

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