The Linnean Society of London ZOOLOGICAL Journal of the Linnean Society

Zoological Journal of the Linnean Society, 2009, **156**, 455–464. With 5 figures

A new genus of xenophyophores (Foraminifera) from Japan Trench: morphological description, molecular phylogeny and elemental analysis

BÉATRICE LECROQ[1]*, ANDREW JOHN GOODAY[2], MASASHI TSUCHIYA[3] and JAN PAWLOWSKI[1]

[1]*Department of Zoology and Animal Biology, University of Geneva, Switzerland*
[2]*National Oceanographic Center, Southampton, Empress Dock, European Way, Southampton, SO14 3ZH, UK*
[3]*Institute for Research on Earth Evolution, Japan Agency for Marine-Earth Science and Technology (JAMSTEC), Yokosuka, Kanagawa 237-0061, Japan*

Received 28 April 2008; accepted for publication 19 June 2008

The deep-sea floor is inhabited by a number of unusual and enigmatic taxa, unknown in shallow waters. These include the xenophyophores, a group of giant protists that construct fragile agglutinated tests. Here, we describe ***Shinkaiya lindsayi* gen. et sp. nov.**, a new xenophyophore collected by the submersible Shinkai 6500 at a depth of 5435 m near the Japan Trench. The phylogenetic analysis performed on its complete small-subunit ribosomal DNA (SSU rDNA) sequence confirms that ***Sh. lindsayi* sp. nov.** is a foraminiferan that is closely related to another xenophyophore, *Syringammina corbicula* Richardson, 2001, and to a monothalamous (single-chambered) foraminiferan *Rhizammina algaeformis* Brady, 1879. In terms of morphology, the new genus resembles *Syringammina*, but its test wall is thicker, softer, and more weakly cemented. Moreover, the SSU rDNA sequences of the two genera are highly divergent. Mass spectra analyses reveal unusually high concentrations of some elements, such as lead, uranium, and mercury. The granellare system (the cytoplasm and the organic sheath that encloses it) is apparently devoid of barite crystals, which are usually abundant as intracellular inclusions in xenophyophores, but is rich in mercury (with 12 times the concentration of mercury found in the surrounding sediment). Fecal pellets retained within a tubular system (stercomare) concentrate heavy metals, including lead and uranium (respectively, two and six times more than that of the sediment). Based on a comparison of the compositions of the agglutinated test wall, the granellare, the stercomare, and the surrounding sediment, we discuss the impact of xenophyophores on their habitat. *Zoological Journal of the Linnean Society*, 2009, **156**, 455–464.

ADDITIONAL KEYWORDS: deep-sea – mass spectrometry – microscopy – ribosomal DNA – xenophyophorea.

INTRODUCTION

Despite many years of study, the fauna of the deep-sea remains poorly known. The xenophyophores are one particularly enigmatic group. These spectacularly large protists are extremely abundant in productive parts of the deep ocean. They are benthic deposit feeders that build an agglutinated test, often greater than 10 cm in diameter, consisting mainly of foreign particles (xenophyae), and with a wide variety of morphologies. Xenophyophores are often very fragile, easily fragmented, and have no proven fossil record (Levin, 1994). This may be one of the reasons why they were poorly studied until recently, despite their wide occurrence in the deep sea, and their importance for bioturbation. Indeed, the enhanced particules deposition in their vicinity would provide food and refuge to their associate fauna, which increase the biological mixing of the sediment (Levin *et al.*, 1986). *Syringammina fragilissima* Brady, 1883, the first species to be described, was classified as a foraminiferan. Later, however, xenophyophores were considered successively as sponges (Haeckel, 1889),

*Corresponding author. E-mail: beatrice.lecroq@unige.ch

members of an independent class of Rhizopoda (Schulze, 1907), or as a new eukaryotic phylum (Lee, Leedale & Bradbury, 2000). Recently, molecular studies showed that *Syringammina corbicula* Richardson, 2001 is indeed related to monothalamous foraminiferans (Pawlowski *et al.*, 2003). Nevertheless, the monophyly of the group remains unproven.

Fourteen genera and almost 60 species of xenophyophores are now described (Gooday & Tendal, 2000). Large species are epifaunal, but a few smaller, infaunal species are also known. Most resemble agglutinated foraminifera, in having a test composed of foreign particles. The internal organization of xenophyophores is distinctive. The multinucleate cytoplasm and the organic tube that encloses it comprise together the granellare system. Faecal pellets (stercomata) enclosed within an organic sheath form the stercomare system. Another distinctive feature of the xenophyophores is the presence of barium sulphate crystals (granellae) throughout the cytoplasm, and sometimes within the stercomare. The crystallography of these crystals has been investigated (Hopwood, Mann & Gooday, 1997), but their function, if any, is still a matter of debate.

Xenophyophores are often abundant beneath productive waters, where the flux of organic matter to the seafloor is high (Tendal, 1972). Their diets probably comprise detrital particles obtained by suspension feeding (Tendal, 1972), surface-deposit feeding (Lemche *et al.*, 1976), or by being trapped within the folds and spaces of the often morphologically complex test (Levin & Thomas, 1988). It is possible that organic material concentrated in this way is digested within invaginations of the cell wall, and that the indigestible remnants are accumulated into stercomata (Tendal, 1979; Hopwood *et al.*, 1997). It has also been suggested that stercomares are used to cultivate bacteria as an additional food source (Tendal, 1979). Some support for this idea is provided by studies of lipid biomarkers, which suggest a diet rich in bacteria (Laureillard, Méjanelle & Sibuet, 2004). Large, epifaunal xenophyophores may constitute important habitat structures on the seafloor, providing refuges and possibly sustenance for numerous small metazoans (Levin & Thomas, 1988; Levin & Gooday, 1992) and foraminifera (Hughes & Gooday, 2004).

In this paper, we describe a new species and genus of xenophyophore from the North-West Pacific, and discuss its phylogenetic position according to the complete small-subunit ribosomal DNA (SSU rDNA) sequence. We also performed a chemical analysis of different parts of the organism, and compared this with the surrounding sediment.

MATERIAL AND METHODS

Sample collection

The single specimen was collected by an MBARI-type push core during the RV Yokosuka cruise YK07/15 to the Japan Trench off Sanriku, using the submersible Shinkai 6500 (dive 1037; 38°14.8175′N, 147°00.1885′E; water depth, 5435 m; October 2007). After recovery, the specimen was split into two main pieces: one to be deposited in the National Museum of Nature and Science, Tokyo, and the other to be used for analyses. Fragments of the specimen were either fixed in formalin (for morphology investigations) or guanidine buffer (for DNA analyses); the rest was immediately frozen at –20 °C.

Microscopy

Fragments of *Shinkaiya lindsayi* gen. et sp. nov. were broken open and examined with a light microscope. Nuclei were observed under a UV microscope after the granellare strands had been stained for 3 min in a 50% solution of 4′,6-diamidino-2-phenylindole (DAPI). Other fragments were critical-point dried, before being coated with platinium and examined in a scanning electron microscope (SEM), operating at 1.5 kV (Jeol 6300F, field emission). For transmission electronic microscopy observations (TEM; Phillips CM12, tungsten filament), fragments of the specimen were dehydrated in a series of graded alcohols and propylene oxide before being embedded in EPON resin. Semithin sections (0.6–0.7-μm thick) were stained with a mixture of methylene blue and Azur II. Thin sections (60–70-nm thick) were contrasted with lead citrate and uranyl acetate, and were viewed on coated 200-μm nickel grids in a graphite holder. Energy dispersive X-ray spectrographic microanalyses (EDAX) was performed in conjunction with TEM.

Mass spectrometry

Fragments were analysed by inductively coupled plasma mass spectrometry (ICPMS; Agilent 7500). Pieces of the test, stercomare, and granellare were separately dissolved in a mixture of nitric and hydrofluoric acid prior to being analysed. Two additional sediment samples were prepared in the same way: one from the same site as *Shinkaiya* (1037), the other from another site (1036; 39°24.1602′N, 144°26.1275′E; water depth, 6406 m; October 2007) approximately 145 nautical miles away.

Molecular and phylogenetic analyses

The complete SSU rDNA of *Sh. lindsayi* sp. nov. was obtained by PCR amplifications and cloning according to the protocol described in Schweizer *et al.* (2008).

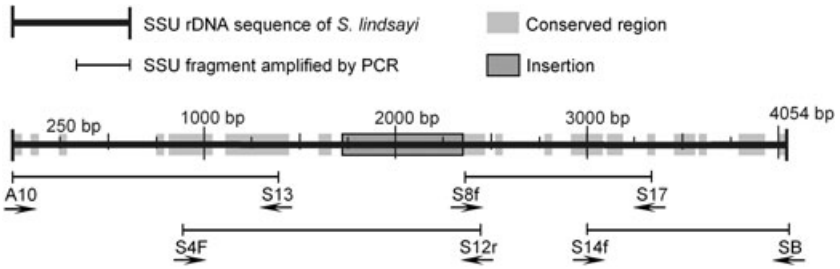

Figure 1. Schematic representation of the small-subunit ribosomal DNA (SSU rDNA) sequence of ***Shinkaiya lindsayi* gen. et sp. nov.**, showing the conserved regions, as well as the largest insertion and primers used for DNA amplifications.

Several overlapping fragments of SSU rDNA were separately amplified using foraminiferal-specific primers: A10, 5′-CTCAAAGATTAAGCCATGCAAGT GG-3′; s4F, 5′-TCTAAGGAACGCAGCAGG-3′; s13, 5′-GCAACAATGATTGTATAGGC-3′; s8F, 5′-TCGATG GGGATAGTTGG-3′; s12r, 5′-GATYAGATACCGTCG TAGTC-3′; s14f, 5′-ACTTGAAGGAATTGACGG-3′; s17, 5′-CGGTCACGTTCGTTGC-3′; or eukaryotic universal primer sb, 5′-TGATCCTTCTGCAGGTTCACC TAC-3′ (Fig. 1). Five DNA extractions from five different fragments of the specimen were used for molecular work. For each PCR product, three or four clones were sequenced. We also sequenced the complete SSU of *Rhizammina algaeformis* Brady, 1879 (from a specimen collected during the ANDEEP 2002 cruise in the Weddell Sea; 64°00.9′S, 39°06.3′W; water depth, 4730 m), which appeared as a sister group of *Sy. corbicula* in a previous study (Pawlowski *et al.*, 2003). Sequences were compared with 30 other foraminiferan sequences, and were manually aligned using SEAVIEW software (Galtier, Gouy & Gautier, 1996). The GC content, number of informative sites, and sequence divergence were determined with PHYLO_WIN (Galtier *et al.*, 1996). The tree was built using the maximum-likelihood method with the Treefinder program (Jobb, von Haeseler & Strimmer, 2004), using the general time-reversible (GTR + G + I) model with four rates categories, and with 1000 replicates for bootstrap analysis.

RESULTS

Systematic description

Rhizaria Cavalier-Smith, 2002

Foraminifera d'Orbigny, 1826

Xenophyophorea Schulze, 1904

Psamminidae Haeckel, 1889

Shinkaiya gen. nov.

Type species: Shinkaiya lindsayi gen. et sp. nov.

Generic diagnosis: Large xenophyophore: at least 8 cm in diameter and 5-cm high. Test fragile, approximately cylindrical in shape, and forming tightly-meshed, reticulated structure composed of bar-shaped elements (~0.5 cm in diameter), separated by open spaces. Test with smooth outer surface; wall relatively thick, soft, weakly cemented, and composed of fine sediment particles. Scattered internal xenophyae (agglutinated particles), mainly radiolarian tests, present.

Derivation of name: The name of the new genus is derived from the Japanese submersible Shinkai 6500, operated by JAMSTEC, which was used to collect the specimen.

Remarks: The new genus resembles species of the genus *Syringammina*, in particular the type species *Sy. fragilissima*. The genera are similar in the general shape and construction of the test, which consists of a framework of bar-like elements, forming a tightly-meshed, often reticulated structure. Another species, *Syringammina reticulata* Gooday, 1996, has a similar arrangement of test elements, although the body form is flattened rather than domed. The main morphological difference between the new genus and *Syringammina* is the nature of the test wall. In *Syringammina*, the wall is brittle, with a smooth inner surface, and consists of 'tightly cemented xenophyae' (Tendal, 1972). These comprise mainly fine sand grains and small foraminiferan tests in *Sy. fragilissima*. *Shinkaiya*, on the other hand, is characterized by a relatively thick wall that is soft rather than brittle, and consists mainly of clay-sized sediment particles. Unlike *Syringammina*, in which the particles are confined to the test wall, the lumen of the test in *Shinkaiya* includes scattered internal xenophyae. Our distinction of these two genera is supported by molecular data showing an important genetic distance between *Sh. lindsayi* sp. nov. and *Sy. corbicula*. Unfortunately, DNA sequences are not yet available for *Sy. fragilissima*.

Shinkaiya lindsayi gen. et sp. nov.

Diagnosis: As for genus.

Derivation of name: The species is named after the biologist Dhugal Lindsay, who collected the specimen.

Type specimen: The single specimen (and therefore the holotype) was recovered from a push core taken by the Shinkai 6500 submersible from the North Pacific, east of the Japan Trench (38°14.8175′N, 147°00.1885′E; water depth, 5435 m). The major fragment is deposited in the National Museum of Nature and Science, Tokyo (registration number: NSMT-Pr 241).

Morphological description

Test form and structure: The test forms a short, approximately cylindrical structure, with a fairly flat upper surface. It measures at least 8 cm in diameter, with ~5 cm of test being exposed above the sediment surface. At the base of the test, 1–2 cm long root-like structures extend into the sediment. The test comprises a system of anastomosing branches, typically 0.5 cm in diameter, forming a meshwork with open spaces ranging from 1 to 3 cm in size (Fig. 2A, B). On the upper surface of the test, these branches tend to form an approximately reticulated pattern. The test wall is delicate, soft, and 300-μm thick. It is light brown in colour, and is mainly composed of fine-grain sediment particles with scattered darker particles, and with occasional larger radiolarian tests (up to 200 μm in diameter) and quartz grains (Fig. 3D).

Test interior: Usually, the test branches are basically hollow, but there are some internal xenophyae, mainly isolated radiolarian tests, but also quartz grains and sponge spicules (Fig. 3A). Occasionally, the two sides of the test adjoin, leaving almost no lumen.

Cytology: The interior contains prominently developed granellare and stercomare strands, which are intimately intertwined inside the test branches, but without any obvious connections between them (Fig. 2D). The stercomare and granellare are not equally distributed within the specimen. Some test branches contain stercomare but no granellare, although the reverse has not been observed.

The granellare strands are pale yellowish (straw-coloured), and branch in an irregular manner (Fig. 2D). The diameter is highly variable (50–200 μm). Sometimes, a thick granellare section gives rise to a cluster of four or five much narrower branches. Where the granellare runs along the length of a test section, the branches may merge; however, these anastomose are not common in the test fragments examined. The organic sheath is very thin, delicate, and has a non-reflective surface (Fig. 3C). No granellae (barite crystals) are visible within the cytoplasm when squashed preparations of granellare fragments are viewed under a high-power microscope. The DAPI staining of the cytoplasm revealed numerous nuclei (roughly 15×10^5 mm^{-3}), of between 2 and 4 μm in diameter (Fig. 2E, F). Although the cytoplasmic ultrastructure had been largely destroyed by freezing, nuclei and a Golgi apparatus were recognizable in TEM sections, and at least one stercome was present within the cytoplasm. Barite crystals were not observed in any of the sections examined.

The stercomare system occupies a greater volume of the test interior than the granellare (Fig. 2C). The strands are usually attached loosely to the inner surface of the wall, but in places they project into the test lumen (Fig. 3A). They are dark grey, almost black, and the thin organic sheath that encloses the stercomata masses has a distinctly reflective, slightly iridescent surface. The strands range from 30 to 200 μm in diameter, and their width is often uneven; lobate sections separated by constrictions sometimes develop. Some branches end blindly with rounded terminations. Anastomoses have not been observed, although branches sometimes adjoin without merging. Branching, which is usually dichotomous, may be very frequent. The branches often run in different directions. However, in the more tubular sections of the test, the stercomare strands extend for 100 μm without branching, and run more or less parallel with the granellare strands.

The stercomata are between 10 and 15 μm in diameter (Fig. 3B). The TEM observations reveal that the organic envelope enclosing the stercomare is of even thickness: 1-μm thick (Fig. 3E). The envelope appears rather homogeneous and featureless, except for an outer layer that in places separates from the underlying part to form a loop-like structure (Fig. 3F). An iron peak is evident in the EDAX spectra. The TEM sections of stercomare revealed the presence of cytoplasm associated with stercomata (Fig. 3E, F). The cytoplasm is present around the margins of the stercomare mass, but is inside the organic envelope. Stercomata are composed mainly of flake-like mineral particles. The EDAX microanalysis revealed peaks for silica, aluminium, magnesium, and iron, suggesting that these particles are composed of clay minerals. Barium was also detected within the stercomata. In one case, this element was associated with a crystal. The barite composition of this crystal, however, remains uncertain, because it also yielded a peak for calcium. A sharp peak for titanium was associated with another crystal, presumably rutile.

Life position

The specimen was epibenthic. It projected from the seafloor, with the root-like lower part being buried in

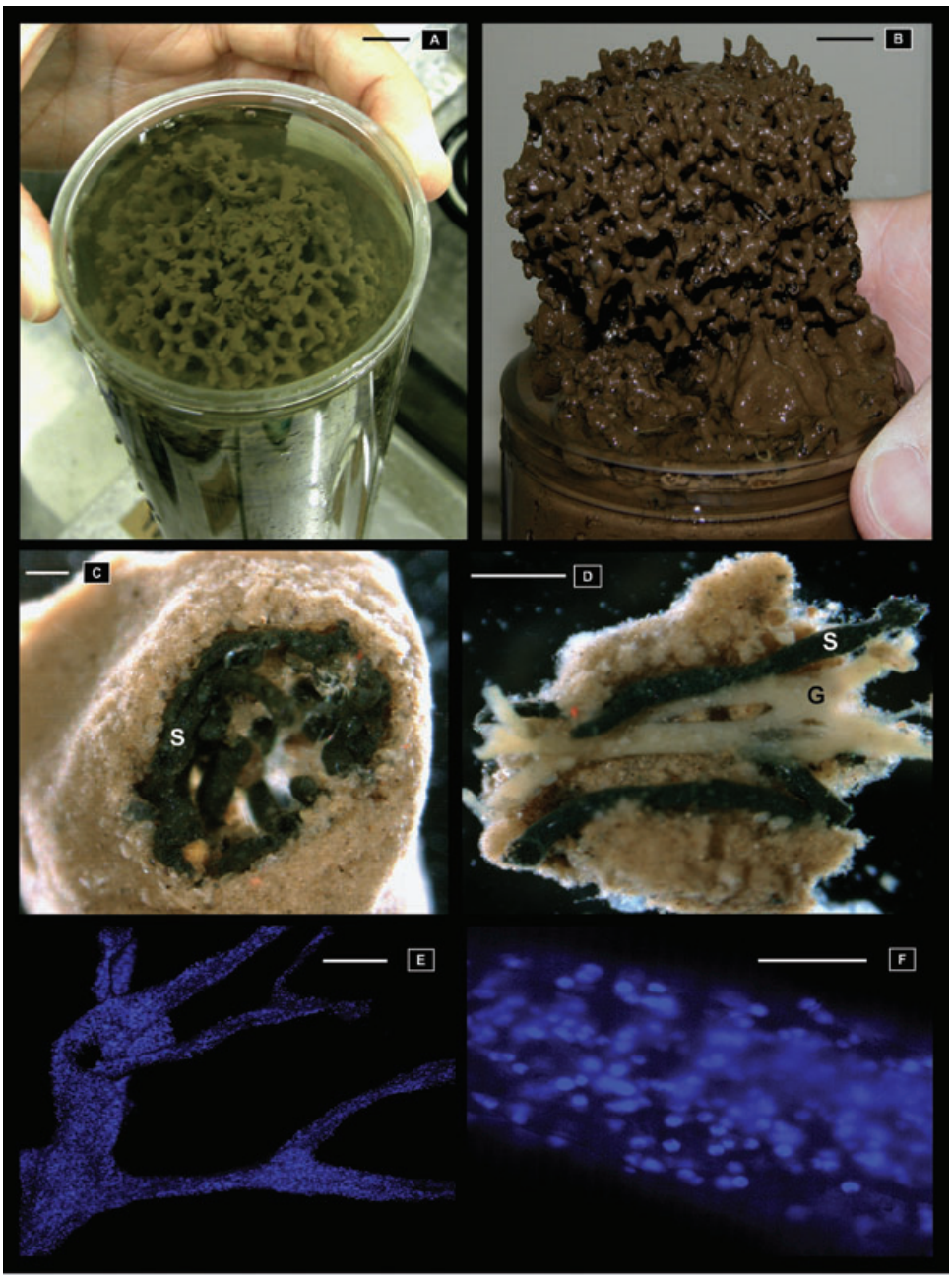

Figure 2. ***Shinkaiya lindsayi*** **gen. et sp. nov.** A, holotype specimen in its push core, just after collection (the authors assumed that this was a whole specimen, almost unbroken by the corer tube). B, holotype specimen out of its core. C, D, microscopic views of fragments, revealing the internal organization (G, granellare; S, stercomare). C, transversal view showing the dark stercomare strings. D, the fragment is open along a longitudinal axis, displaying the obvious whitish granellare and the stercomare. E, F, fragments of granellare stained with diaminidophenylindol (DAPI), revealing thousands of nuclei in the cytoplasm. Scale bars: 15 mm (A), 15 mm (B), 250 μm (C), 500 μm (D), 250 μm (E), and 30 μm (F).

the sediment. It was found among numerous other unidentified xenophyophores of different sizes.

Molecular characterization

The total length of the SSU rDNA was 4054 bp, and all of the clones sequenced were identical. The sequence alternates between conserved regions and variable regions among foraminiferans, with a long insertion of 624 bp starting in the variable region E23 at position 1744 bp (Fig. 1). The GC content of *Sh. lindsayi* sp. nov. (32.2%) is similar to that of *Sy. corbicula* (34.1%). The sequence divergence between

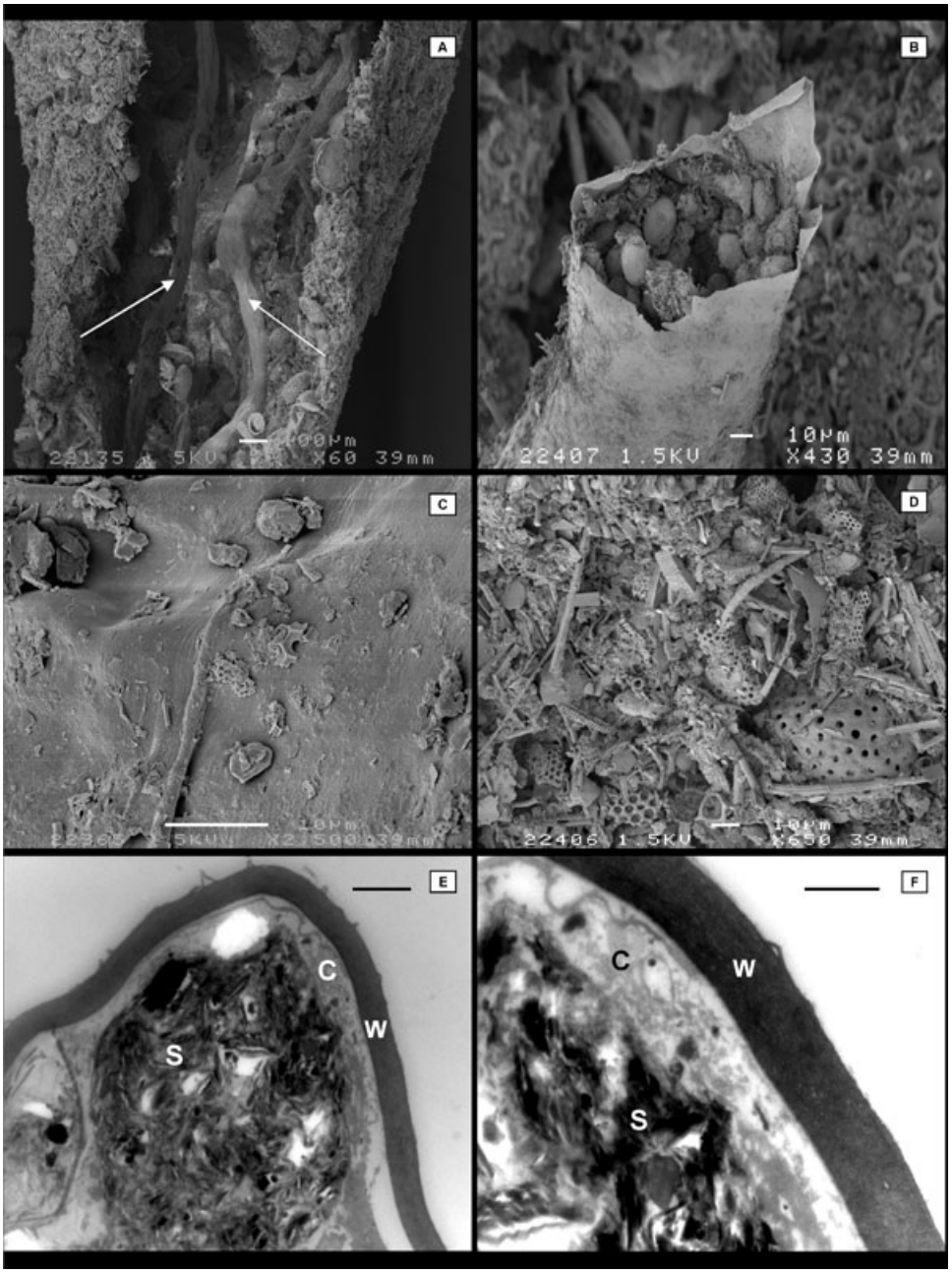

Figure 3. ***Shinkaiya lindsayi*** **gen. et sp. nov.** A, scanning electron micrograph (SEM) of an open tube, showing its inner surface with many radiolarian tests, a granellare string (right-hand arrow), and a stercomare string (left-hand arrow). B, SEM image of an open stercomare string, containing stercomata (spherical pellets). C, SEM image of the organic sheath of the granellare. D, SEM image showing details of the external surface of the test, with agglutinated material. E, F, transmission electronic microscopy (TEM) images of a stercomare section, showing its wall (W), stercomata (S), and cytoplasm (C). Scale bars: 100 µm (A), 10 µm (B–D), 2 µm (E), 1 µm (F).

the two xenophyophores is 23.6%, whereas it is 30.2% between *Sh. lindsayi* sp. nov. and *R. algaeformis*.

In the phylogenetic tree obtained by the ML method (Fig. 4), *Sh. lindsayi* sp. nov. clusters with *Sy. corbicula*, and the two xenophyophores form a sister group of *R. algaeformis*. This topology is supported by high bootstrap values (94 and 100%, respectively). The clade consisting of *Sh. lindsayi* sp. nov., *Sy. corbicula*, and *R. algaeformis* branches at the base of polythalamous (multichambered) foraminiferans, including rotaliids, textulariids, and robertinids.

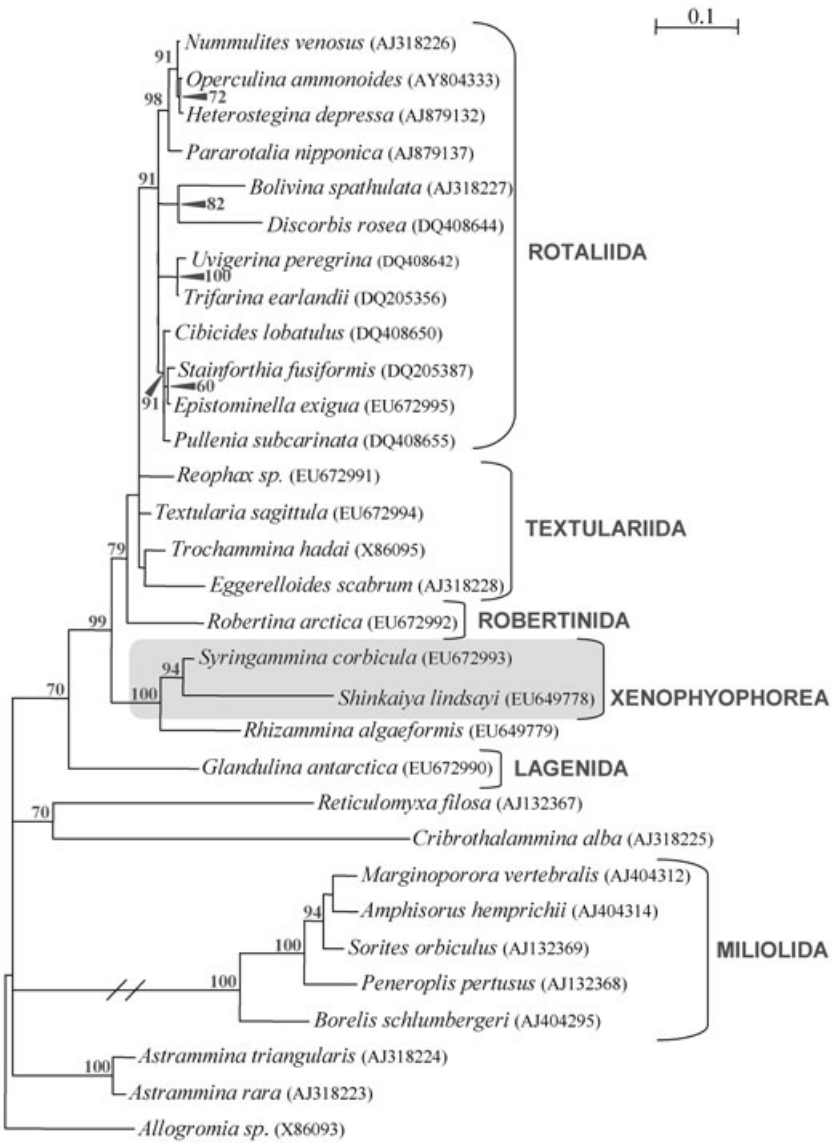

Figure 4. Phylogenetic position of ***Shinkaiya lindsayi* gen et sp. nov.** among Foraminifera, based on complete small-subunit ribosomal DNA (SSU rDNA) gene sequences. The tree was obtained using the maximum-likelihood method with the general time-reversible (GTR + G + I) model, with four rates categories, and 1000 replicates for bootstrap analysis. Only bootstrap support values higher than 70% are indicated.

Remarks

As discussed above, the new species is similar to some species of *Syringammina* in the construction of the test from reticulated bar-like elements. There is a particular resemblance between *Sh. lindsayi* sp. nov. and *Sy. reticulata* in the constant diameter, dimensions, and arrangement of the tubes (compare Fig. 2A with Gooday, 1996: pl. 7). However, in addition to the differences in wall structure noted above, the overall morphology of the test is distinctly flattened in *Sy. reticulata*, but is more or less equidimensional in *Sh. lindsayi* sp. nov.

Elemental composition

Mass spectrometry analyses were performed separately on pieces of the stercomare, granellare, and on intact fragments of the specimen, as well as on environmental samples from the area where the specimen was collected (site 1037) (Fig. 5). Aluminium, barium, and magnesium were present inside the stercomare, where concentrations were more than 30% higher than in the sediment. These elements were less abundant in the granellare than in the surrounding sediment (site 1037). They occur in roughly the same concentration in the intact fragment (mainly test)

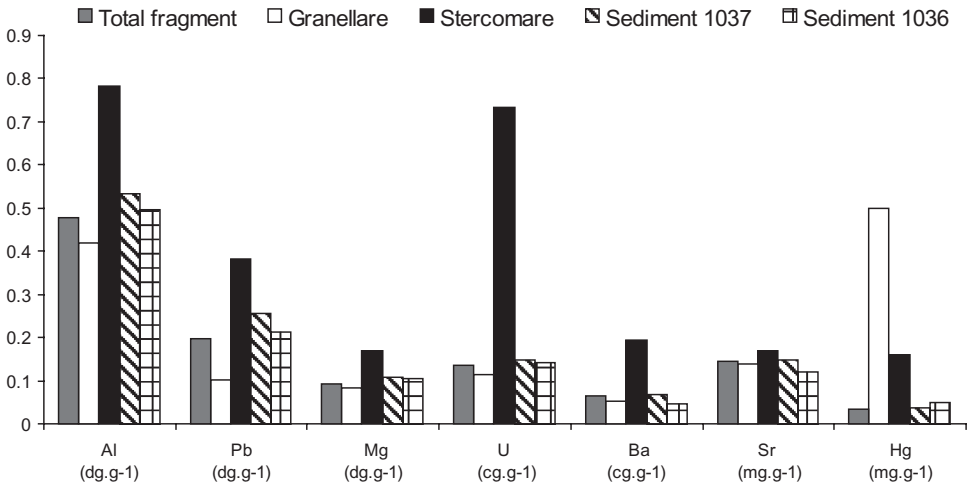

Figure 5. Inductively coupled plasma mass spectrometry (ICPMS) values for the composition of the total fragment and different structural parts of ***Shinkaiya lindsayi* gen. et sp. nov.** (total fragment), and of the environmental sediment. The mass of elemental aluminium (Al), lead (Pb), magnesium (Mg), uranium (U), barium (Ba), strontium (Sr), and mercury (Hg), per gram of dry material, is shown. A semiquantitative method has been used for Pb, U, and Hg.

and in the environment. Consistent with microscopic observations of barite crystals, barium occurs in the stercomata but not in the cytoplasm. Lead, mercury, and uranium concentrations are also higher (two, four, and six times higher, respectively) inside the stercomare than in the sediment. The concentration of mercury in the granellare is 12 times that in the sediment.

DISCUSSION

Phylogenetic position

Several authors have regarded xenophyophores as a distinct higher taxon at the level of subclass (Tendal, 1972), class (Tendal, 1996; Gooday & Tendal, 2000), or even phylum (Tendal, 1989). Pawlowski *et al.* (2003), however, showed that *Sy. corbicula* is a foraminiferan, based on a complete analysis of the SSU rDNA gene. Here, we present evidence that a second xenophyophore species is also a foraminiferan, thus strengthening the case that this enigmatic group does not represent a distinct eukaryotic taxon.

The phylogenetic position of *Shinkaiya* as a sister group to *Syringammina* supports the monophyly of the xenophyophores. However, the two species for which DNA sequences are available are both classified within Psamminidae. It is possible that members of Stannomidae, the other xenophyophore family, characterized by the presence of proteinaceous fibres (linellae) within the test, will branch outside the clade. Moreover, there are still too few complete SSU sequences of monothalamous foraminiferans, and missing data could artefactually bring *Shinkaiya* and *Syringammina* together.

The sequence divergence between *Sh. lindsayi* sp. nov. and *Sy. corbicula* is remarkably high (23.6% compared with 13.9% between *Astrammina rara* Rhumbler, 1931 and *Astrammina triangularis* Earland, 1933, which are placed in the same genus), and supports their separation into distinct genera. Both xenophyophore sequences also seem to be closely related to that of *R. algaeformis*, another monothalamous foraminiferan of uncertain taxonomic origin. Like *Shinkaiya* and *Syringammina*, *Rhizammina* contains stercomata and cytoplasmic strands within its tubular test. It has been proposed that *R. algaeformis* should be placed in the superfamily Komokiacea, based on the overall test morphology and the presence of stercomata (Gooday & Cartwright, 1987; Cartwright, Gooday & Jones, 1989). Our study suggests that *Rhizammina* is related to xenophyophores. Whether komokiaceans also group with the xenophyophores is unknown. Komokiacean sequences are needed to answer this question.

Elemental composition

Elemental analyses of *Sh. lindsayi* sp. nov. revealed that the granellare are surprisingly poor in barite. Our TEM observations, together with microanalysis, identified a few barite crystals in the stercomare, but failed to find any in the cytoplasm. This surprising result could be a temporary state, or a specific feature of the new species. Tendal (1972) also reports an absence of granellae in a few species of xenophyophores, including several stannomid species and *Reticulammina labyrinthica* Tendal, 1972. However, mass spectra analyses confirmed a weak concentra-

tion of barium inside the granellare of *Sh. lindsayi* sp. nov. We therefore cannot exclude the possibility that the observed granellare sections were poor in crystals, and are not representative of the granellare as a whole.

Another striking result of the mass spectra analysis is the extremely high concentration of mercury inside the granellare system. This result is astonishing considering the toxicity of mercury. It is highly improbable that only the granellare sample was contaminated. Mercury is lipophilic, and thus could be retained inside lipid droplets within the cytoplasm. Moreover, resistance to mercury is widespread among microorganisms, and some marine bacteria are known to convert water-soluble inorganic mercury and methylmercury to the volatile elemental form (Poulain *et al.*, 2007). It is possible that some xenophyophores also perform this detoxification process.

Other heavy metals, for example, lead, seem to be concentrated in the stercomare, as previously described by Tendal, Swinbanks & Shirayama (1982) for *Occultammina profunda* Tendal, Swinbanks & Shirayama, 1982. The inorganic remnants of digested particles taken up from the environment accumulate in the stercomata, which as a result may become enriched in non-nutritive substances like heavy metals. Because xenophyophores do not release these digestive wastes, they probably modify the chemical composition of the sediment, at least locally. Indeed, Swinbanks & Shirayama (1986b) showed that xenophyophores may drastically change the distribution of some elements in deep-sea sediment profiles. They also demonstrate that high levels of natural radiation occur in xenophyophores, as a result of the presence of ^{226}Ra in the intracellular barite crystals, and suggested that this radiation would induce numerous genetic mutations (Swinbanks & Shirayama, 1986a). As noted above, there are no obvious barite crystals in the cytoplasm of *Sh. lindsayi* sp. nov. However, radiation could arise from the high concentrations of uranium in the stercomata of this species. It is interesting to note that the excessively long branch of *Sh. lindsayi* sp. nov. in our phylogenetic tree could suggest an accelerated evolution rate of its ribosomal genes. Measurement of the radiation emanating from xenophyophores may enhance our knowledge of the respective contributions of natural and artificial radioelements, thereby improving assessments of deep-sea pollution.

As they seem to concentrate many elements from the environment, xenophyophores may directly affect the composition of deep-sea sediments, especially because they can be extremely numerous on the abyssal seafloor. For example, densities reach almost 1000 xenophyophores per 100 m^2 at a depth of 4000 m off North-West Africa (Tendal & Gooday, 1981). Information about this group, its diversity, biology, and ecology, is still scarce. The elemental analysis must be extended to other species and genera of xenophyophores to confirm that they concentrate high levels of heavy metals and radioactive elements, compared with the sediment, and in this way modify the chemistry of their environment. This could reveal how far they are involved in global biogeochemical cycles, as well as improving our knowledge of their role in deep-sea ecosystems.

ACKNOWLEDGEMENTS

We would like to thank: the captain, crew members, and scientists of the Yokosuka YK07-15 cruise, and especially Dhugal Lindsay and Frédéric Sinniger; José Fahrni (University of Geneva), for the DAPI staining; Francine Voinesco, Antonio Mucciolo, and Michel Bonin, for the microscopy (Université de Lausanne); Dominique Robin and Ricardo Stouvenel (Ecole d'ingénieur de Genève), for the ICPMS analyses; and finally Ana Aranda Da Silva for great discussions. The project was supported by a grant from the Swiss National Science Foundation (3100A0-100415).

REFERENCES

Cartwright NG, Gooday AJ, Jones AR. 1989. The morphology, internal organization and taxonomic position of *Rhizammina algaeformis* Brady, a large, agglutinated, deep-sea foraminifer. *Journal of Foraminiferal Research* **19:** 115–125.

Galtier N, Gouy M, Gautier C. 1996. SEAVIEW and PHYLO_WIN: two graphic tools for sequence alignment and molecular phylogeny. *Computer applications in the biosciences* **12:** 543–548.

Gooday AJ, Cartwright N. 1987. Rhizammina algaeformis: a giant komokiacean foraminifer? *Deep Sea Newsletter* **13:** 13–15.

Gooday AJ, Tendal OS. 2000. Class Xenophyophorea Schulze 1904. In: Lee JJ, Leedale GF, Bradbury P, eds. *The illustrated guide to the protozoa*, 2nd edn. Lawrence, KS: Allen Press, 1086–1097.

Haeckel E. 1889. Report on the Deep-Sea Keratosa. Report on the Scientific Results of the Voyage of H. M. S. Challenger during the years 1873–76. *Zoology* **32** (part 82)**:** 1–92.

Hopwood JD, Mann S, Gooday AJ. 1997. The crystallography and possible origin of barium sulphate in deep-sea rhizopod protists (Xenophyophorea). *Journal of the Marine Biological Association of the United Kingdom* **77:** 969–987.

Hughes JA, Gooday AJ. 2004. Associations between living benthic foraminifera and dead tests of *Syringammina fragilissima* (Xenophyophorea) in the Darwin Mounds region (NE Atlantic). *Deep-Sea Research I* **51:** 1741–1758.

Jobb G, von Haeseler A, Strimmer K. 2004. TREEFINDER: a powerful graphical analysis environment for molecular phylogenetics. *BMC Evolutionary Biology* **4:** 18.

Laureillard J, Méjanelle L, Sibuet M. 2004. Use of lipids to study the trophic ecology of deep-sea xenophyophores. *Marine Ecology Progress Series* **270:** 129–140.

Lee JJ, Leedale GF, Bradbury P. 2000. *The illustrated guide to the protozoa*, 2nd edn. Society of protozoologists. Lawrence, KS: Allen Press

Lemche H, Hansen B, Madsen FJ, Tendal OS, Wolff T. 1976. Hadal life as analysed from photographs. *Videnskabelige meddelelser fra Dansk naturhistorisk forening* **139:** 263–336.

Levin LA. 1994. Paleoecology and ecology of xenophyophores. *Palaios* **5:** 32–41.

Levin LA, DeMaster DJ, McCann LD, Thomas CL. 1986. Effects of giant protozoans (Class: Xenophyophorea) on deep-sea-mount benthos. *Marine Ecology Progress Series* **29:** 99–104.

Levin LA, Gooday AJ. 1992. Possible roles for xenophyophores in deep-sea carbon cycling. In: Rowe GT, Pariente V, eds. *Deep-sea food chains and the global carbon cycle*. The Netherlands: Kluwer Academic Publishers, 93–104.

Levin LA, Thomas CL. 1988. The ecology of xenophyophores (Protista) on eastern Pacific seamounts. *Deep-Sea Research* **35:** 2003–2027.

Pawlowski J, Holzmann M, Fahrni J, Richardson SL. 2003. Small subunit ribosomal DNA suggests that the xenophyophorean Syringamma corbicula is a foraminiferan. *Journal of Eukaryotic Microbiology* **50:** 483–487.

Poulain AJ, Ní Chadhain SM, Ariya PA, Amyot M, Garcia E, Campbell PG, Zylstra GJ, Barkay T. 2007. Potential for mercury reduction by microbes in the high arctic. *Applied and Environmental Microbiology 7* **73:** 2230–2238.

Schulze FE. 1904. Über den Bau und die Entwicklung gewisser Tiefsee-Organismen. *Sitzungsberichte der Königlich-preussischen Akademie der Wissenschaften zu Berlin* **53:** 1387.

Schulze FE. 1907. Die Xenophyophoren, eine besondere Gruppe der Rhizopoden. *Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer 'Validivia' 1898–1899* **11:** 1–55.

Schweizer M, Pawlowski J, Kouwenhoven TJ, Guiard J, van der Zwaan B. 2008. Molecular phylogeny of Rotaliida (Foraminifera) based on complete small subunit rDNA sequences. *Marine Paleontology* **66:** 233–246.

Swinbanks DD, Shirayama Y. 1986a. High levels of natural radionuclides in a deep-sea infaunal xenophyophore. *Nature* **320:** 354–357.

Swinbanks DD, Shirayama Y. 1986b. A model of the effect of an infaunal xenophyophore on 210Pb distribution in deep-sea sediment. *La mer* **24:** 69–74.

Tendal OS. 1972. A monograph of the Xenophyophora (Rhizopodea, Protozoa). *Galathea Report* **12:** 7–103.

Tendal OS. 1979. Aspects of the biology of Komokiacea and. *Xenophyophoria. Sarsia* **64:** 13–17.

Tendal OS. 1989. Phylum Xenophyophora. In: Margulis L, Corlis JO, Melkonian M, Chapman DJ, eds. *Handbook of the protoctista*. Boston, MA: Johnes and Bartlett Publisher, 135–138.

Tendal OS. 1996. Synoptic checklist and bibliography of the Xenophyophorea (Protista), with a zoogeographic survey of the group. *Galathea Report* **17:** 79–101.

Tendal OS, Gooday AJ. 1981. Xenophyophoria (Rhizopoda, Protozoa) in bottom photographs from the bathyal and abyssal NE Atlantic. *Oceanologica Acta* **4:** 415–422.

Tendal OS, Swinbanks DD, Shirayama Y. 1982. A new infaunal xenophyophore (Xenophyophorea, Protozoa) with notes on its ecology and possible trace fossil analogues. *Oceanologica Acta* **5:** 325–329.