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Small Subunit Ribosomal DNA Suggests that the Xenophyophorean *Syringammina corbicula*[1] is a Foraminiferan

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ABSTRACT. Xenophyophorea are giant deep-sea rhizopodial protists of enigmatic origins. Although species were described as Foraminifera or sponges in the early literature, the xenophyophoreans are currently classified either as a class of Rhizopoda or an independent phylum. To establish the phylogenetic position of Xenophyophorea, we analysed the small subunit (SSU) rRNA gene sequence of *Syringammina corbicula* Richardson, a newly described xenophyophorean species from the Cape Verde Plateau. The SSUrDNA analyses showed that *S. corbicula* is closely related to *Rhizammina algaeformis*, a tubular deep-sea foraminiferan. Both species branch within a group of monothalamous (single-chambered) Foraminifera, which include also such agglutinated genera as *Toxisarcon*, *Rhabdammina*, and *Saccammina*, and the organic-walled genera *Gloiogullmia* and *Cylindrogullmia*. Our results are congruent with observations of similar cytoplasmic organisation in *Rhizammina* and *Syringammina*. Thus, the Xenophyophorea appear to be a highly specialised group of deep-sea Foraminifera.

Key Words. Deep-sea, Foraminifera, Phylogeny, Ribosomal RNA, Protista Xenophyophorea.

XENOPHYOPHOREA are giant rhizopodial protists widely distributed in the deep sea at bathyal and abyssal depths. The xenophyophoreans are particularly abundant in regions of high food supply, for example, beneath productive surface waters or on the summits and flanks of seamounts (Levin 1994; Levin and Tomas 1988). Their often large, morphologically complex tests provide a substrate, refuge, and source of food for numerous small-sized metazoans and protists and may contribute to the maintenance of high local species diversity in areas where they are abundant (Gooday 1991; Levin et al. 1986).

The Xenophyophorea are the largest deep-sea protists, ranging in size from a few millimetres up to 25 cm (Tendal 1990). Their main diagnostic morphological features are: (1) an agglutinated test composed of foreign particles (''xenophyae''), (2) a cytoplasm organised as a multinucleate plasmodium enclosed within a branching system of organic tubes (granellare), (3) strings of stercomata (stercomare) closely associated with the granellare system, and (4) numerous intracellular barium sulphate crystals (granellae) (Tendal 1972). Some Xenophyophorea have been reported to possess granuloreticulopodia (Richardson 2001), biflagellated gametes, and heterokaryotic nuclei (Tendal 1972). However, observations of living xenophyophoreans are very rare (Gooday et al. 1993) and our knowledge of their cell biology, reproduction, and life cycle is limited.

The class of Xenophyophorea presently includes 14 genera and almost 60 described species (Gooday and Tendal 2000; Tendal 1996). Identification of xenophyophoreans is often difficult because their fragile tests fragment easily, have relatively few distinct morphological features, and are often morphologically variable. Xenophyophoreans can be easily mistaken for poorly preserved fragments of sponges, coelenterates, bryozoans or ascidians, or regarded as inorganic conglomerates (Tendal 1972). The first xenophyophorean was described as a primitive foraminiferan (Brady 1883). Later, Haeckel (1889) classified the xenophyophoreans as a group of deep-sea sponges, but his classification was strongly criticized by sponge specialists. Schultze (1907), who was the first to clearly demonstrate the protistan nature of Xenophyophorea, considered them to be an independent class of Rhizopoda. This taxonomic status has been generally accepted in recent protist classifications, in which Xenophyophorea are placed either as a class of Rhizopoda (Corliss 1994), or as an independent class or phylum within Eukaryota (Lee et al. 2000). Because of a lack of molecular data, the Xenophyophorea have not been included in recent taxonomic revision of the protists (Cavalier-Smith 2002).

In this paper, we present the phylogenetic analysis of small subunit (SSU) rRNA gene sequences obtained from *Syringammina corbicula*, a newly described species of Xenophyophorea (Richardson 2001), indicating that this species is a foraminiferan.

MATERIALS AND METHODS

DNA extraction. Living specimens of *Syringammina corbicula* were collected in December 1998, during cruise 159, leg 7 of the *R/V Knorr* (Woods Hole Oceanographic Institution). All specimens were retrieved from a single site on the Cape Verde Plateau (N 18° 27.7′, W 21° 01.6′), at a depth of 3,106 m using a multiple corer (Richardson 2001). A specimen designated for molecular work was frozen at −80 °C immediately after being collected. It was transferred frozen to the laboratory in Geneva, where it was dissected under a binocular microscope, in sterile conditions. Several fragments of granellare were isolated under UV-irradiated hood, using sterile tools to avoid contamination by foreign DNA. Each fragment was washed in sterile seawater and cleaned with brush under a binocular microscope. The microscopic examination of all fragments of granellare taken for DNA extraction did not reveal the presence of any other protists. The DNEasy plant mini kit (Qiagen, Santa Clarita, CA) was used for DNA extraction.

DNA amplification, cloning and sequencing. The SSUrDNA was amplified by PCR, following the protocol described in Holzmann et al. (2003). Several fragments of the SSUrRNA gene were obtained using foraminiferal specific primers (A10–s13; s8f–s17; s14f–sB) or, whenever it was possible, the eukaryotic universal primer pairs (s6–s14r; s15r–s20r) (Table 1). PCR products were cloned and sequenced as described in Holzmann et al. (2003). For each PCR product, 2–3 clones were sequenced in both directions.

To ascertain that the obtained sequences originate from *Syringammina* and not from any other foraminiferal contaminant, not only have we thoroughly cleaned the extracted material but also we have examined the sequences from 6 extractions of different fragments of granellare. Moreover, we used universal eukaryotic primers to check whether any other eukaryotic DNA is present in our samples. Because all DNA extracts gave the same sequence, with both specific and universal primers, we assumed that the sequence is that of *S. corbicula*.

Phylogenetic analysis. Sequences were aligned manually to the large database of foraminiferan sequences, using the Sea-

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[1] GenBank accession number for SSU rDNA sequence of *S. corbicula*: AJ514856

Table 1. List of primers used in this study.

Name	Sequence	Specificity	Orientation
sA10	5′ CTC AAA GAT TAA GCC ATG CAA GTG G 3′	foraminifera	forward
s13	5′ GCA ACA ATG ATT GTA TAG GC 3′	foraminifera	reverse
s8f	5′ TCG ATG GGG ATA GTT GG 3′	foraminifera	forward
s17	5′ CGG TCA CGT TCG TTG C 3′	foraminifera	reverse
s14f	5′ ACT TGA AGG AAT TGA CGG 3′	foraminifera	forward
sB	5′ TGA TCC TTC TGC AGG TTC ACC TAC 3′	universal	reverse
s6	5′ C(CT)G CGG TAA TTC CAG CTC 3′	universal	forward
s14r	5′ CCG TCA ATT (TC)CT TTA AGT 3′	universal	reverse
s15r	5′ GTG GTG CAT GGC CGT 3′	universal	forward
s20r	5′ GAC GGG CGG TGT GTA CAA 3′	universal	reverse

view software (Galtier et al. 1996). For analyses of complete SSUrDNA, 1,081 sites were selected, including 506 variable and 402 phylogenetically informative sites. Analyses of partial SSUrDNA were done using 595 sites, including 198 variable and 128 phylogenetically informative sites. Phylogenetic analyses were performed using the maximum likelihood (ML) method using the tree-building algorithm of FASTDNAML (Olsen et al. 1994) and the neighbor joining (NJ) method, applied to distances corrected using K2, HKY, and LogDet models. All characters were equally weighted and the transition-transversion ratio estimated from the data was set to 1.08 and 0.89 for analyses of complete and partial SSUrDNA, respectively. The reliability of internal branches was assessed by bootstrapping (Felsenstein 1985) with 1,000 resamplings for the NJ and 100 resamplings for the ML tree, respectively. The Phylo_win program (Galtier et al. 1996) was used for distance computations using various models, NJ and ML tree-building, and bootstrapping. The GenBank accession numbers for all sequences used in our analyses are given in Table 2.

RESULTS AND DISCUSSION

Phylogenetic analysis of complete SSUrDNA sequences shows that *Syringammina corbicula* branches among Foraminifera (Fig. 1A). The group is very well supported in both analyses (100% bootstrap values), presenting a long stem lineage due to the numerous foraminiferal specific nucleotide substitutions. The position of the Foraminifera in the eukaryotic tree (Fig. 1A) differs from the previously published SSUrDNA phylogenies (Pawlowski and Holzmann 2002). To avoid the long-branch attraction artefacts, we excluded all fast evolving eukaryotic lineages from our analyses (Berney and Pawlowski 2003). As a result, the Foraminifera group with the Cercozoa, in agreement with phylogenies derived using sequences from actin (Keeling 2001) and ubiquitine (Archibald et al. 2003). The position of Foraminifera as the sister-group to the filosean *Gromia oviformis* is congruent with analyses of actin and RNA polymerase sequences (unpubl. data). The topology obtained using the ML method (Fig. 1A) is congruent with the topology of NJ trees obtained using HKY and LogDet substitution models, but it differs from the NJ trees obtained using K2 model, where long branch of Foraminifera cluster among Amoebozoa (data not shown).

To establish the position of *Syringammina corbicula* among Foraminifera, we compared its sequence to the partial SSUrDNA sequences of 29 foraminiferal species (Fig. 1B). In all analyses, *S. corbicula* clustered with *Rhizammina algaeformis* within a clade of monothalamous Foraminifera that includes also such agglutinated genera as *Toxisarcon*, *Saccammina*, and *Rhabdammina*, and the organic-walled genera *Gloiogullmia* and *Cylindrogullmia*. This clade corresponds to lineage C in a recently published phylogeny of monothalamous Foraminifera (Pawlowski et al. 2002). It is supported by high bootstrap values and it is the sister-group to the clade comprised of monothalamous lineages, including *Psammosphaera* and some unidentified allogromiids, as well as the polythalamous Rotaliida and Textulariida. The relationship between *Syringammina* and *Rhizammina* is well supported in all types of analyses (Fig. 1B).

Our data showing that *Syringammina corbicula* is a foraminiferan would suggest that this species possesses the granuloreticulopodia. Until now, all we know about xenophyophorean pseudopodia was based on few observations of cytoplasmic extensions in fixed specimens (Riemann et al. 1993; Tendal 1972) and observation of possible pseudopodial traces surrounding individuals photographed in situ on the seafloor (Lemche et al. 1976). Observations of granuloreticulopodia in *S. corbicula* (Richardson 2001) could provide an independent line of evidence for foraminiferan origins of Xenophyophorea. However, it remains to be determined if their organisation and ultrastructure conforms to the refined definition of foraminiferan reticulopodia (Bowser and Travis 2002).

Placement of *Syringammina* among Foraminifera based on molecular data is in agreement with the initial classification of this genus as a large agglutinated foraminiferan (Brady 1883), and its subsequent placement in the foraminiferal families Rhabdamminidae (Rhumbler 1913), Hyperamminidae (Cushman 1950), or Astrorhizidae (Loeblich and Tappan 1964). *Syringammina* was included among Xenophyophorea by Tendal (1972), who pointed, however, to its strong similarity to Foraminifera. The xenophyophoreans and foraminiferans share several common features, not only in gross morphology of their test. Some Foraminifera (for example *Reticulomyxa filosa*) possess a multinucleate plasmodium similar to that observed in xenophyophoreans (Pawlowski et al. 1999). Other foraminiferans are known to have nuclear dimorphism (Lee et al. 1991), perhaps similar to the differentiation of nuclei observed in some xenophyophoreans (Tendal 1972). Hopwood et al. (1996) drew attention to similarities in the cellular organization of the xenophyophore *A. ramuliformis* and the foraminiferan *Rhizammina algaeformis*. Interestingly, *Rhizammina* appears as closely related to *Syringammina* in our analyses. This is congruent with the morphological similarities of both genera that have a basically tubular test, with tubes containing a thread of cytoplasm and strands of stercomata (Cartwright et al. 1989; Gooday, pers. info.).

The distinction of xenophyophoreans is based principally on the presence of some specific features, such as the granellare, the stercomare, and intracellular barite crystals. However, in view of our study, these features should be interpreted as autapomorphies of a derived group of deep-sea Foraminifera rather than those of an independent eukaryotic taxon. *Syringam-*

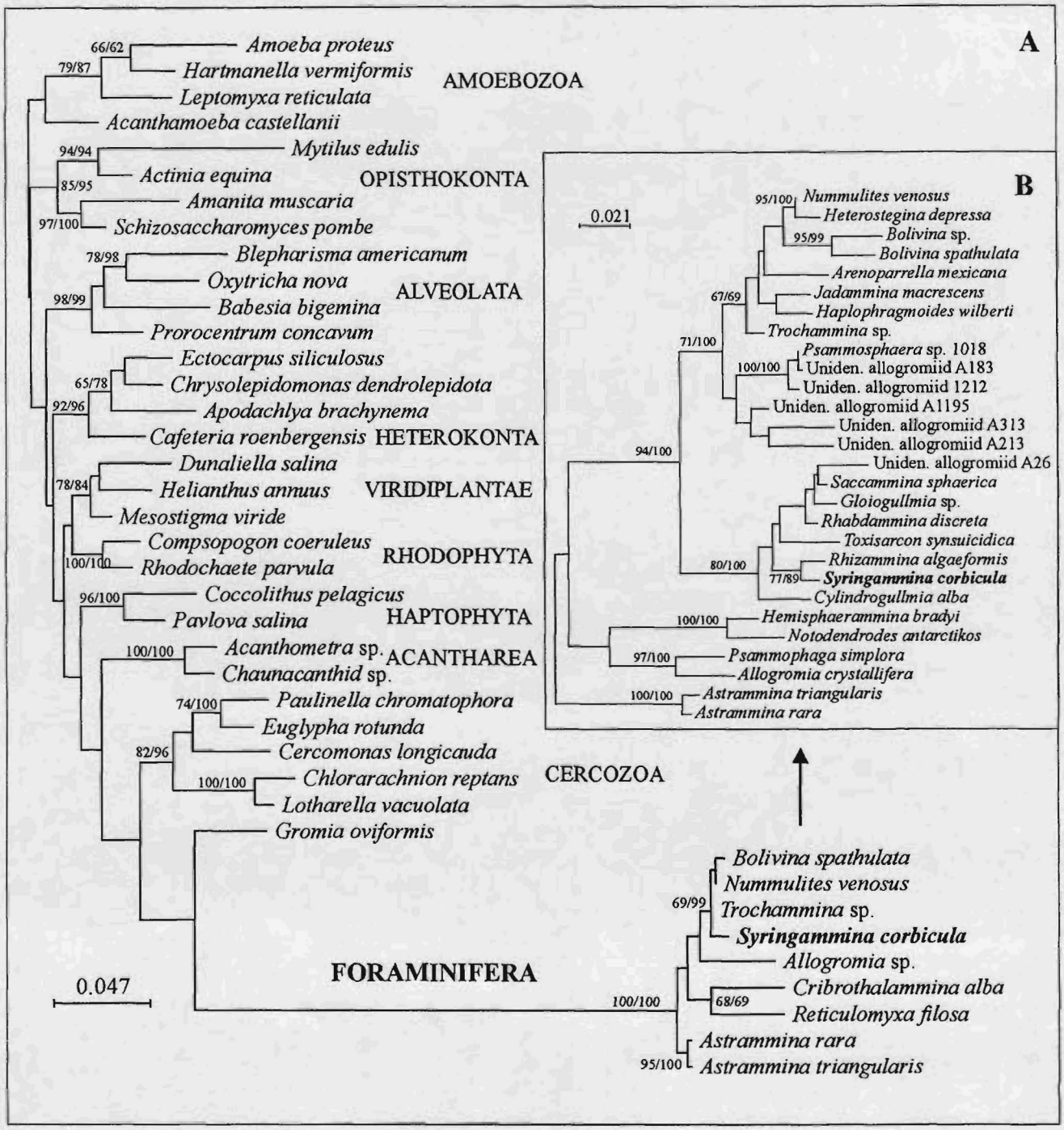

Fig. 1. Phylogenetic position of xenophyophorean *Syringammina corbicula* among eukaryotes (**A**) and Foraminifera (**B**) inferred from small subunit rRNA gene sequences. Both trees were obtained using the maximum likelihood method. Numbers at the nodes in both trees indicate bootstrap support values, higher than 60%, for maximum likelihood and neighbor joining analyses, respectively.

mina corbicula possesses all typical xenophyophorean morphological features and therefore it can be considered as representative of the entire group. Nevertheless, to test the monophyly of Xenophyophorea and confirm their foraminiferan origins, the molecular study of other species and ultrastructural examination of their pseudopodia will be necessary.

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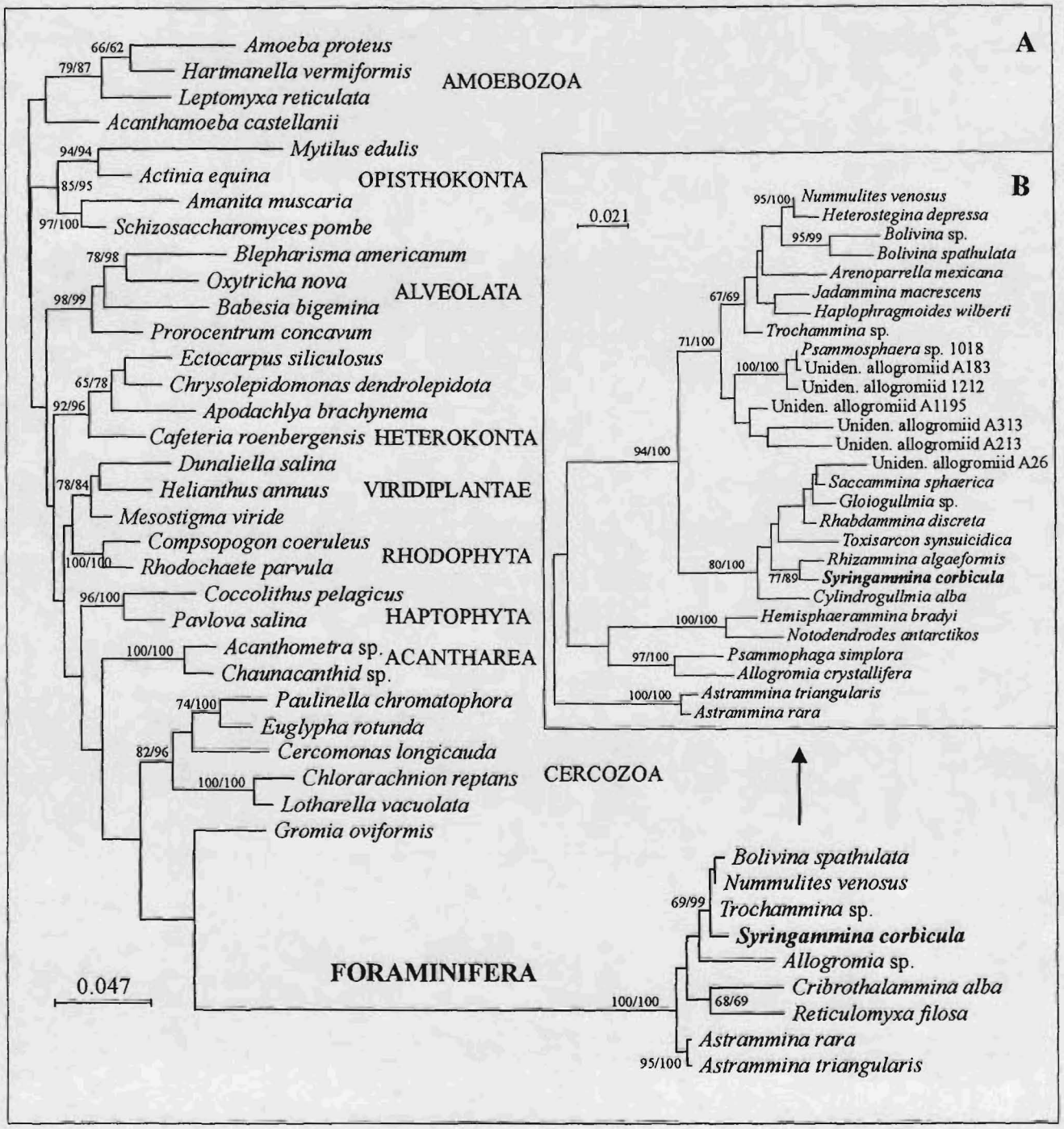

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Table 2. GenBank accession number of all sequences used in this work.

Phylum	Species	Accession number
Amoebozoa	*Amoeba proteus*	AJ314604
	Hartmanella vermiformis	AF426157
	Leptomyxa reticulata	AF293898
	Acanthameoba castellanii	M13435
Opisthokonta	*Mytilus edulis*	L33448
	Actinia equina	AJ133552
	Amanita muscaria	AF026631
	Schizosaccharomyces pombe	X58056
Alveolata	*Blepharisma americanum*	M97909
	Oxytricha nova	X03948
	Babesia bigemina	X59604
	Prorocentrum concavum	Y16237
Heterokonta	*Ectocarpus siliculosus*	L43062
	Chrysolepidomonas dendrolepidota	AF123297
	Apodachlya brachynema	AJ238663
	Cafeteria roenbergensis	L27633
Viridplantae	*Dunaliella salina*	M84320
	Helianthus annuus	AF107577
	Mesostima viride	AF408245
Rhodophyta	*Compsopogon coeruleus*	AF342748
	Rhodochaete parvula	AF139462
Haptophyta	*Coccolithus pelagicus*	AJ246261
	Pavlova salina	AF102987
Acantharea	*Acanthometra* sp.	AF063240
	Chaunacanthid sp.	AF018158
Cercozoa	*Paulinella chromatophora*	X81811
	Euglypha rotunda	X77692
	Cercomonas longicauda	AF101052
	Chlorarachnion reptans	X70809
	Lotharella vacuolata	AF054890
	Gromia oviformis	AJ457811
Foraminifera	*Allogromia* sp.	X86093
	Allogromia crystallifera	AJ317986
	Arenoparrella mexicana	AJ307741
	Astrammina rara	AJ318223
	Astrammina triangularis	AJ318224
	Bolivina sp.	Z69613
	Bolivina spathulata	AJ318227
	Cribrothalammina alba	AJ318225
	Cylindrogullmia alba	AJ317983
	Gloiogullmia sp.	AJ307751
	Haplophragmoides wilberti	AJ312436
	Hemisphaerammina bradyi	AJ311216
	Heterostegina depressa	AJ514841
	Jadammina macrescens	AJ307742
	Notodendrodes antarctikos	AJ311213
	Nummulites venosus	AJ311212
	Psammophaga simplora	AJ317985
	Psammosphaera sp. 1018	AJ307743
	Reticulomyxa filosa	AJ132367
	Rhabdammina discreta	AJ514852
	Rhizammina algaeformis	AJ514853
	Saccammina sphaerica	AJ514855
	Syringammina corbicula	AJ514856
	Toxisarcon synsuicidica	AJ315955
	Trochammina sp.	X86095
	Uniden. Allogromiid 1212	AJ307744
	Uniden. Allogromiid A1195	AJ307746
	Uniden. Allogromiid A313	AJ307748
	Uniden. Allogromiid A213	AJ307748
	Uniden. Allogromiid A213	AJ307747
	Uniden. Allogromiid A26	AJ307752

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LITERATURE CITED

Archibald, J. M., Longet, D., Pawlowski, J. & Keeling, P. J. 2003. A novel polyubiquitin structure in Cercozoa and Foraminifera: evidence for a new eukaryotic supergroup. *Mol. Biol. Evol.*, **20**:62–66.

Berney, C. & Pawlowski, J. 2003. Revised small subunit rRNA analysis provides further evidence that Foraminifera are related to Cercozoa. *J. Mol. Evol.*, **57**:1–8.

Bowser, S. S. & Travis, J. L. 2002. Reticulopodia: structural and behavioral basis for the suprageneric placement of granuloreticulosean protists. *J. Foramin. Res.*, **32**:440–447.

Brady, H. B. 1883. *Syringammina*, a new type of arenaceous Rhizopoda. *Proc. R. Soc.*, **35**:55–161.

Cartwright, N. G., Gooday, A. J. & Jones, A. R. 1989. The morphology, internal organization, and taxonomic position of *Rhizammina algaeformis* Brady, a large, agglutinated deep-sea foraminifer. *J. Foramin. Res.*, **19**:115–125.

Cavalier-Smith, T. 2002. The phagotrophic origin of eukaryotes and phylogenetic classification of Protozoa. *Int. J. Syst. Evol. Microbiol.*, **52**:297–354.

Corliss, J. O. 1994. An interim utilitarian ("user-friendly") hierarchical classification and characterization of the protists. *Acta Protozool.*, **33**: 1–51.

Cushman, J. A. 1950. Foraminifera, their Classification and Economic Use. Harvard University Press, Cambridge, MA. p. 1–605.

Felsenstein, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution*, **39**:783–791.

Galtier, N., Gouy, M. & Gautier, C. 1996. SEAVIEW and PHYLO_WIN: two graphic tools for sequence alignment and molecular phylogeny. *Comput. Appl. Biosci.*, **12**:543–548.

Gooday, A. J. 1991. Xenophyophores (Protista, Rhizopoda) in box-core samples from the abyssal northeast Atlantic Ocean (Biotrans area): their taxonomy, morphology and ecology. *J. Foramin. Res.*, **21**:197–212.

Gooday, A. J. & Tendal, O. S. 2000. Class Xenophyophorea Schulze 1904. *In*: Lee, J. J., Leedale, G. F. & Bradbury, P. (ed.), The Illustrated Guide to the Protozoa, 2nd ed., Allen Press, Lawrence, KS. p. 1086–1097.

Gooday, A. J., Bett, B. J. & Pratt, D. N. 1993. Direct observation of episodic growth in an abyssal xenophyophore (Protista). *Deep-Sea Res.*, **40**:2131–2143.

Haeckel, E. 1889. Report on the Deep-Sea Keratosa. *Rep. Challenger*, **32**:1–92.

Holzmann, M., Habura, A., Giles, H., Bowser, S. S. & Pawlowski, J. 2003. Freshwater foraminiferans revealed by analysis of environmental DNA samples. *J. Eukaryot. Microbiol.*, **50**:135–139.

Hopwood, J. D., Mann, S. & Gooday, A. J. 1996. The crystallography and possible origin of barium sulphate in deep-sea rhizopod protists (class Xenophyophorea). *J. Mar. Biol. Assoc. UK*, **77**:969–987.

Keeling, P. J. 2001. Foraminifera and Cercozoa are related in actin phylogeny: two orphans find a home? *Mol. Biol. Evol.*, **18**:1551–1557.

Lee, J. J., Leedale, G. F. & Bradbury, P. 2000. The Illustrated Guide to the Protozoa, 2nd ed., Allen Press, Lawrence, KS.

Lee, J. J., Faber, W. W., Anderson, R. O. & Pawlowski, J. 1991. Lifecycles of foraminifera. *In*: Lee, J. J. & Anderson, R. O. (ed.), Biology of Foraminifera. Academic Press, London. p. 285–334.

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

Levin, L. A. 1994. Paleoecology and ecology of xenophyophores. *Palaios*, **9**:32–41.

Levin, L. A. & Thomas, C. L. 1988. The ecology of xenophyophores (Protista) on eastern Pacific seamounts. *Deep-Sea Res.*, **35**:2003–2027.

Levin, L. A., DeMaster, D. J., McCann, L. D. & Thomas, C. L. 1986. Effects of giant protozoans (Class: Xenophyophorea) on deep-seamount benthos. *Mar. Ecol. Prog. Series*, **29**:99–104.

Loeblich, A. R. & Tappan, H. 1964. Treatise of Invertebrate Paleontology. Part C. Protista. University of Kansas Press.

Olsen, G. J., Matsuda, H., Hagstrom, R. & Overbeek, R. 1994. FastDNAml: a tool for construction of phylogenetic trees of DNA sequences using maximum likelihood. *Comp. Appl. Biosci.*, **10**:41–48.

Pawlowski, J. & Holzmann, M. 2002. Molecular phylogeny of Foraminifera—a review. *Europ. J. Protistol.*, **38**:1–10.

Pawlowski, J., Bolivar, I., Fahrni, J., de Vargas, C. & Bowser, S. S. 1999. Molecular evidence that *Reticulomyxa filosa* is a freshwater naked foraminifer. *J. Eukaryot. Microbiol.*, **46**:612–617.

Pawlowski, J., Holzmann, M., Berney, C., Fahrni, J., Cedhagen, T. & Bowser, S. S. 2002. Phylogeny of allogromiid Foraminifera inferred from SSU rRNA gene sequences. *J. Foramin. Res.*, **32**:334–343.

Rhumbler, L. 1913. Die Foraminiferen (Thalamorphen) der Plankton Expedition. *Systematik. Ergebn. Atlant. Ozean Planktonexpd. Humboldt-Stift.* **3c**:1–331.

Richardson, S. L. 2001. *Syringammina corbicula* sp. nov. (Xenophyophorea) from the Cape Verde Plateau, E. Atlantic. *J. Foramin. Res.*, **31**:201–209.

Riemann, F., Tendal, O. S. & Gingele, F. X. 1993. *Reticulammina antarctica* nov. spec. (Xenophyophora, Protista) from the Weddell Sea, and aspects of the nutrition of xenophyophores. *Polar Biol.*, **13**:543–547.

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

Tendal, O. S. 1972. A monograph of the Xenophyophoria (Rhizopodea, Protozoa). *Galathea Report,* **12**:7–99.

Tendal, O. S. 1990. Phylum Xenophyophora. *In:* Margulis, L., Corliss, J. O., Melkonian, M. & Chapman, D. J. (ed.), Handbook of Protoctista. Jones & Bartlett Publishers, Boston, MA. p.135–138.

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

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