A new monothalamous foraminiferan from 1000 to 6300 m water depth in the Weddell Sea: morphological and molecular characterisation

Andrew J. Gooday[a,*], Maria Holzmann[b], Jackie Guiard[b],
Nils Cornelius[a], Jan Pawlowski[b]

[a]*Southampton Oceanography Centre, Empress Dock, European Way, Southampton SO14 3ZH, UK*
[b]*Department of Zoology and Animal Biology, University of Geneva Sciences III, CH1211 Geneva 4, Switzerland*

Abstract

We describe *Bathyallogromia weddellensis* gen. & sp. nov., a deep-water, monothalamous foraminiferan from bathyal and abyssal sites in the western Weddell Sea. The species is characterised by a delicate, almost spherical, organic-walled test, a low, broad projecting apertural region, and light grey or greenish cytoplasm containing mineral grains and other inclusions. Molecular phylogenetic analyses, based on small subunit rRNA gene sequences, indicate that *Bathyallogromia* is an independent lineage branching within a clade of monothalamous foraminiferans, which also includes such genera as *Saccammina*, *Gloiogullmia*, *Cylindrogullmia*, *Rhabdammina*, *Toxisarcon* and *Pilulina* (?). Lack of significant genetic differences between specimens collected at depths ranging from 1000 to 6300 m suggests that *B. weddellensis* is adapted to conditions that span a broad bathymetric range.
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1. Introduction

Relatively few species of monothalamous (single-chambered) organic-walled foraminiferans ('allogromiids') have been described from the deep sea and most of these are fairly robust forms belonging to genera such as *Placopsilinella*, *Nodellum* and *Resigella*. In fact, delicate, undescribed allogromiid species are common and diverse in deep-sea settings (Gooday, 2002; Gooday et al., 2001, 2004). The purpose of this paper is to formally describe one of these species on the basis of samples obtained at bathyal and abyssal sites in a poorly studied region of the western Weddell Sea. The description is based on traditional morphological criteria combined with characterisation of molecular genetic sequences from specimens collected along a bathymetric gradient. The

*Corresponding author. Tel.: +44-2380-516353; fax: +44-2380-596247.

E-mail address: ang@soc.soton.ac.uk (A.J. Gooday).

availability of molecular data from different stations enables us to address the question of whether the new species exhibits genetic differentiation in relation to water depth.

2. Materials and methods

2.1. Sampling sites

Most of the material was collected at a series of stations in the western Weddell Sea during R/V *Polarstern* Cruise ANT-XIX/4 (Brandt et al., 2003) (Table 1; Fig. 1). Stations 131–134 were located along a transect down the continental slope on the eastern side of the Antarctic Peninsula (1080–4060 m). Stations 135–138 were located on the Weddell Abyssal Plain (4680–4980 m). Station 142 was situated at 6330 m depth in the South Sandwich Trench at the eastern extremity of the Scotia Sea.

The seafloor in the western Weddell Sea is overlain by Weddell Sea deep water and Weddell Sea bottom water. Bottom-water oxygen concentrations are not available from our sites but sediments at all the sites appeared to be well-oxygenated. The stations studied exhibited a variety of sediment types reflecting different hydrodynamic regimes (Howe, 2003). Clayey silt occurred at Stations 137 and 138, silty clays at Stations 131, 134–136, silty sand at Station 133 and sandy silts at the trench station (142). These sediments are interpreted as contourite deposits (Stations 131 and 133), a glacigenic hemipelagite (Station 132), hemipelagites (Stations 134–137, 142) and a pelagite (Station 138). The contourites suggest moderate along-slope current activity, for which there is some photographic evidence at Station 131 on the lower slope (3055 m water depth).

2.2. Shipboard procedures

The allogromiids were collected between the 5th and 17th of March 2002. Sediment samples were obtained using either a box-core or a multiple corer equipped with 12 tubes, each of 57 mm internal diameter. As soon as possible after collection, the upper 1 cm or so of surface sediment was scooped off and then immediately sieved through 500 and 125 μm screens in a cool room set at 2 °C. These unfixed residues were stored in the cool room for periods of several hours to several days. Living foraminifera were then sorted under a binocular microscope in a Petri dish of seawater kept cool in a dish of ice. Specimens for morphological study were fixed in buffered 10% formalin and stored in plastic centrifuge vials. Specimens for molecular analyses were transferred to microtubes containing 60 μl of guanidine DNA extraction buffer. The DNA extracts contained from 1 to 10 specimens per tube.

Some additional specimens were picked from the 150–300 μm and 63–125 μm fractions of samples used for a quantitative study of foraminiferal faunal characteristics (Cornelius and Gooday, 2004). These specimens were used to calculate the relative abundance of the new species.

2.3. Morphological study

Specimens for morphological study were photographed in water under a Wild M440 stereomicroscope using reflected light. For more detailed examination, the allogromiids were placed in glycerol in a cavity slide and examined and photographed under an Olympus BH2 photomicroscope. The results were recorded in Ilford Delta 100ASA film and scanned into a computer. Test measurements were made to the nearest 10 μm using an eyepiece graticule fitted to a Wild M50 dissecting microscope.

2.4. Molecular analysis

A fragment of the SSU rRNA gene was amplified by PCR with the primer pair s14F3 (5′ ACG CA(AC) GTG TGA AAC TTG) and sB (5′ TGA TCC TTC TGC AGG TTC ACC TAC), as described in Pawlowski (2000). In some cases, the PCR products were re-amplified using nested primer s14F1 (5′ AAG GGC ACC ACA AGA ACG C). The amplified PCR products were purified using a High Pure PCR Purification Kit (Roche Diagnostics), then either sequenced

Table 1
Station data

Station	Latitude (°S)	Longitude (°W)	Depth (m)	Phytodetritus	Environmental conditions	Number of specimens examined	
						Morphology	Molecular
131#7	65°19.45′	51°30.98′	2986	Thin surface veneer of greenish material	Dark, greenish-grey silty clay; moderate current activity; interpreted as contourite deposit	13	6
131#9	65°18.54′	51°31.93′	2986				
131#10	65°19.56′	51°34.31′	3000				
132#5	65°17.66′	53°22.98′	2002	Somewhat thicker layer of greenish material	Dark greenish-grey sandy silt; sluggish current; interpreted as a glacigenic hemipelagite	32	12
132#7	65°17.66′	53°22.98′	1982				
133	65°20.23′	54°12.65′	1166	No obvious phytodetritus	Greenish-grey silty sand; interpreted as contourite	0	2
134	65°19.90′	48°5.55′	4060	Quite a lot of phytodetritus present	Greenish-grey silty clay; interpreted as hemipelagite	0	8
135#6	64°59.94′	43°00.68′	4670	Sparse amounts of phytodetritus	Surficial sediment very soft and watery; Greenish-grey silty clay; interpreted as hemipelagite	21	5
135#8	65°00.01′	42°59.91′	4678				
136#6	64°00.94′	39°06.31′	4730	A few cores with some fluffy surface material	Dark greenish-grey silty clay; interpreted as hemipelagite	46	8
136#8	64°01.64′	39°05.14′	4736				
137#6	63°44.99′	33°47.80′	4735	Some cores with quite a lot of brownish-green phytodetritus, but amounts very variable	Dark greenish-grey silty clay; interpreted as low-energy hemipelagite	2	10
137#8	63°45.03′	33°47.95′	4735				
138#3	62°57.69′	27°53.60′	4490	More or less complete layer of degraded-looking (brownish) phytodetritus in some cores but amounts very variable	Dark greenish-grey clayey silt containing biogenic siliceous material and volcanic glass; interpreted as low-energy hemipelagite	10	0
138#5	62°57.81′	27°53.99′	4500				
138#7	62°58.00′	27°53.85′	4500				
138#9	62°57.90′	27°54.11′	4500				
138#11	62°58.02′	27°54.06′	4500				
142	58°50.81′	23°58.55′	6326	No obvious phytodetritus	Dark greyish-brown sandy silt; interpreted as hemipelagite or pelagite	0	5

Sediment data and environmental interpretation from Howe (2003). Information about phytodetritus from Vanreusel and De Mesel (2003) and Gooday (unpublished).
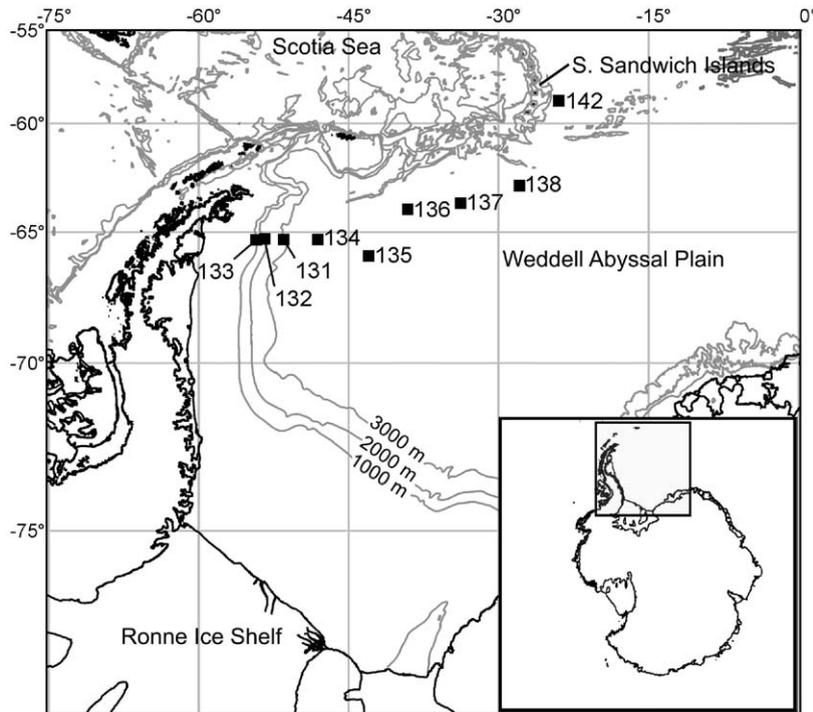
Fig. 1. Location of sampling sites in the Weddell Sea.

directly or ligated into pGEM-T Vector system (Promega) and cloned in XL-2 Ultracompetent Cells (Stratagene). Sequencing reactions were prepared by using an ABI-PRISM Big Dye Terminator Cycle Sequencing Kit and analysed with an ABI-377 DNA sequencer (Perkin-Elmer), all according to the manufacturer's instructions.

Sequences were aligned manually to the large database of foraminiferan sequences, using the Seaview software (Galtier et al., 1996); 592 sites were selected for analysis, including 218 variable and 156 informative sites. Phylogenetic analyses were performed with the neighbour joining (NJ) method (Saitou and Nei, 1987), applied to distances corrected using the Kimura 2 parameters model (Kimura, 1980), the Hasegawa–Kishino–Yano model (Hasegawa et al., 1985) and the LogDet model (Lockhart et al., 1994), and the maximum likelihood (ML) method using the tree-building algorithm of FASTDNAML (Olsen et al., 1994). All characters were equally weighted and the transition-transversion ratio was set to 0.914. The reliability of internal branches was assessed by bootstrapping (Felsenstein, 1985) with 1000 re-sampling for the NJ and 100 re-sampling 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.

3. Systematics

We follow recent suprageneric classifications (Loeblich and Tappan, 1987; Sen Gupta, 1999) by placing the new genus in the Order Allogromiida. However, molecular genetic studies suggest that the monothalamous foraminifera currently accommodated within the Order Allogromiida (organic walls) and the Order Astrorhizida (agglutinated walls) include a number of phylogenetic lineages (clades) that cut across these traditional, morphology-based taxa (Pawlowski et al., 2002b, 2003). Moreover, none of the lineages so far recognised
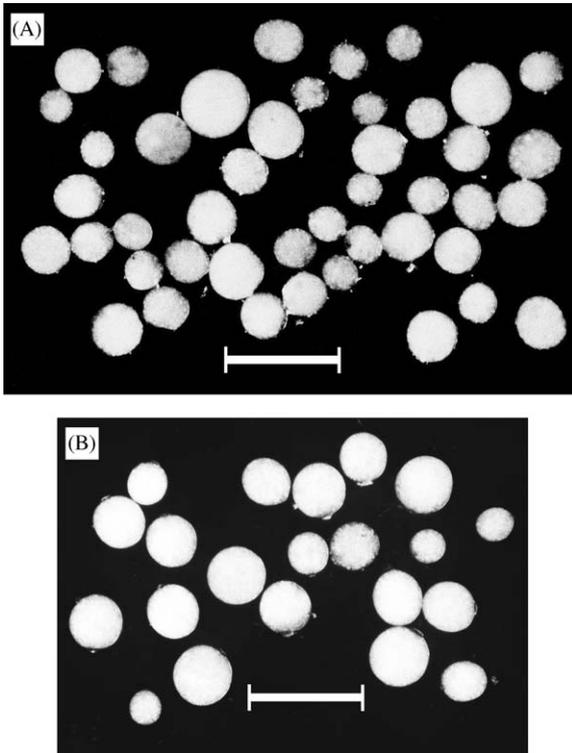
Fig. 2. *B. weddellensis* gen. & sp. nov. Specimens photographed in water using reflected light. (A) Station 136 (4730 m water depth); the 10 largest specimens in this collection are deposited under reg. no. SMF XXVII 7510; (B) Station 135 (4670 m). Scale bar = 500 μm.

corresponds to any of the allogromiid families and subfamilies defined by Loeblich and Tappan (1987). In view of the uncertainty in the higher level classification of monothalamous foraminifera resulting from these molecular investigations, we have avoided placing the new genus in an existing allogromiid family:

Class Foraminifera Lee, 1990
Order Allogromiida Loeblich and Tappan, 1961
Genus *Bathyallogromia* gen. nov.

Derivation of name: *Bathy* (Greek)—deep, referring to the deep-water habitat of this *Allogromia*-like morphotype.

Diagnosis: Test monothalamous, almost spherical, 140–450 μm in diameter; wall transparent,

proteinaceous, with smooth outer surface devoid of agglutinated grains; single aperture located in the centre of low, broad projecting region; cytoplasm light grey or greenish, containing various inclusions which often include mineral particles.

Remarks: Molecular evidence suggests that the new genus is not closely related to morphologically similar monothalamous taxa such as *Allogromia*. Instead, it appears to belong to a clade which includes most deep-sea monothalamous foraminiferal species so far examined (see Discussion). A comparison with morphologically similar species is given below.

Type species: *Bathyallogromia weddellensis* sp. nov.

Derivation of name: Refers to the Weddell Sea, Antarctica.

Type material: The holotype is from ANDEEP Station 136 (64°01′S, 39°06′W; 4735 m water depth) in the western Weddell Sea. It is deposited in the Senckenburg Museum, Frankfurt, Germany, under registration number SMF XXVII 7509. Ten paratypes (the largest specimens among those illustrated in Fig. 2A) are deposited under registration no. SMF XXVII 7510.

Other material examined: ANDEEP Stations 131 (65°19′S, 51°23′W; 3000 m water depth) 13 specimens; Station 132 (65°17.66′S, 53°23′W; 2000 m water depth) 32 specimens; Station 135 (65°00′S, 43°00′W; 4675 m water depth) 21 specimens; Station 137 (63°45′S, 33°47.9′W; 4735 m water depth) 2 specimens; Station 138 (62°58′S, 27°54′W; 4500 m water depth) 10 specimens.

Diagnosis: As for genus.

Description

Test morphology: The test is light in colour and approximately spherical to broadly oval in shape (Fig. 2). One hundred and twenty four specimens had the following dimensions: length (measured along the axis passing through the aperture) 150–450 μm (mean 251 μm, standard deviation 54 μm), width 140–440 μm (mean 231 μm, standard deviation 53 μm) (Fig. 3), length/width ratio 0.88–1.37 (mean 1.09, standard deviation 0.08). The aperture is situated on a broad, low, mound-like projection with sloping sides and a slightly
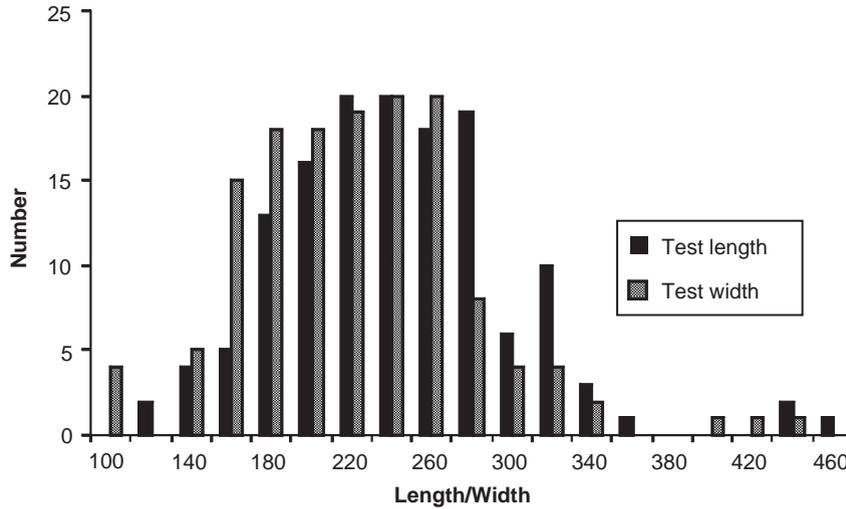
Fig. 3. *B. weddellensis* gen. & sp. nov. Histogram of test length and width values from 140 specimens from Stations 131, 132, 135–138.

uneven outer edge (Figs. 4A, C, E and F). This 'apertural collar' is only visible when the test is orientated correctly. A thread of cytoplasm usually extends along the axis of the mound to the aperture. A corresponding invagination of the cytoplasm ('peduncular sheath') forms an inward extension of the aperture into the cytoplasm (Figs. 5A and B), although this feature is often indistinct and is not visible in all specimens. The test wall is transparent and colourless and appears as a thin but distinct line under a compound microscope. When placed in glycerol, specimens from sites > 4000 m water depth retain their shape, whereas those from the 2000 and 3000 m sites tend to shrink.

Cell contents: When specimens are mounted in glycerol and viewed under a compound microscope, the cytoplasm appears finely granular. A single large nucleus, 30–36 μm in diameter, is sometimes visible (Figs. 4B and 5E). The cytoplasm contains numerous other inclusions, including mineral grains, that are scattered throughout the cytoplasm and not concentrated in any particular area (Figs. 5C, D, F).

Remarks

Comparison with other species: In terms of size and overall test morphology, the new species resembles *Allogromia laticollaris* Arnold, a well-known shallow-water allogromiid that occurs in intertidal to shallow subtidal areas around the coasts of North America and Europe (Arnold, 1948, 1955). An obvious morphological feature of *A. laticollaris* is the presence of a well-developed 'peduncular sheath', an internal extension of the apertural structure that occupies more than a half of the diameter of some specimens. A similar structure is sometimes visible in *B. weddellensis* but is never so clearly developed. The new species often possesses intracellular mineral grains and lacks the deep orange coloration of *A. laticollaris*, although the latter feature could reflect differences in diet. *B. weddellensis* also resembles *Allogromia crystallifera* Dahlgren, described from 80 to 100 m water depth in the Gullmar Fjord, Swedish west coast (Dahlgren, 1962). Both species accumulate intracellular mineral grains but *A. crystallifera* is larger (usually 500–700 μm) with an oval outline and a tubular apertural structure. Other *Allogromia* species, reviewed by Rhumbler (1904), are poorly characterised and difficult to compare with our new species. The best known is *Allogromia ovoidea* Rhumbler, a species that occurs off Bergen (Norway), in the North Sea off Kiel, and in the Adriatic. It has a more elongate shape than *B. weddellensis* and yellow to reddish or brown cytoplasm.
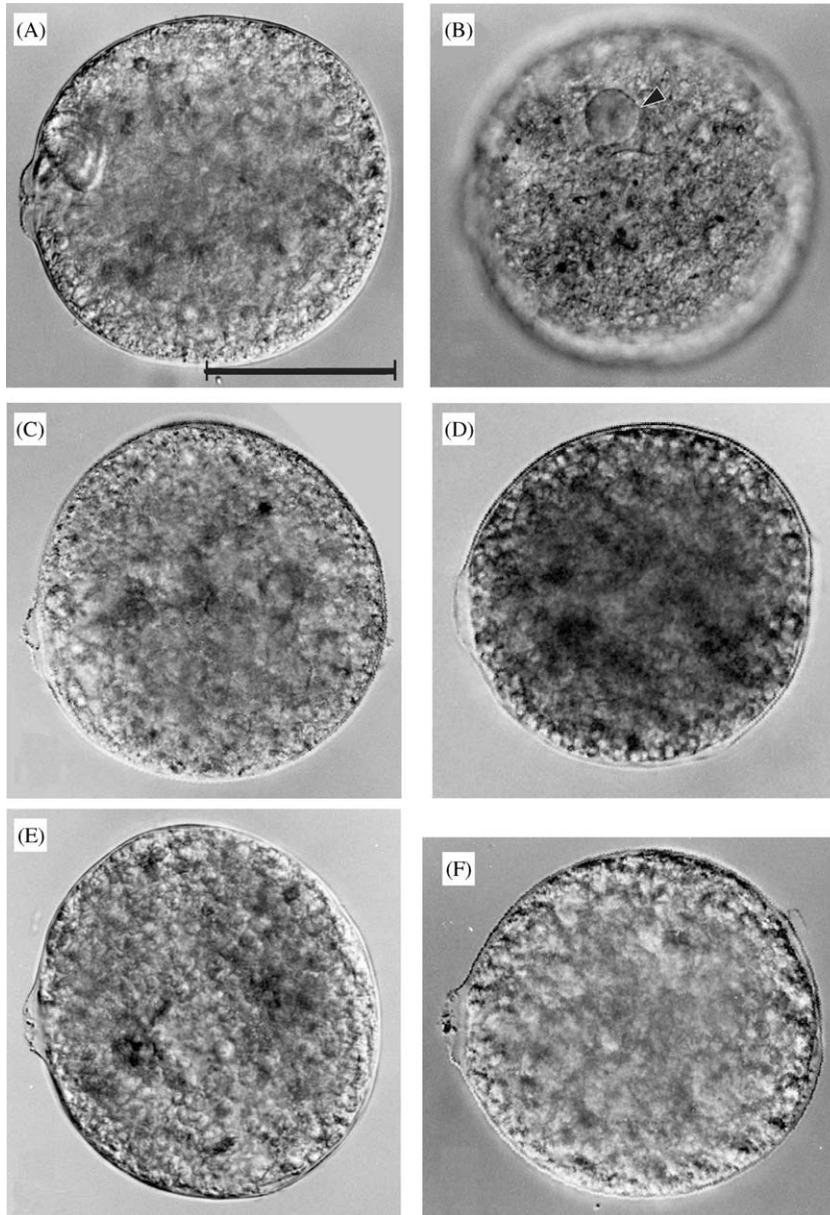
Fig. 4. *B. weddellensis* gen. & sp. nov. Specimens mounted in glycerol and photographed using transmitted light. (A,B) Holotype from Station 136 (4740 m), reg. no. SMF XXVII 7509; (C) Station 136; (D) Station 135 (4670 m); (E,F) Station 131 (3000 m). Arrowhead indicates nucleus. Scale bar = 100 μm.

Variation in cell contents: The colour of the cell body and the nature of its inclusions exhibit considerable inter-station variability. The main variations are as follows.

Station 136 (type locality; 4740 m water depth). The cytoplasm is greyish or greenish-grey and the cell contents varied and heterogeneous. Transparent, angular mineral grains are present in all
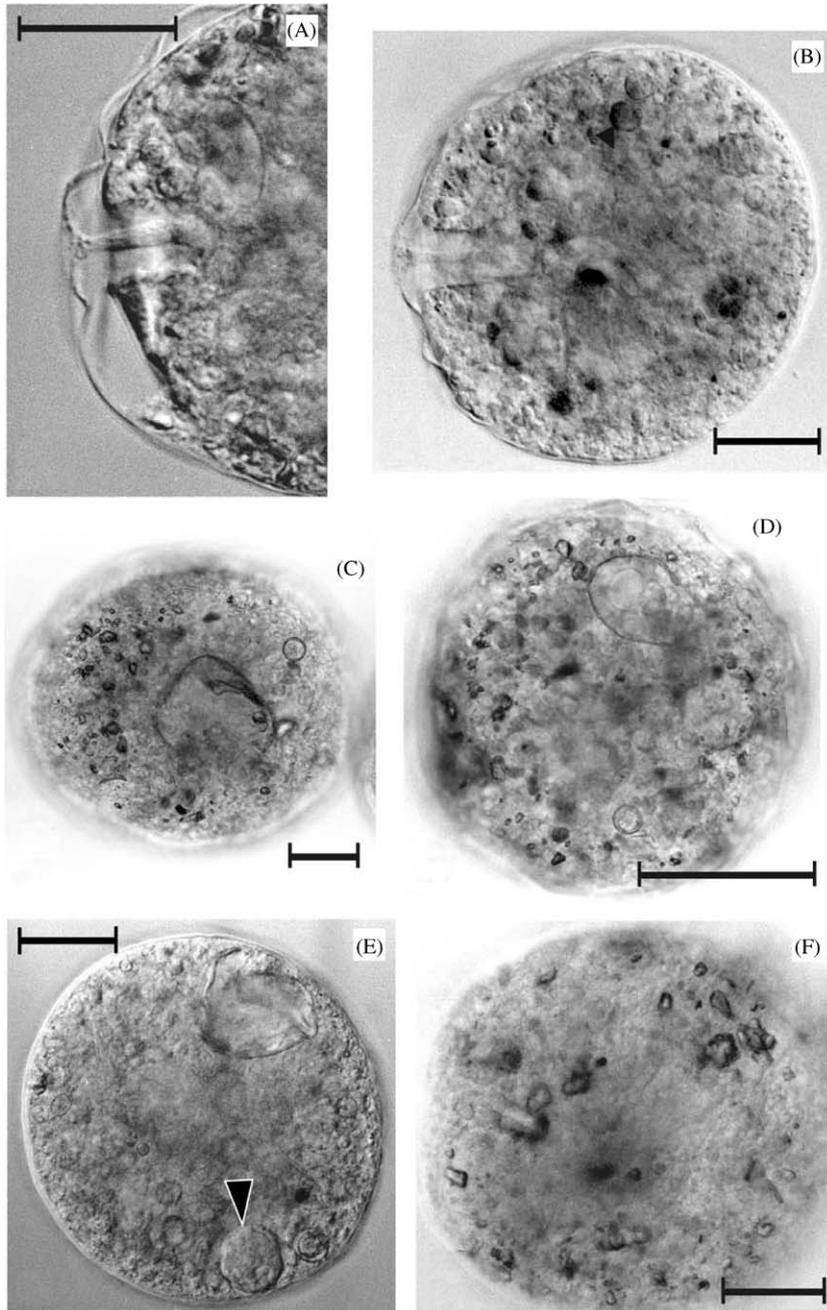
Fig. 5. *B. weddellensis* gen. & sp. nov. Specimens from type locality (Station 136) mounted in glycerol and photographed using transmitted light. (A) Aperture with short peduncular sheath; (B) specimen with focus on peduncular sheath; (C–F) specimens with focus on mineral grains and other cellular inclusions. Arrowhead indicates nucleus. Scale bars = 50 μm.

specimens and are sometimes common. A variety of transparent, vacuole-like inclusions of varying shapes and sizes, some of them (16–18-μm diameter) resembling red blood cells, are also present. Fairly large, transparent, sack-like and flask-shaped structures (Figs. 5C–E) and curved, linear inclusions occur in many specimens.

Station 135 (4680 m). The pale greenish-grey cytoplasm contains variable numbers of the small, transparent 'vacuoles' resembling red blood cells. Some larger inclusions, usually transparent but occasionally dark in colour, are also present. Obvious mineral grains occur in some specimens but are not as common as at the type locality.

Station 138 (4500 m). The cytoplasm is greenish and tiny spherical bodies, possibly algal cells, are numerous. Large, colourless 'vacuoles' occur occasionally but obvious mineral grains are rare.

Station 131 (3000 m). Most specimens are packed with small, transparent, vacuole-like structures, while others contain numerous small, rounded, brownish particles. One specimen contains a single diatom.

Station 132 (2000 m water depth). The cytoplasm is greenish, possibly due to the presence of numerous small inclusions that may be algal cells. More obvious inclusions include spherical, transparent 'vacuoles', a variety of angular mineral grains, some black but most colourless, occasional spicule-like particles, and rarely, large, stercomata-like bodies.

These variations may reflect differences in the availability of food particles, in particular, the small algal cells which impart a greenish colour to the cytoplasm. The greenish colour was most evident at Stations 132 and 138 where a phytodetrital layer was fairly well developed (Table 1). There is no evidence that dietary preferences vary from station to station.

Molecular characterisation

Phylogenetic position: Phylogenetic analysis of partial SSU rRNA gene sequences shows that *B. weddellensis* branches within a clade of monothalamous foraminiferans which, together with some monothalamous lineages (*Psammosphaera* + five undetermined allogromiids) and the polythalamous rotaliids and textulariids, form a well-supported (95/99%) radiation in the 'crown' of foraminiferal tree (Fig. 6). This clade, corresponding to lineage C in Pawlowski et al. (2002b), comprises a considerable variety of morphotypes, ranging from organic-walled allogromiids (*Gloiogullmia*, *Cylindrogullmia*) to large spherical agglutinated saccamminids (*Pilulina*?, *Saccammina*), tubular rhabdamminids (*Rhabdammina*), and the large agglutinated amoeboid genus *Toxisarcon*. The grouping of these genera is supported by high bootstrap values in all analyses (97/100%).

The position of *B. weddellensis* within the clade is not well established. In all analyses, *B. weddellensis* branches as a sister group to an undescribed allogromiid (J6) from Mediterranean caves, which probably represents the same genus. However, the relationships between *Bathyallogromia* and other genera grouping in the same clade depend on the type of analysis and model of nucleotide substitution. In the ML tree, *Bathyallogromia* branches as a sister group to *Saccammina sphaerica*, another deep-sea species that also occurs in the Weddell Sea (Fig. 6). In the NJ K2 and LogDet trees, however, *Bathyallogromia* branches between the clade (*Gloiogullmia* + *Rhabdammina* + *Saccammina* + *Toxisarcon*) and *Cylindrogullmia*, while in the NJ HKY tree, it branches at the base of the clade, as a sister group to all other genera (data not shown). None of these positions is supported by higher bootstrap values, suggesting that the relationships within the *B. weddellensis* clade cannot be resolved using the SSU rRNA gene sequences.

Intraspecific variations: Phylogenetic analysis of 22 sequences of *B. weddellensis*, representing 16 isolates from eight stations, shows very small intraspecific variations (Fig. 7). Eighteen sequences form a homogenous group with sequence divergence lower than 0.5%. Within this group, the sequences of cloned PCR products from the same isolate show the same level of divergence as the directly sequenced PCR products from different isolates, suggesting that the 0.5% divergence corresponds to the intra-individual variation among different copies of rRNA gene in *B. weddellensis*. There are four sequences that differ from this group by about 1% sequence divergence (isolates 3337, 3341, 3362, 3434 in Fig. 7). These sequences may represent either the rapidly
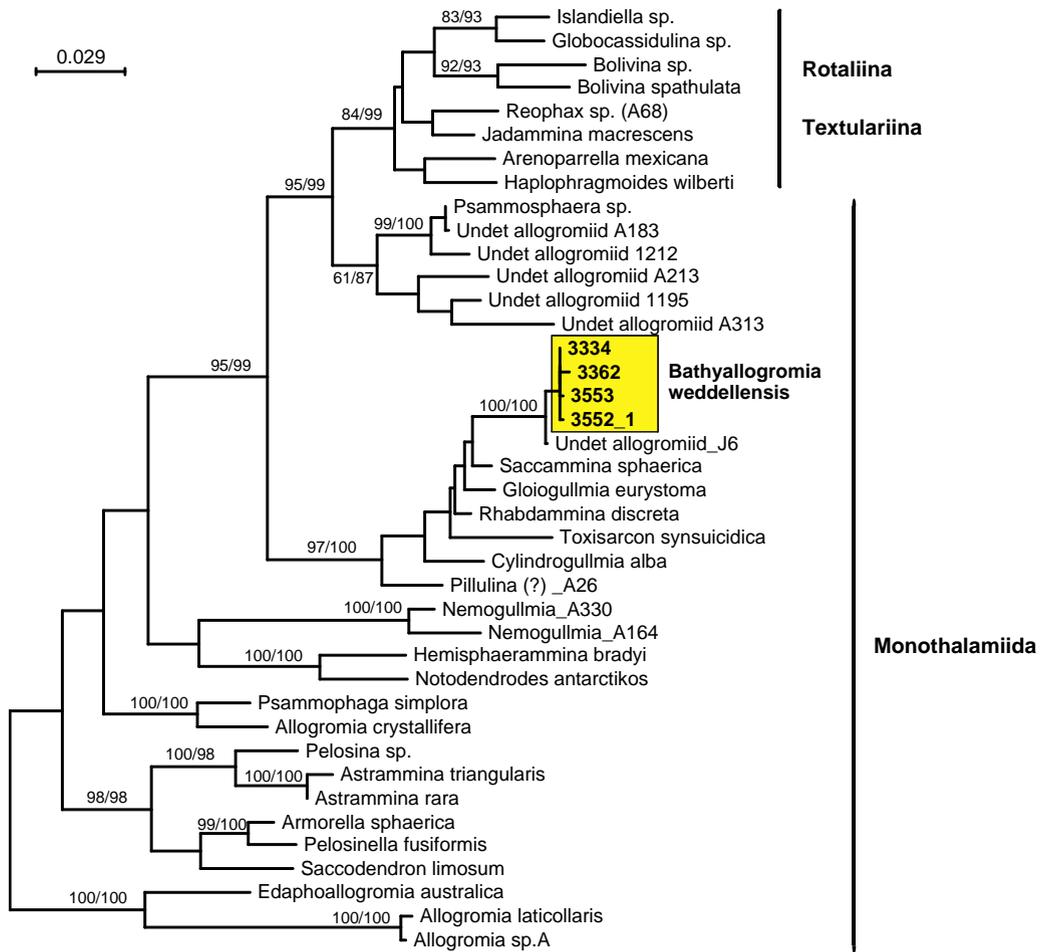
Fig. 6. Phylogenetic position of *B. weddellensis* gen. & sp. nov. inferred from partial SSU rRNA gene sequences (592 sites), using ML method. Numbers above the branches indicate bootstrap support values for ML and NJ K2 analyses. Only the bootstrap values higher than 60% are indicated.

evolving copies of rRNA genes or a cryptic speciation of *B. weddellensis*. For comparison, the sequence divergence between 22 sequences of *B. weddellensis* and the most closely related sequence of the undescribed Mediterranean allogromiid (J6) averages 5–6%.

Our analyses do not show any genetic difference between isolates of *B. weddellensis* collected from different depths. The isolates from six stations, with depths ranging from 1080 to 6330 m, group together in the clade of 18 sequences (Fig. 7). Among the remaining four sequences, three originating from stations 131 and 134 are not

represented in the main clade. The intermediate depths of these two stations, 3050 and 4060 m, respectively, indicate that the divergence of these sequences is not related to water depth.

Distribution and relative abundance: B. weddellensis occured in the Weddell Sea from 1080 m to 6330 m water depth. The new species was represented by three individuals (= 1% of total 'live' foraminiferal fauna) in a multiple core subsample ($3.45 \, cm^2$ surface area) from Station 132 (2000 m), five individuals (= 2% of total) in a subsample from Station 131 (3000 m water depth), and 16 individuals (= 11% of total) in a subsample from
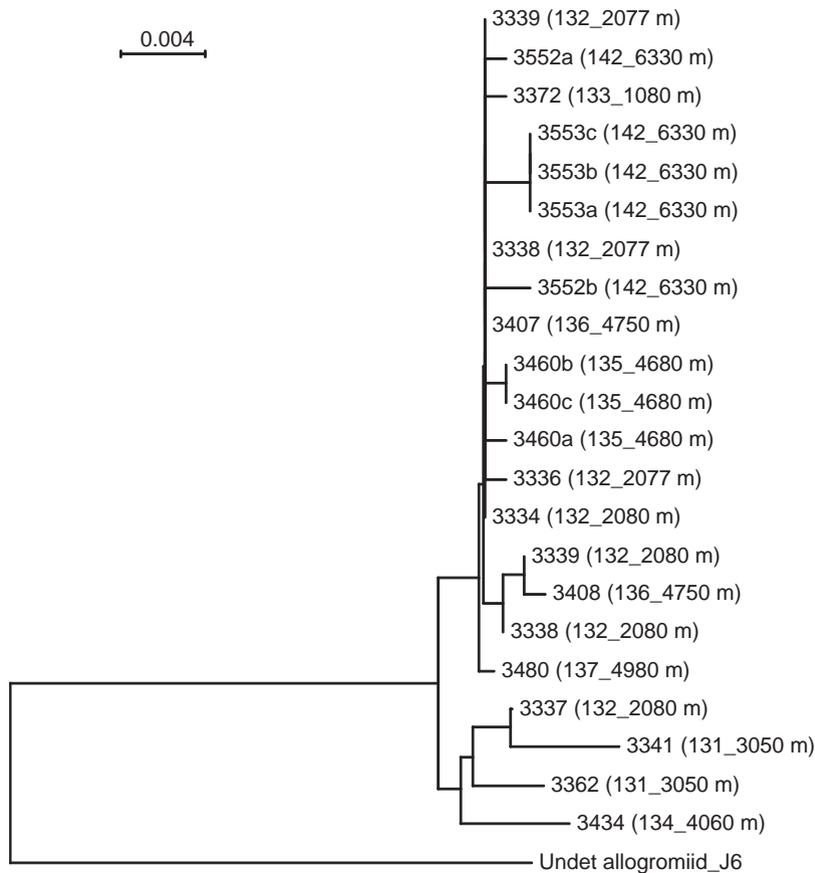
Fig. 7. Intraspecific variations between isolates of *B. weddellensis* gen. & sp. nov. collected from different water depths. The tree is inferred by analysis of 884 sites of the SSU rRNA gene using NJ K2 method. Each isolate is described by a four-digit number corresponding to its number in the Forams DNA collection. For each isolate, the station and its depth are given in brackets. The sequences of cloned PCR products of the same isolate are indicated by letters a–c. The sequence of the undescribed allogromiid J6 is used as an outgroup because this appears to be the species most closely related to *B. weddellensis*.

Station 137 (5000 m). Specimens of *B. weddellensis* were not found in subsamples from Stations 133 and 134 (1000 and 4000 m, respectively); cores obtained at Stations 135, 136 and 138 have not yet been analysed quantitatively.

4. Discussion

DNA sequences of the new species diverge from those of its closest known relative (the undescribed species J6) by an average of 5–6%. There are no strict rules for defining foraminiferal species using molecular data. In a study of foraminifera from the coastal Explorers Cove site, Pawlowski et al. (2002a) used a 5% sequence divergence as a lower limit to define 'species' (phylotypes). According to this criterion, *Bathyallogromia weddellensis* and J6 are distinct species, a conclusion consistent with their geographical separation.

The molecular evidence indicates that *B. weddellensis* is not related to either *Allogromia laticollaris* or to *A. crystallifera*, the two species which it most closely resembles morphologically. The former species branches together with *Edaphoallogromia australica* at the base of our tree

(Fig. 6), and the second branches with *Psammophaga simplora* in the clade that groups morphotypes with mineral inclusions. Interestingly, there is little morphological relation between *Bathyallogromia* and other genera which are included in the same clade. These vary from spherical to tubular or amoeboid forms. The clade also encompasses a variety of different wall types, ranging from organic (*Gloiogullmia, Cylindrogullmia*) to loosely agglutinated (*Toxisarcon*) and firmly agglutinated (*Rhabdammina, Saccammina*). One species (*Pilulina*?) possesses a finely agglutinated test which is protected by a second coarsely agglutinated cyst. These new molecular analyses support previous indications that gross test morphology and wall type are poor taxonomic characters for phylogenetic systematics of monothalamous foraminiferans (Pawlowski et al., 2002b). Finding morphological or ultrastructural features that provide reliable indicators of taxonomic relationships above the generic level remains a challenge for future studies of this group.

A remarkable feature of *B. weddellensis* is the fact that individuals are genetically almost identical across a very wide bathymetric range, from 1100 m to > 6000 m. This suggests that there is continuous gene flow between bathyal and abyssal populations. Some other foraminiferal species also appear to have broad depth ranges; for example, *Adercotryma glomeratum* is reported to occur from 197 to 3400 m in the Arctic Ocean (Wollenburg and Kuhnt, 2000). In the absence of molecular data, however, it is not possible to be certain that these populations represent a single species (Gooday et al., 2004). Our results contrast sharply with evidence for genetic differentiation among invertebrate species on continental slopes at lower latitudes in the Northern Hemisphere. Chase et al. (1998) found that populations of the bivalve *Deminucula atacellana* from slope (< 2500 m water depth) and rise (> 2500 m) sites in the NW Atlantic were genetically distinct over a horizontal distance of only 134 km, despite the good dispersion capabilities of this species. Considerable genetic differentiation exists within upper bathyal (457–1102 m water depth) populations of the gastropod *Frigidoalvania brychia* from the same area (Quattro et al., 2001). Cryptic speciation is

reported among populations of the scavenging amphipod *Eurythenes gryllus* from different depth zones in the North Atlantic and central North Pacific (France and Kocher, 1996) and four molluscan morphospecies from 500 to 5000 m depth on the NE United States continental margin (Etter et al., 1999). Recent modelling studies suggesting that speciation can occur more easily along an environmental gradient (e.g. water depth) than in the absence of a gradient (Doebeli and Dieckmann, 2003) are consistent with these results. Why *B. weddellensis* has such a broad bathymetric range in the Weddell Sea is not clear, particularly since it is also associated with a variety of different sediment types within this range (Table 1). Possibly, this pattern is related to the wide dispersion potential of foraminiferal propagules (Alve and Goldstein, 2002, 2003), coupled with the existence of a virtually isothermal water column around the Antarctic continent. It has been suggested that the lack of a temperature barrier in the Antarctic water column facilitates the penetration of species from shallower into deeper waters (Tyler and Young, 1998; Tyler et al., 2000).

Bathyallogromia weddellensis or closely related species may be widely distributed geographically in the deep ocean. Specimens that are morphologically very similar to those from the Weddell Sea occur in the Indian Ocean (Gooday, 1994, Fig. 3c therein) and at the Porcupine Abyssal Plain (Gooday, unpublished). However, confirmation that these forms represent the same species must await molecular characterisation.

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