



## A new ‘saccamminid’ genus (Rhizaria: Foraminifera), from 4400 m water depth in the Nazaré Canyon (NE Atlantic)

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### Abstract

We describe *Bithekammina occulta*, a new monothalamous agglutinated foraminiferan (‘saccamminid’) collected in multicore samples at 4400 m on the terrace of the lower Nazaré Canyon on the Portuguese margin. The test is spherical to oval, up to ~400 µm in length, with a simple circular aperture. The wall has a very smooth surface with a distinct sheen in reflected light. It is <10 µm thick and composed of very fine agglutinated plate-like clay particles and a thin inner organic layer. The most distinctive feature of the new species is that the test is contained within an agglutinated case (‘secondary test’) composed mainly of larger (10–50 µm) quartz grains. The case is equipped with a long, narrow tube that originates near the aperture of the inner test and presumably acts as a channel through which pseudopodia are deployed. Secondary agglutinated structures have been described in a number of foraminifera, but never before in a ‘saccamminid’.

**Key words:** ‘Saccamminid’, monothalamous foraminifera, Portuguese margin, Nazaré canyon, cyst, secondary agglutinated structure

### Introduction

There is a growing appreciation of the importance of monothalamous foraminifera in both coastal (e.g. Habura *et al.* 2008) and deep-water (e.g. Gooday 2002; Gooday 2004; Cedhagen *et al.* 2009) settings. In contrast to multi-chambered foraminifera, these ‘primitive’ forms often have relatively simple tests with ‘soft’ flexible walls. The ‘saccamminids’, which typically have a flask-shaped agglutinated test with a single terminal aperture, constitute one important monothalamous group. ‘Saccamminids’ are particularly common and diverse in the deep sea (Gooday 1986a; Cornelius and Gooday 2004). Here, we describe a new genus and species of saccamminid from the Nazaré canyon on the Portuguese margin. A remarkable feature of this taxon is that the organism is enclosed in an agglutinated case or ‘secondary test’. Secondary agglutinated structures have been described in a number of foraminifera but never, as far as we are aware, in a ‘saccamminid’.

This study is based on material collected as part of HERMES (Hotspot Ecosystem Research on the Margins of European Seas), an integrated project funded by the European Union that terminated in March 2009 and continues as HERMIONE. The main purpose of the HERMES project was to investigate the biodiversity of ‘hotspot’ ecosystems, including submarine canyons, around the European margins (Weaver *et al.* 2004, 2009). The Nazaré Canyon on the Portuguese margin is one of Europe’s largest and most spectacular submarine canyons and a main focus of biological and geological research during HERMES (Tyler *et al.* 2009).

### Material and methods

**Sampling sites.** The Nazaré canyon is located off the southern part of the Portuguese Atlantic coast. The canyon head is located very close to land, but is not associated with a river. The entire system is up to 27 km wide and 94

km long (Lastras *et al.* 2009). Several authors have divided it into upper, middle and lower sections (Vanney and Mougénot 1990; Schmidt *et al.* 2001; van Weering *et al.* 2002; de Stigter *et al.* 2007), but because the upper and middle sections show no significant differences in morphology or sedimentary features, Arzola *et al.* (2008) grouped them together. This upper part merges into the lower section where the canyon widens abruptly at the base of the continental slope, around 4000 m water depth. The lower section is gently sloping with a relatively subdued topography and terraces developed on either side of the wide, flat-floored channel. Here, currents are generally too weak to move sediment, although occasional gravity flows transport sediment through the lower canyon onto the abyssal plains (de Stigter *et al.*, 2007). Our sampling site is located on a terrace next to the main channel at 4300 m depth. The area is characterised by sandy sediments with numerous mica flakes and carbonised plant detritus, overlain by a thin layer of hemipelagic sediment.

**Sampling and laboratory methods.** Samples were obtained using a multicore (Barnett *et al.* 1984) during R.R.S. *Charles Darwin* Cruise 179 (CD 179, 14 April to 17 May, 2006; Billett 2006) (Table 1). As soon as possible after recovery, the cores (cross-sectional area 25.5 cm<sup>2</sup>) were taken to a shipboard temperature-controlled laboratory adjusted to the appropriate bottom-water temperature. They were sliced into 0.5 cm layers down to 2 cm and then 1 cm layers down to 10 cm; each layer was fixed and preserved in 10% formalin buffered with borax. In the laboratory, sediment slices were sieved through a series of screens (mesh sizes 300 and 150 µm) and each sieve fraction stained overnight in rose Bengal. The residues were placed in water in a Petri dish and 'live' (stained) foraminiferal specimens extracted using a fine glass pipette under a Wild M5 dissecting microscope.

**TABLE 1.** Sampling station data and number of specimens of *Bithekammia occulta* recovered from each multicore.

Station and Deployment	Position		Depth (m)	Specimens	
	° N	° S		Live	Dead (empty)
56847#6	39°59.28'	10°33.32'	4403	19	60
56847#7	39°59.25'	10°33.43'	4404	7	14
56859#2	39°59.32'	10°33.20'	4405	14	42

**SEM and elemental composition.** Specimens of the new species were photographed using a digital camera (Nikon Coolpix 4500) attached to either a Leica binocular microscope or an Olympus BH-2 compound photomicroscope. Test measurements were made to the nearest 10 mm using an eyepiece graticule fitted to a Wild M50 dissecting microscope. One specimen was washed very carefully in distilled water to remove the formalin and was left to dry naturally. It was then coated by gold-palladium in an Edwards Sputter Coater S150B for 4.5 minutes, and examined in a LEO1450VP scanning electron microscope (SEM), using a voltage of 15kV, a probe current of 30pA, and a working distance (WD) varying from between 7mm and 15mm. X-ray elemental microanalysis was undertaken using a PGT light element EDS detector using a WD of 19mm and an acquisition time of 60 seconds.

**Vertical distribution.** The average living depth of 'live' saccamminids (ALD<sub>s</sub>), and the average depth of occurrence of empty agglutinated cases (ADDC<sub>s</sub>), were calculated according to Jorissen *et al.* (1995) and Aranda da Silva (2005), respectively.

## Systematic description

The type material is deposited in the Natural History Museum, London.

## Supergroup Rhizaria Cavalier-Smith, 2002

### Class Foraminifera d'Orbigny, 1826

### Family Saccamminidae Brady, 1884

### ***Bithekammia* gen. nov.**

The systematic division of higher taxa based on morphology has little support from molecular studies (Pawlowski *et al.* 2002). We therefore recognise the family Saccamminidae only in order to provide a systematic context for our new taxa that is consistent with previous studies.

**Etymology.** The first part of the name (the suffix *bi*) means two; the middle part (*theka*) derives from the Greek *theke* (θηκη) meaning case or test; the last part (*-ammia*) is a common ending for generic names of agglutinating foraminiferans and is derived from the Greek word *amos* (αμμος), meaning sand.

**Type species.** *Bithekammia occulta* Aranda da Silva and Gooday

**Diagnosis.** Test free, monothalamous, spherical to ovate in shape, and generally 200–400 µm in size. Test surface very smooth, translucent with diffuse silvery highlighted in reflected light. Single aperture forms round opening with slightly raised rim but otherwise without any associated structures. Wall thin and composed largely of tiny (usually 1–2 µm) plate-like clay particles overlying organic lining. Cell body with large nucleus, but without any other obvious inclusions. Test typically enclosed within larger, more coarsely agglutinated case ('secondary test'), which gives rise to long, narrow tubular extension that corresponds to the aperture of the primary test.

**Remarks.** The most interesting characteristic of *Bithekammia* is the fact that the test is enclosed in an outer agglutinated case, a feature not present in any other named 'saccamminid'. The test itself resembles that of the newly-described genus *Niveus* Altin, Habura & Goldstein 2009 (type species *N. flexilis*) in being rather small, flexible and ovate in shape with an outer surface composed of tiny, flake-like clay particles. In *N. flexilis*, however, these particles overlie a much thicker inner organic lining, so that the test appears to have an organic wall when viewed under a dissecting microscope. The organic lining is thin in our new genus and the wall is separated from the cell body by what appears to be an open space, which is wider near the distal end than the proximal end. Another recently described 'saccamminid' genus, *Leptammia* Cedhagen, Gooday & Pawlowski 2009 (type species *L. flavofusca*), is much larger (up to 2 mm diameter) than *Bithekammia* and has a thicker test wall. It also has a clearly developed endosolenial tube, a feature absent in *Bithekammia*.

Apart from the presence of a secondary agglutinated case, *Bithekammia* differs from *Ovammia* (type species *O. opaca* Dahlgren, 1962) in having an oval rather than egg-shaped to fusiform shape, a much thinner and more finely agglutinated test wall, and in lacking a well-developed endosolenial tube.

### ***Bithekammia occulta* gen. et sp. nov.**

**Derivation of name.** *Occulta*, derives from the Latin *occultus*, which means hidden, mysterious. In this case it refers to the fact that the inner 'saccamminid' is easily overlooked within its outer agglutinated casing.

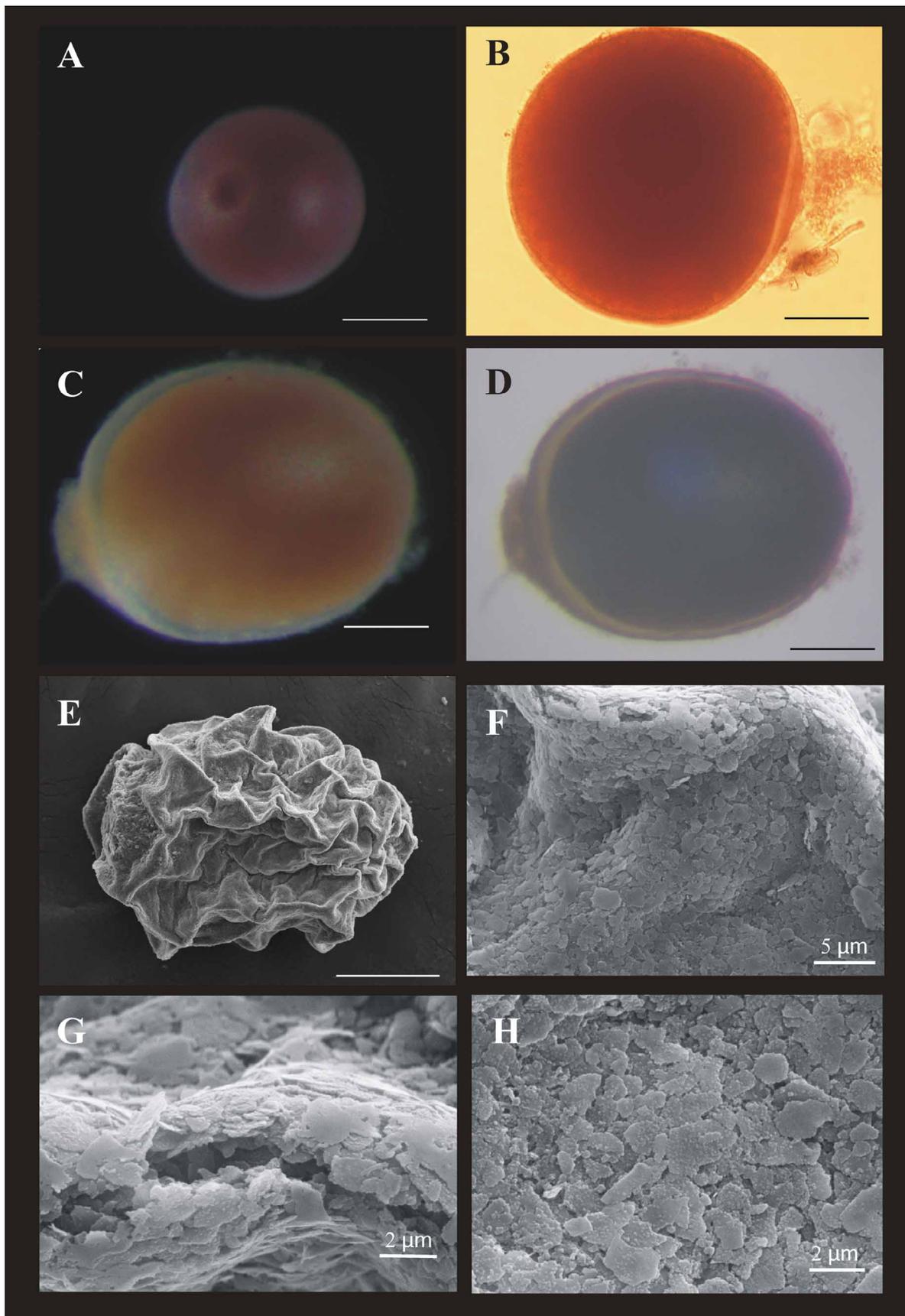
**Type material.** The holotype (Pl. 2 fig. A), from Station 56859#2 in the Nazaré canyon, is deposited under reg. no. ZF5241. Paratype 1 (Pl. 2, fig. B) and paratype 2 (Pl. 2, fig. C,D), from the same station, are deposited under reg. nos ZF5242 and ZF5243, respectively. All of the type specimens originate from the 0.5–1.0 cm sediment layer.

**Diagnosis.** As for genus

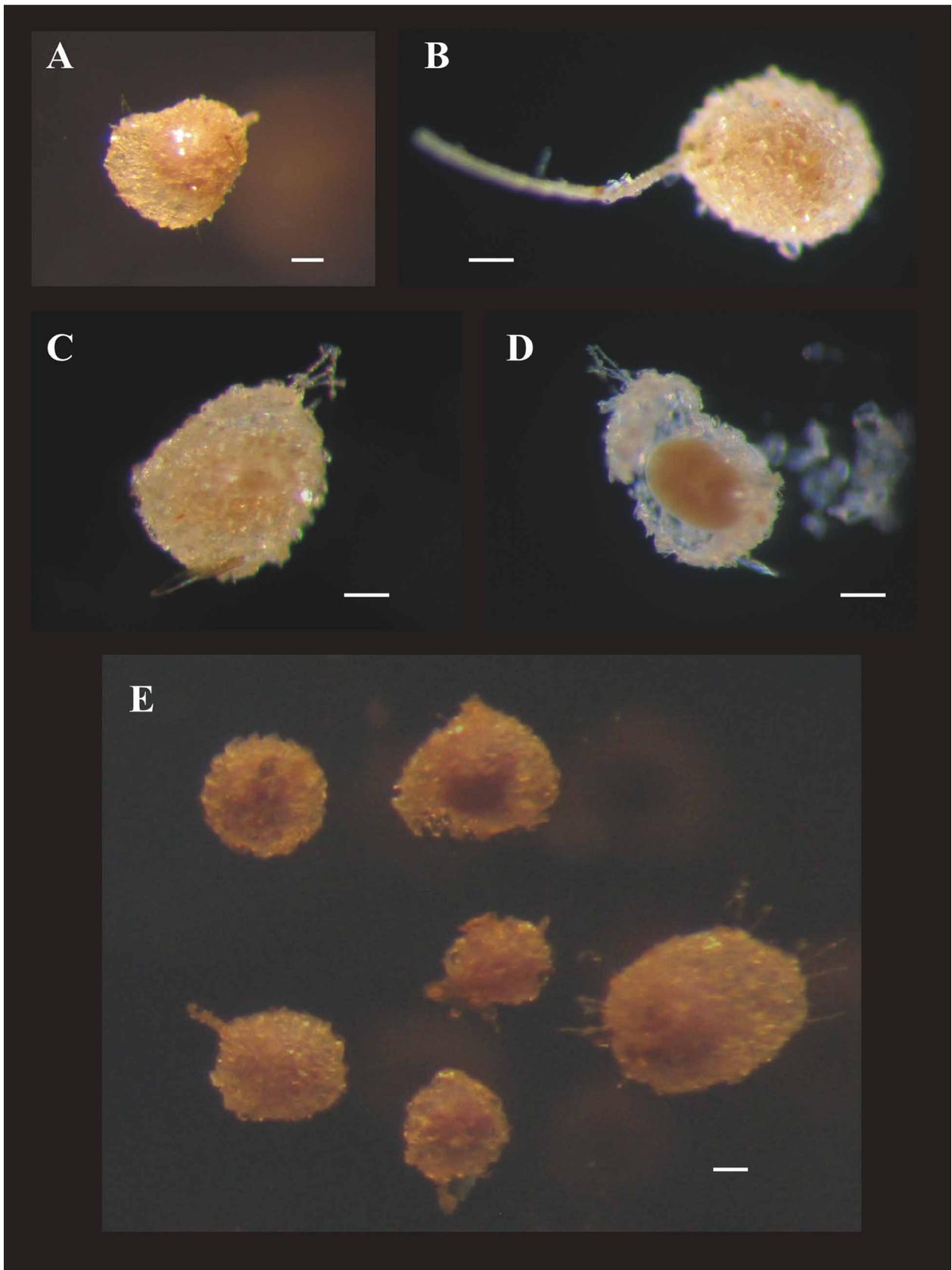
#### **Description. Test:**

**Morphology.** The test is broadly oval to circular in outline, with a smoothly rounded proximal end and a circular cross section (Plate 1, figs A–D). The distal end is slightly flattened with a single aperture. This is a simple opening 25–30 µm diameter, with an indistinct, slightly raised rim and without any associated structures. Fine detritus typically accumulates around the aperture. Five specimens had the following dimensions: length 210–413 µm (mean 308 ± 88.6 µm), maximum width 210–370 (mean 279 ± 64.8 µm).

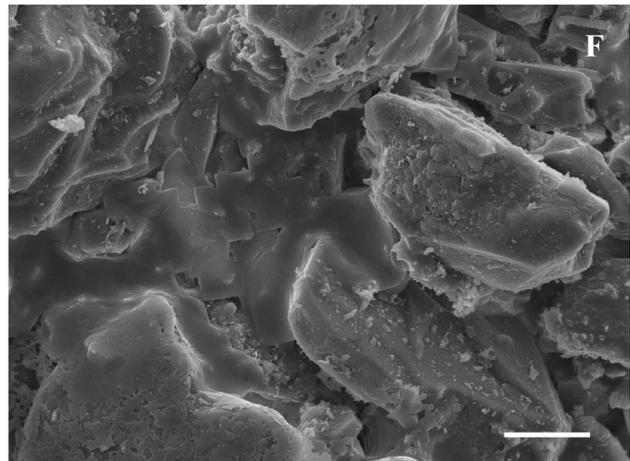
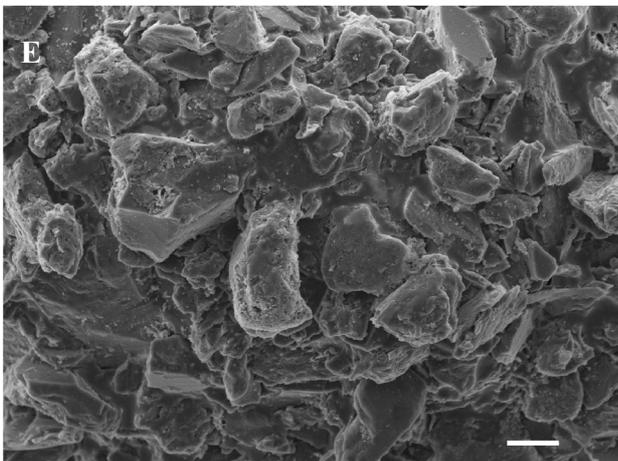
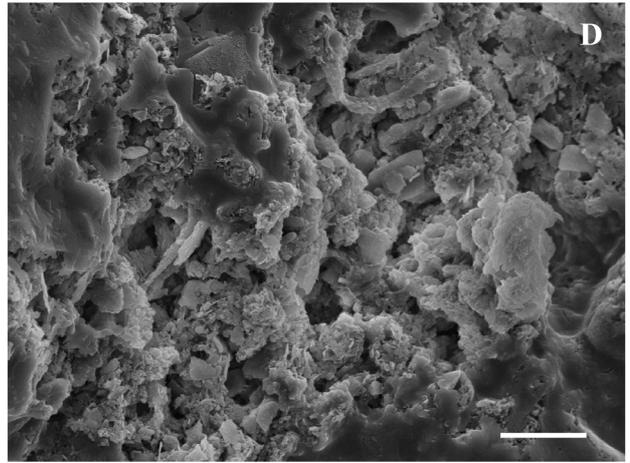
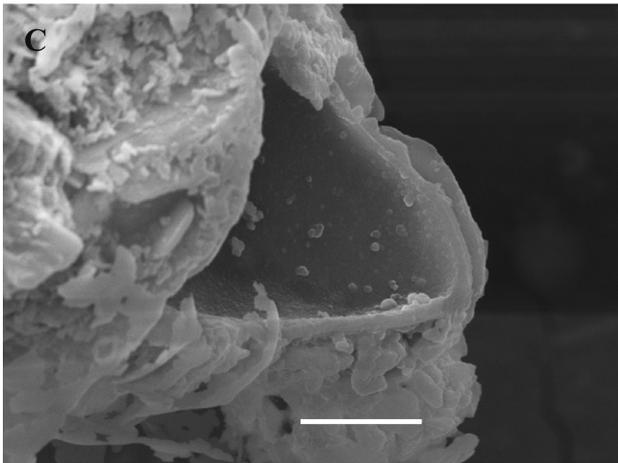
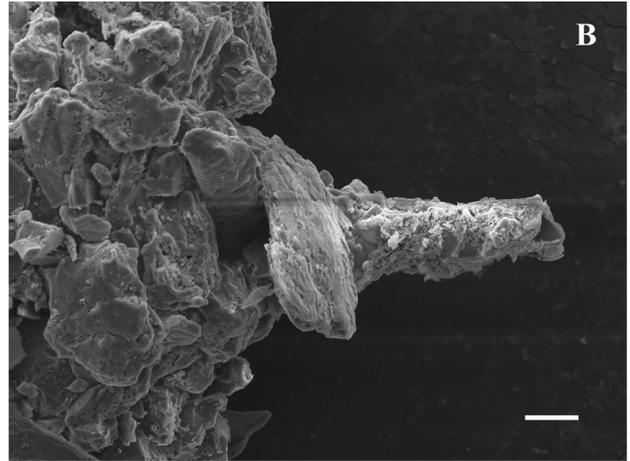
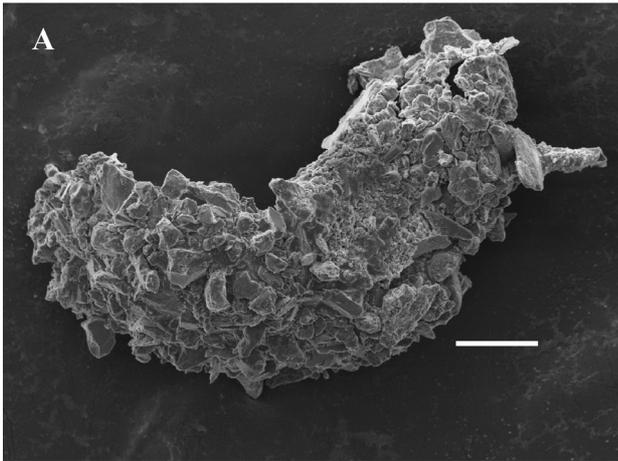
**Wall structure and composition.** The test wall is translucent and the rose-Bengal-stained cell body is clearly visible through it when the test is immersed in water and viewed in reflected light; it is more or less transparent in transmitted light (Plate 1, figs B, D). The surface is very smooth, unwrinkled, with a diffuse, silvery, reflective sheen (Plate 1, figs A, C). The wall is clearly defined and very thin (<5 µm), particularly at the proximal end, but slightly thicker (up to 15 µm) around the aperture. It is composed of several layers of very fine plate-like particles (1–5 µm, but usually 1–2 µm in size) that overlie an organic lining (Plate 1, figs E–H). X-ray microanalysis reveals strong peaks for Si and Al and smaller peaks for K, Ca, Mg, and Fe, consistent with a clay mineral composition (Figure 1). When dried for SEM, the test wall crumples but still retains its integrity (Plate 1, fig. E).



**PLATE 1.** *Bithekammina occulta* **gen. et sp. nov.** A and B. Reflected and transmitted light photographs of specimen from Station 56859#2 core (4–5 cm layer). C–D Reflected and transmitted light photographs of specimen from Station 56859#2 core (0.5–1 cm layer). E–H. SEM images of the same specimen. E. Entire test, which crumpled when dried onto the stub. F–H. Details of agglutinated particles. Scale bars = 100 µm except where indicated otherwise.

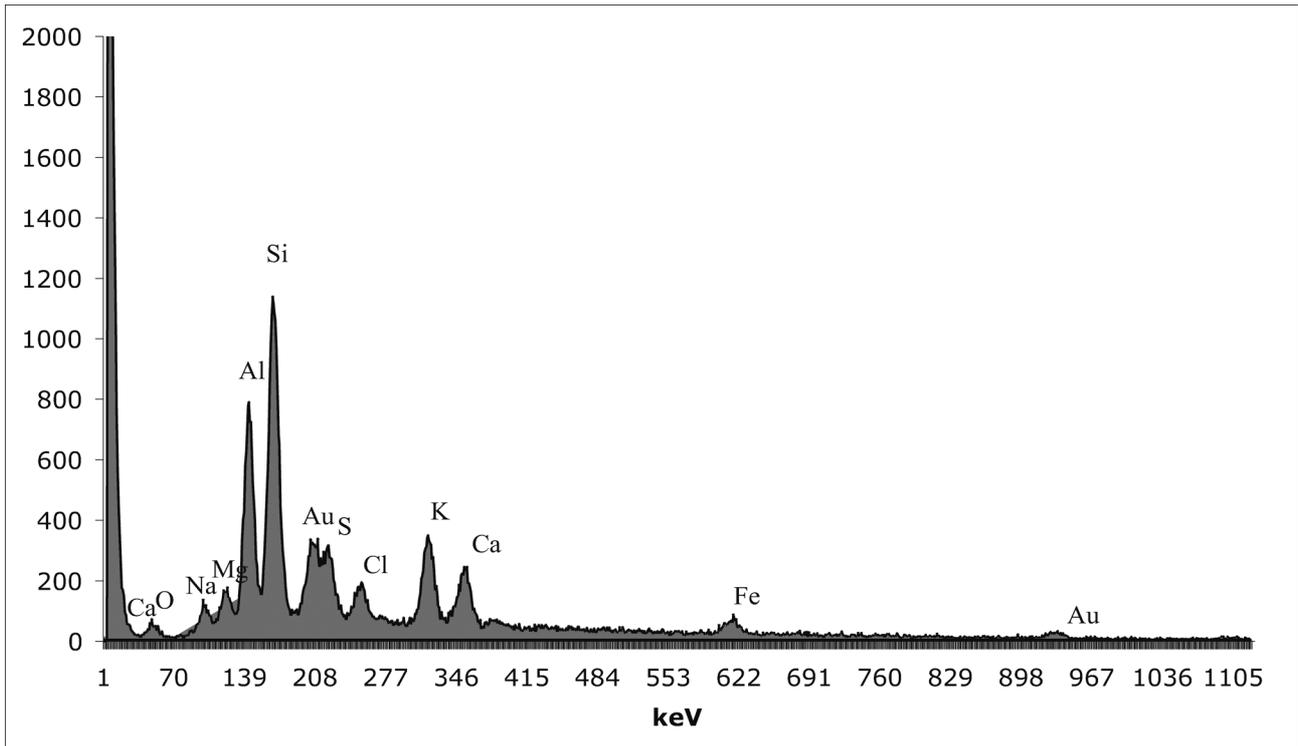


**PLATE 2.** *Bithekammina occulta* **gen. et sp. nov.**, scale bars = 100  $\mu$ m. A. Transmitted light photograph from holotype, reg. no. ZF5241, from Station 56859#2 0.5–1 cm. B. Transmitted light photograph from paratype 1, reg. no. ZF5242, from Station 56859#2 0.5–1 cm. C and D. Transmitted light photograph from paratype 2, reg. no. ZF5241, from Station 56859#2 0.5–1 cm. E. Transmitted light photograph from specimens from Station 56859#2 1–1.5 cm.

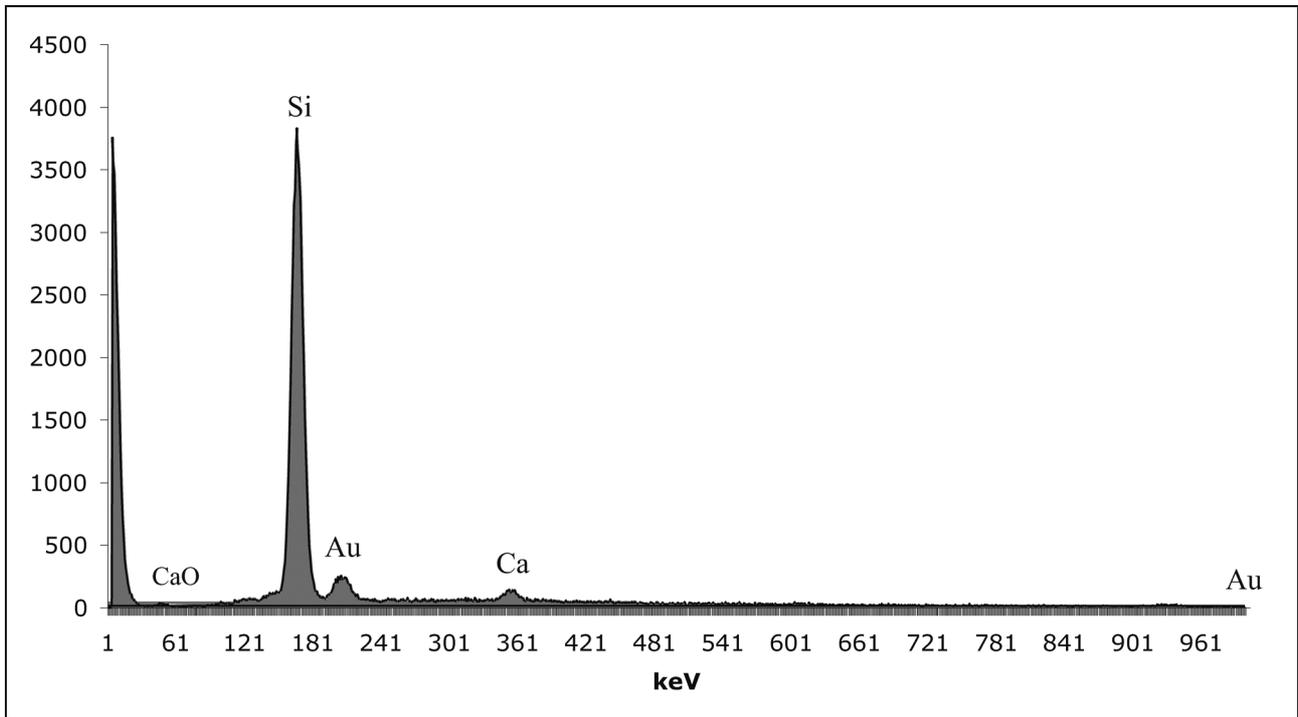


**PLATE 3.** *Bithekammina occulta* **gen. and sp. nov.** SEM images of the outer case of specimen shown in Plate 1, figs C–H; Station 56859#2, 0.5–1 cm layer. B, C. Detail of the tubular extension showing organic lining. D. Surface of tubular extension. E, F. Details of main part of casing. Scale bars = 100  $\mu\text{m}$  (A), 20  $\mu\text{m}$  (B, E), 10  $\mu\text{m}$  (D, F), 5  $\mu\text{m}$  (C).

*Test contents.* The cell body is well defined and either fills the test cavity almost completely, or is separated from the wall by a narrow space, which is apparently empty (Plate 1, figs B, D). When viewed through the test wall, the cytoplasm appears dense and very finely granular with no obvious large inclusions such as stercomata. A large nucleus (~50- $\mu\text{m}$  diameter) is visible in one specimen. An endosolenial tube is not clearly developed although a lighter area of cytoplasm immediately inside the aperture of one specimen when viewed in transmitted light suggests that such structure may be present.



**FIGURE 1.** X-ray microanalysis of the surface of the 'saccaminid' test (specimen illustrated in Plate 1, figs C–H; 0.5–1.0 cm layer of the core from Station 56859#2).



**FIGURE 2.** X-ray microanalysis of a larger grain in the outer agglutinated case (specimen 1 illustrated in Plate 3, figs A–F; 0.5–1.0 cm layer of the core from Station 56859#2).

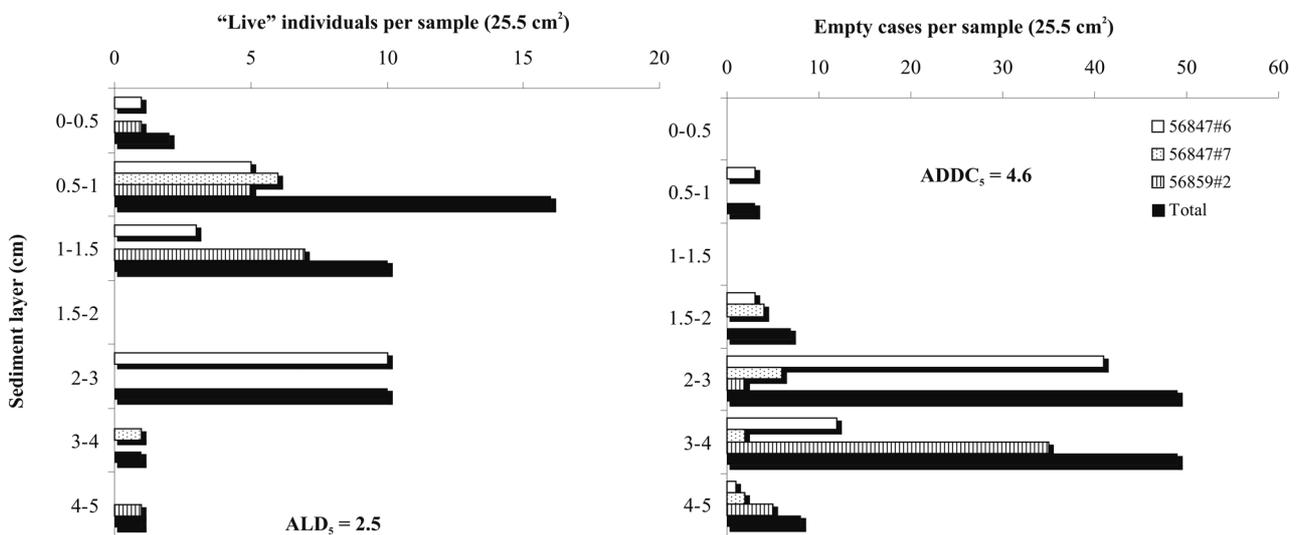
**Outer agglutinated case:**

*Morphology.* In all available specimens, the test is contained within an outer agglutinated casing (secondary test) within which it lies fairly loosely (Plate 2). This structure is spherical to oval in shape. A narrow tubular extension, which is orientated on the same axis as the aperture of the inner test, is sometimes clearly developed. How-

ever, this structure is not always evident. When present, it presumably acts as a channel through which pseudopodia are deployed (Plate 2, fig. B) Eleven specimens had the following dimensions; length 364–770  $\mu\text{m}$  (mean  $496 \pm 117 \mu\text{m}$ ), width 287–539 (mean  $428 \pm 96 \mu\text{m}$ ). The tubular extension ranged in length from 40 to 840  $\mu\text{m}$  (shorter tubes were probably broken) with a width of 14 to 42  $\mu\text{m}$ .

**Wall composition and structure.** The outer case is fragile, breaking easily when poked with a needle. It is composed mainly of irregularly-shaped grains, 10–50  $\mu\text{m}$  in size (Plate 3, figs E,F), which yield X-ray spectra dominated by Si and are presumably composed of quartz (Figure 2). Much smaller clay-sized particles are also present between the larger grains. The tubular extension is composed mainly of these smaller (< 10  $\mu\text{m}$ ) grains (Plate 3, fig. A,B,D). An organic matrix partially obscures some of the grains on the outer surface, and what appears to be an organic lining is visible in SEM photographs of the tubular extension (Plate 3, fig. C).

**Vertical distribution in the sediment.** In three replicate cores (56847#6, 56847#7 and 56859#2), *Bithekammina occulta* was concentrated in the upper 3 cm of the sediment with only scattered specimens occurring at deeper sediment layers between 3 and 5 cm, the maximum depth sampled (Figure 3). The overall average living depth ( $\text{ALD}_s$ ) was 2.5. In addition to ‘live’ ‘saccamminids’, we also encountered empty outer cases. These were more abundant than the ‘live’ specimens and were found in deeper sediment layers (Figure 3). The average depth of occurrence of empty cases ( $\text{ADDC}_s$ ) was 4.6. All three replicate cores showed different numbers of ‘live’ and empty cases at each of the sediment layers, suggesting patchiness in the occurrence of this species.



**FIGURE 3.** Vertical distribution within the sediment profile (> 150  $\mu\text{m}$ ) *Bithekammina occulta* gen. and sp. nov. from CD 179. A. ‘Live’ (stained) specimens,  $\text{ALD}_s$  = Average Living Depth. B. Dead (empty) cases,  $\text{ADDC}_s$  = Average Depth of Dead agglutinated cases.

## Discussion

The most distinctive feature of the new species is the fact that the test is enclosed in a permanent agglutinated casing. Monothalamous foraminifera are known to inhabit pre-existing structures, including the empty tests of other foraminifera (Gooday, 1986b; Moodley, 1990). However, because all the available specimens were found inside a casing, and the base of the tubular extension of the casing corresponds closely with the test aperture, we believe that this structure is a kind of secondary test made by the new species.

Foraminifera sometimes construct secondary agglutinated structures of various kinds. Many species, both agglutinated and calcareous, surround their tests with cysts (e.g. Heinz *et al.*, 2005). These are generally rather thick, loosely constructed structures, not comparable to the casing described here. Rather more similar are the cysts of a ‘saccamminid’ species (*Saccamminid* sp. 1) from the North Carolina slope, described by Gooday *et al.* (2001) as being an ‘elongate secondary agglutinated structure (‘cyst’), up to 4 mm long, composed of very loosely cemented quartz grains’. However, these cysts, which unfortunately were not illustrated by Gooday *et al.* (2001),

sometimes contained more than one ‘saccamminid’ and are pressed directly against the test wall of the inhabitants rather than loosely containing them. Gooday *et al.* (2005) and Sabbatini *et al.* (2007) described some allogromiids from Svalbard fjords in which the organic-walled test was encased within an agglutinated sheath. Again, unlike the delicate casing in *Bithekammina*, this sheath is pressed tightly against the organic test wall from which it is often difficult to detach. Bowser *et al.* (1995) recognized that the tests of some agglutinated foraminifera, including species of *Notodendrodes*, *Astrammina* and *Vanhoeffenella*, contained an allogromiid-like cell body (including a typical endosolenial tube) enclosed within an organic theca. They suggested that the ‘allogromiid’ was the fundamental organism and the agglutinated test constituted a secondary structure. The agglutinated test of these ‘allogromiids incognito’ may be comparable to the secondary casing in *Bithekammina*, although it is usually a more complex structure, particularly in the case of notodendrodids. Another obvious difference is that the test is inhabited by an organic-walled allogromiid rather than an agglutinated ‘saccamminid’. Christiansen (1965) described a supposed benthic form of the planktonic species *Globigerinoides rubra* that constructed a ‘mud house’, resembling an oval cyst but equipped with a long, branched tubular extension through which pseudopodia were deployed. Finally, some species of the calcareous genus *Cibicides* construct sometimes elaborate agglutinated tubes (Nyholm 1961; Alexander *et al.*, 1987). Although morphologically different, and different by being temporary feeding structures, these structures are perhaps more closely comparable to the permanent agglutinated case of *Bithekammina* than the other agglutinated structures mentioned above. In particular, they act as pseudopodial guides, which is also a likely function for the tubular extensions of *Bithekammina* cases.

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## References

- Alexander, S.P. & Delaca, T.E. (1987) Feeding adaptations of the foraminiferan *Cibicides refulgens* living episodically and parasitically on the Antarctic scallop *Adamussium colbecki*. *Biological Bulletin*, 173, 136–159.
- Altin, D.Z., Habura, A. & Goldstein, S.T. (2009) A New Allogromiid Foraminifer *Niveus flexilis* nov. gen., nov. sp., from Coastal Georgia, USA: Fine Structure and Gametogenesis. *Journal of Foraminiferal Research*, 39, 73–86.
- Aranda da Silva, A. (2005) *Benthic Protozoa community attributes in relation to environmental gradients in the Arabian Sea*. Ph.D thesis. School of Ocean and earth Sciences, Southampton.
- Arzola, R.G., Wynn, R.B., Lastras, G., Masson, D.G. & Weaver, P.P.E. (2008) Sedimentary features and processes in the Nazaré and Setúbal submarine canyons, west Iberian margin. *Marine Geology*, 250, 64–88.
- Barnett, P.R.O., Watson, J. & Connelly, D. (1984) A multiple corer for taking virtually undisturbed samples from shelf, bathyal and abyssal sediments. *Oceanologica Acta*, 7, 399–408.
- Billet, D.S.M. (2006) Hotspot ecosystem research in the Setúbal, Lisbon, Cascais and Nazaré canyons on the Portuguese continental margin. *RRS Charles Darwin cruise 179*. 14 Apr–17 May 2006. Southampton Oceanography Centre, Cruise Report No. 13.
- Bowser, S.S., Gooday, A.J., Alexander, S.P. & Bernhard, J.M. (1995) Larger agglutinated foraminifera of McMurdo Sound, Antarctica: Are *Astrammina rara* and *Notodendrodes antarcticos* allogromiids incognito? *Marine Micropaleontology*, 26, 75–88.
- Cavalier-Smith, T. (2002) The phagotrophic origin of eukaryotes and phylogenetic classification of protozoa. *International Journal of Systematic and Evolutionary Microbiology*, 52, 297–354.
- Cedhagen, T., Gooday, A.J. & Pawlowski, J. (2009) A new genus and two new species of saccamminid foraminiferans (Protista, Rhizaria) from the deep Southern Ocean. *Zootaxa*, 2096, 9–22.

- Christiansen, B.O. (1965) A bottom form of the planktonic foraminifer *Globigerinoides rubra* (D'Orbigny, 1839). *Publicazione of the Stazione Zoologica di Napoli*, 34, 197–202.
- Cornelius, N. & Gooday, A.J. (2004) 'Live' (stained) deep-sea benthic foraminiferans in the western Weddell Sea: trends in abundance, diversity and taxonomic composition along a depth transect. *Deep-Sea Research Part II-Topical Studies in Oceanography*, 51, 1571–1602.
- Dahlgren, L. (1962) A new monothalamous foraminifer, *Ovammmina opaca* n. gen., n. sp., belonging to the family Saccamminidae. *Zoologiska Bidrag från Uppsala*, 33, 197–200.
- de Stigter, H.C., Boer, W., de Jesús Mendes, P.A., Jesús, C.C., Thomsen, L., van den Berg, G.D. & van Weering, T.C.E. (2007) Recent sediment transport and deposition in Nazaré Canyon, Portuguese continental margin. *Marine Geology*, 246, 144–164.
- Gooday, A.J. (1986a) Meiofaunal foraminiferans from the bathyal Porcupine Seabight (Northeast Atlantic) - size structure, standing stock, taxonomic composition, species diversity and vertical distribution in the sediment. *Deep-Sea Research Part A*, 33, 1345–1373.
- Gooday, A.J. (1986b) Soft-shelled Foraminifera in meiofaunal samples from the bathyal northeast Atlantic. *Sarsia*, 71, 275–287.
- Gooday, A.J. (2002) Organic-walled allogromiids: aspects of their occurrence, diversity and ecology in marine habitats. *Journal of Foraminiferal Research*, 32, 384–399.
- Gooday, A.J. (2004) Soft-walled, monothalamous benthic foraminiferans in the Pacific, Indian and Atlantic Oceans: aspects of biodiversity and biogeography. *Deep-Sea Research Part I-Oceanographic Research Papers*, 51, 33–53.
- Gooday, A.J., Bowser, S.S., Cedhagen, T., Cornelius, N., Hald, M., Korsun, S. & Pawlowski, J. (2005) Monothalamous foraminiferans and gromiids (Protista) from western Svalbard: a preliminary survey. *Marine Biology Research*, 1, 290–312.
- Gooday, A.J., Hughes, J.A. & Levin, L.A. (2001) The foraminiferan macrofauna from three North Carolina (USA) slope sites with contrasting carbon flux: a comparison with the metazoan macrofauna. *Deep-Sea Research Part I-Oceanographic Research Papers*, 48, 1709–1739.
- Habura, A., Goldstein, S.T., Broderick, S. & Bowser, S.S. (2008) A bush, not a tree: The extraordinary diversity of cold-water basal foraminiferans extends to warm-water environments. *Limnology and Oceanography*, 53, 1339–1351.
- Heinz, P., Geslin, E. & Hemleben, C. (2005) Laboratory observations of benthic foraminiferal cysts. *Marine Biology Research*, 1, 149–159.
- Jorissen, F.J., de Stigter, H.C. & Widmark, J.G.V. (1995) A conceptual model explaining benthic foraminiferal microhabitats. *Marine Micropaleontology*, 26, 3–15.
- Lastras, G., Arzola, R.G., Masson, D.G., Wynn, R.B., Huvenne, V.A.I., Huhnerbach, V. & Canals, M. (2009) Geomorphology and sedimentary features in the Central Portuguese submarine canyons, Western Iberian margin. *Geomorphology*, 103, 310–329.
- Moodley, L. (1990) Squatter Behavior in Soft-Shellled Foraminifera. *Marine Micropaleontology*, 16, 149–153.
- Nyholm, K.G. (1961) Morphogenesis and biology of the foraminifer *Cibicides lobatulus*. *Zoologiska Bidrag från Uppsala*, 33, 157–192.
- Pawlowski, J., Holzmann, M., Berney, C., Fahrni, J., Cedhagen, T. & Bowser, S.S. (2002) Phylogeny of allogromiid foraminifera inferred from SSU rRNA gene sequences. *Journal of Foraminiferal Research*, 32(4), 334–343.
- Sabbatini, A., Morigi, C., Negri, A. & Gooday, A.J. (2007) Distribution and biodiversity of stained monothalamous foraminifera from Tempelfjord, Svalbard. *Journal of Foraminiferal Research*, 37, 93–106.
- Schmidt, S., de Stigter, H.C. & van Weering, T.C.E. (2001) Enhanced short-term sediment deposition within the Nazare Canyon, North-East Atlantic. *Marine Geology*, 173, 55–67.
- Tyler, P., Amaro, T., Arzola, R., Cunha, M.R., de Stigter, H., Gooday, A., Huvenne, V., Ingels, J., Kiriakoulakis, K., Lastras, G., Masson, D., Oliveira, A., Pattenden, A., Vanreusel, A., VanWeering, T., Vitorino, J., Witte, U. & Wolff, G. (2009) Europe's Nazaré Submarine Canyon. *Oceanography*, 22, 53–63.
- van Weering, T.C.E., de Stigter, H.C., Boer, W. & de Haas, H. (2002) Recent sediment transport and accumulation on the NW Iberian margin. *Progress in Oceanography*, 52, 349–371.
- Vanney, J.R. & Mougénot, D. (1990) A Gouf-Type Canyon, the Canhao-Da-Nazare (Portugal). *Oceanologica Acta*, 13, 1–14.
- Weaver, P.P.E. & Gunn, V. (2009) Introduction to the Special Issue: HERMES – Hotspot Ecosystem Research on the Margins of European Seas. *Oceanography*, 22, 12–15.
- Weaver, P.P.E., Billett, D.S.M., Boetius, A., Danovaro, R., Freiwald, A. & Sibuet, M. (2004) Hotspot Ecosystem Research on Europe's Deep-Ocean Margins. *Oceanography*, 17, 132–143.