The 'mica sandwich'; a remarkable new genus of Foraminifera (Protista, Rhizaria) from the Nazaré Canyon (Portuguese margin, NE Atlantic)

Andrew J. Gooday[1], Ana Aranda da Silva[2,3], Karoliina A. Koho[4], Béatrice Lecroq[5], Richard B. Pearce[1]

[1]*National Oceanography Centre, Southampton, University of Southampton Waterfront Campus, European Way SO14 3ZH, UK*

[2]*CESAM, Departamento de Biologia, Universidade de Aveiro, Campus universitário de Santiago, 3810-193 Aveiro*

[3]*INETI, Departamento de Geologia Marinha, Estrada da Portela, Zambujal 2721-866 Alfragide, Portugal*

[4]*Utrecht University, Faculty of Geosciences, Budapestlaan 4, 3584 CD Utrecht, The Netherlands*

[5]*Department of Zoology and Animal Biology, University of Geneva, Sciences III, 1211 Geneva 4, Switzerland*

email: ang@noc.soton.ac.uk

ABSTRACT: Based on morphological and molecular characteristics, we describe a new genus and species of monothalamous agglutinated foraminifera, *Capsammina patelliformis,* that occurs mainly at bathyal (1000-3400m) water depths in the Nazaré Canyon off Portugal. The test is strongly flattened, up to 500µm or more in maximum dimension, and 30-80µm thick. It lacks obvious apertures, and is typically composed of 2-3 large, plate-like grains of mica that form the upper and lower surface of the test; these are separated by fine-grained, white agglutinated material ('mortar') forming a ring around the cell body. The cytoplasm, visible through the mica plates, is whitish in colour with few obvious inclusions. Analysis of a fragment of the SSUrDNA gene indicates that *C. patelliformis* belongs in a clade branching with *Crithionina delacai, C. granum* and an undetermined crithioninid species. However, the divergences between the new species and these *Crithionina* species range from 20% to 21%, and are therefore too high to classify it in the same genus. We also transfer a previously described species, *Psammosphaera bowmanni* Heron-Allen and Earland 1912, to *Capsammina* based on its use of mica flakes in test construction. Other monothalamous agglutinated foraminifera, including *Psammosphera* spp., are phylogenetically distant from *Capsammina*. The new species occupies a shallow infaunal microhabitat, living mainly in the top 0.5cm of sediment.

INTRODUCTION

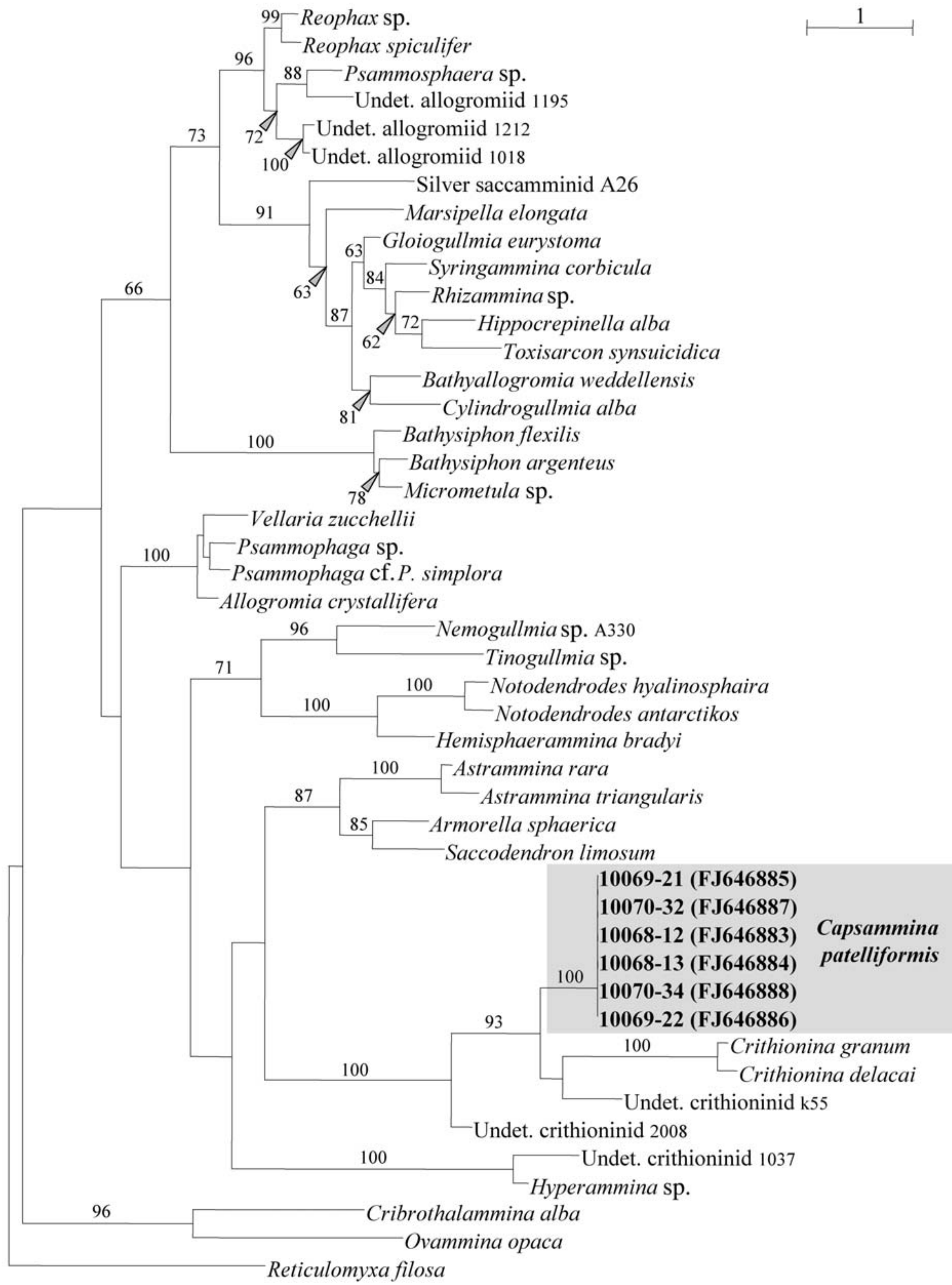
HERMES (Hotspot Ecosystem Research on the Margins of European Seas), an Integrated Project funded by the European Union, aimed among other things to investigate the biodiversity of 'hotspot' ecosystems around the European margins (Weaver et al. 2004). One main focus of HERMES was on submarine canyons, and particularly on the large canyons that traverse the continental slope on the southern part of the Portuguese margin. These canyons were studied during a series of HERMES cruises. The most intensively studied was the Nazaré Canyon, which extends from close to the shoreline to 5000m depth on the Iberian Abyssal Plain. Arzola et al. (2008) describe sedimentary features and processes in the Nazaré Canyon. De Stigter et al. (2007) describe modern sediment transport and deposition. A general account of the morphology, sedimentology, physical oceanography and biology of the Nazaré Canyon is given by Tyler et al. (2008).

Koho et al. (2007) provide an overview of the abundance, species composition, and vertical distribution within the sediment of foraminifera at sites in the axis and on the adjoining terraces of the Nazaré canyon at depths from 146 to 4976m. Among the species they recognise is a peculiar agglutinated form, which they termed the 'mica sandwich' because the test is formed from two mica plates. Koho et al. (2007) assign this species to the genus *Crithionina.* However, our molecular data suggest that it is sufficiently distant from typical *Crithionina* to warrant the establishment of a new genus. The purpose of this paper is to describe the 'mica sandwich' based on HERMES and other material from the Nazaré canyon. The description combines morphological features, mainly test characteristics with phylogenetic molecular data.

METHODS

Study site

Most of our material originated from a 3500-m site located on a terrace in middle part of the Nazaré Canyon. This area is characterised by very high sedimentation rates of up to 32.6g m^{-2} d^{-1} (De Stigter et al. 2007). Piston cores recovered from 40–60m high terraces at ~3500m water depth reveal thick sequences of dark greenish-brown, bioturbated silt-mud turbidites, rich in black carbonaceous fragments and mica flakes (Arzola et al. 2008). Macrofaunal densities at this site are the highest observed anywhere in the canyon (Tyler et al. 2008). The new species was also collected at ~1000-m water depth on the terraces of the upper Nazaré canyon. The upper canyon experiences relatively high sedimentation rates; 14.1g m^{-2} d^{-1} at 927-m water depth (De Stigter et al. 2007). The sediments here are generally medium-fine-grained silt with a modal grain size of ~14µm (De Stigter et al. 2007) and are relatively enriched in labile organic matter with a high phytopigment content (García et al. 2007; García and Thomsen 2008). The high organic-matter content of sediments in the upper Nazaré Canyon is reflected in a shallow (generally <1cm depth in sediment) oxygen penetration depth (Epping et al. 2002).



TEXT-FIGURE 1
Phylogenetic tree based on SSU rDNA partial sequences showing the position of *Capsammina patelliformis* gen. et sp. nov. among the Foraminifera. The tree was obtained using maximum likelihood method with GTR + I + G model of evolution. Only bootstrap values higher than 60% are indicated.

TABLE 1
Station data and number of specimens of *Capsammina patelliformis* recovered from each sample (megacore or *Isis* push core). CD = R.R.S *Charles Darwin,* JC = R.R.S. *James Cook,* PE = RV *Pelagia.*

Cruise	Station	Gear/Dive	°N	°W	Depth (m)	Specimens
Nazaré canyon						
CD179	56851#1	Megacorer	39°49.98′	09°93.28′	3518	37
CD179	56848#1	Megacorer	39°50.00′	09°93.35′	3517	52
JC10	91	*Isis* Dive 46	39°29.82′	09°55.99′	3536	27
JC10	101	Megacorer	39°30.05′	09°55.88′	3466	24
JC10	122	Megacorer	39°30.05′	09°55.88′	3461	7
JC10	127	*Isis* Dive 57	39°29.76′	09°56.04′	3536	37
64PE138	12	Multicorer	39°38.87′	09°14.72′	344	2
64PE138	14	Multicorer	39°30.76′	09°51.05′	2847	1
64PE236	7	Multicorer	39°35.99′	09°24.26′	1160	12
64PE236	13	Multicorer	39°35.87′	09°24.26′	927	18
Whittard canyon						
JC36	053	Megacorer	48°41.08′	11°12.09′	2436	1
JC36	087	*Isis* Dive 115	48°35.84′	09°59.08′	1389	7

A few additional specimens of the new species were obtained in the Whittard Canyon, a large and complex canyon located in the northern part of the Bay of Biscay (Masson 2009).

Sample collection and treatment

Samples were collected during R.R.S. *Discovery* cruise 297 (July 27 to August 16; Weaver 2005), R.R.S. *Charles Darwin* cruise 179 (April 14 to May 17; Billett 2006), legs 2 and 3 of the R.R.S. *James Cook* cruise 10 (June 3 to July 7, 2007; Weaver and Masson 2007) and *James Cook* cruise 36 (June 19 to July 28, 2009; Masson 2009) using either pushcores deployed by the *Isis* ROV or a megacorer equipped with core tubes of 10-cm diameter. As soon as possible after collection, the surficial sediment (usually upper 2cm) was sliced off, sieved on a 125-µm screen in chilled water and selected foraminifera, including specimens of the new species, extracted under a binocular microscope. Specimens for morphological study were fixed in buffered 10% formalin and stored in 2ml cryovials. Specimens for molecular analyses were transferred to microtubes containing 60ml of guanidine DNA extraction buffer. Additional material for morphological study was collected during R.V *Pelagia* cruises 64PE138 (May 1999) and 64PE236 (May 2005) using an 8+4 multiple corer developed by Oktupus GmbH. Cores (6-cm diameter) for foraminiferal analyses were immediately sliced on board down to 10cm depth in the sediment; the top 2cm were cut into 0.5cm-thick-slices and the rest of the core into 1cm slices. The samples were stored in a solution of rose Bengal in 96% ethanol (1g/L) until washed and sieved (63-150µm, >150µm) in the laboratory several months later. The well-stained specimens were picked from the top 5cm of sediment (>150µm fraction only).

Morphological methods

Light photographs of the new species were taken in water using a SLR digital camera (Canon EOS 350D) attached to either a Leica binocular microscope or an Olympus BH-2 compound photomicroscope. Measurements of the test were made to the nearest 10µm using an eyepiece graticule fitted to a Wild M50 dissecting microscope. Selected specimens were examined by scanning electron microscopy (SEM) using either a LEO 1450VP SEM in Southampton or an XL30FEG SEM in Utrecht. The Leo 1450VP SEM is a tungsten filament SEM from which both secondary electron and backscattered electron images were acquired. EHT settings of 15kV and 30kV were used with nominal probe current settings of 750pA and 31pA respectively and a working distance ranging from between 12–19mm. Elemental microanalysis was undertaken using a PGT light element detector.

Molecular methods

DNA of six specimens from three different stations was extracted using guanidine buffer (Pawlowski 2000): two from station 91 (DNA 10068), two from station 101 (DNA 10069) and two from station 127 (DNA 10070). A fragment of the SSU rDNA 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), and re-amplified using nested primer s14F1 (5' AAG GGC ACC ACA AGA ACG C). The amplified PCR products were purified using High Pure PCR Purification Kit (Roche Diagnostics) and then cloned using ultracompetent cells XL2-Blue MRF' (Stratagene) after ligation in the Topo Cloning vector (Invitro Gene). All clones were sequenced in both directions. Sequencing reactions were prepared using an ABI-PRISM Big Dye Terminator Cycle Sequencing Kit and analysed with an ABI-377 DNA sequencer or an ABI-PRISM 3100 (Applied Biosystems), all according to the manufacturer's instructions.

Sequences were compared to 40 other foraminiferan sequences and manually aligned using the Seaview software (Galtier et al. 1996). The maximum likelihood tree was constructed with GTR + I + G model, using Phy_ML program (Guindon and Gascuel 2003).

SYSTEMATIC DESCRIPTION

Supergroup Rhizaria Cavalier-Smith 2002
Phylum Foraminifera Cavalier-Smith 1998

Capsammina Gooday, Aranda da Silva, Koho, Lecroq **gen. nov.**

Derivation of name. Latin ‘capsa’ a box

Type species. Capsammina patelliformis gen. & sp. nov.

Diagnosis. Monothalamous test composed of relatively few large, plate-like grains of mica separated by fine-grained, white agglutinated material (‘mortar’). Obvious aperture(s) absent.

Remarks. Capsammina is distinguished by the structure and composition of its test from other monothalamous foraminifera that lack an obvious aperture. Morphology-based classifications group these forms in the Families Psammosphaeridae and Hemisphaeramminidae (Loeblich and Tappan 1987). *Psammosphaera* is much larger and has a test composed of quartz grains. *Crithionina* has a more rounded shape and the test does not incorporate mica plates. Molecular evidence (see below) indicates that the type species of *Capsammina* belongs in a different phylogenetic clade from *Psammosphaera.*

In addition to the type species, described below, we include *Psammosphaera bowmanni* Heron-Allen and Earland, 1912 in the new genus (Pl. 1). The test of this species was originally described as ‘consisting of a more or less irregularly polyhedral chamber, constructed of small flakes of mica cemented around the edges by a light grey mud-like cement’ (Heron-Allen and Earland 1912).

Capsammina patelliformis Gooday **gen. & sp. nov**.
Plates 2-5

Crithionina sp. (mica sandwich). Koho et al. 2007, Pl. 3, fig. 3

Derivation of name. Patella (L), a plate, referring to the typically plate-like morphology of the test.

Diagnosis. Species of *Capsammina* characterised by strongly flattened test dominated by 2-3 flat, parallel mica plates. Plates separated by more or less oval ring of white mortar composed of fine mineral grains and enclosing cell body. Both mortar and cell body visible though transparent plates.

Type material. The type specimens, from *Isis* Dive 57 (*James Cook* Station 127; 39°29.756', 9°56.041', 3536m water depth) are deposited in the Natural History Museum, London under registration numbers ZF5210 (holotype; Pl. 2, Fig. D), ZF5211 (1 paratype; Pl. 2, Fig. E) and ZF5212-5229 (18 paratypes; Pl. 2, Fig. C).

Other material examined. 17 specimens from the type locality and 153 specimens from other sites in the Nazaré Canyon (Table 1).

Morphological description

The test is usually strongly compressed with flat upper and lower surfaces formed from single plate-like mineral grains, presumed to be mica (Pls. 2, 3). Most of the plates are colourless and yield main peaks for Si, Al and K when examined using elemental X-ray microanalysis under SEM. These are presumably muscovite. Others are brownish in colour and yield peaks for Fe and Ti, in addition to Si, Al and K. These plates are presumably biotite. The mica plates are separated by a mass of small, more equidimensional mineral grains that form a ring around the cell body and appear pure white in colour when viewed in reflected light (Pl. 2). X-ray microanalyses indicate that some larger grains are rich in Si and are presumably quartz. Other smaller grains yield peaks for Si, Al, K, Ca and Fe and are probably rep-

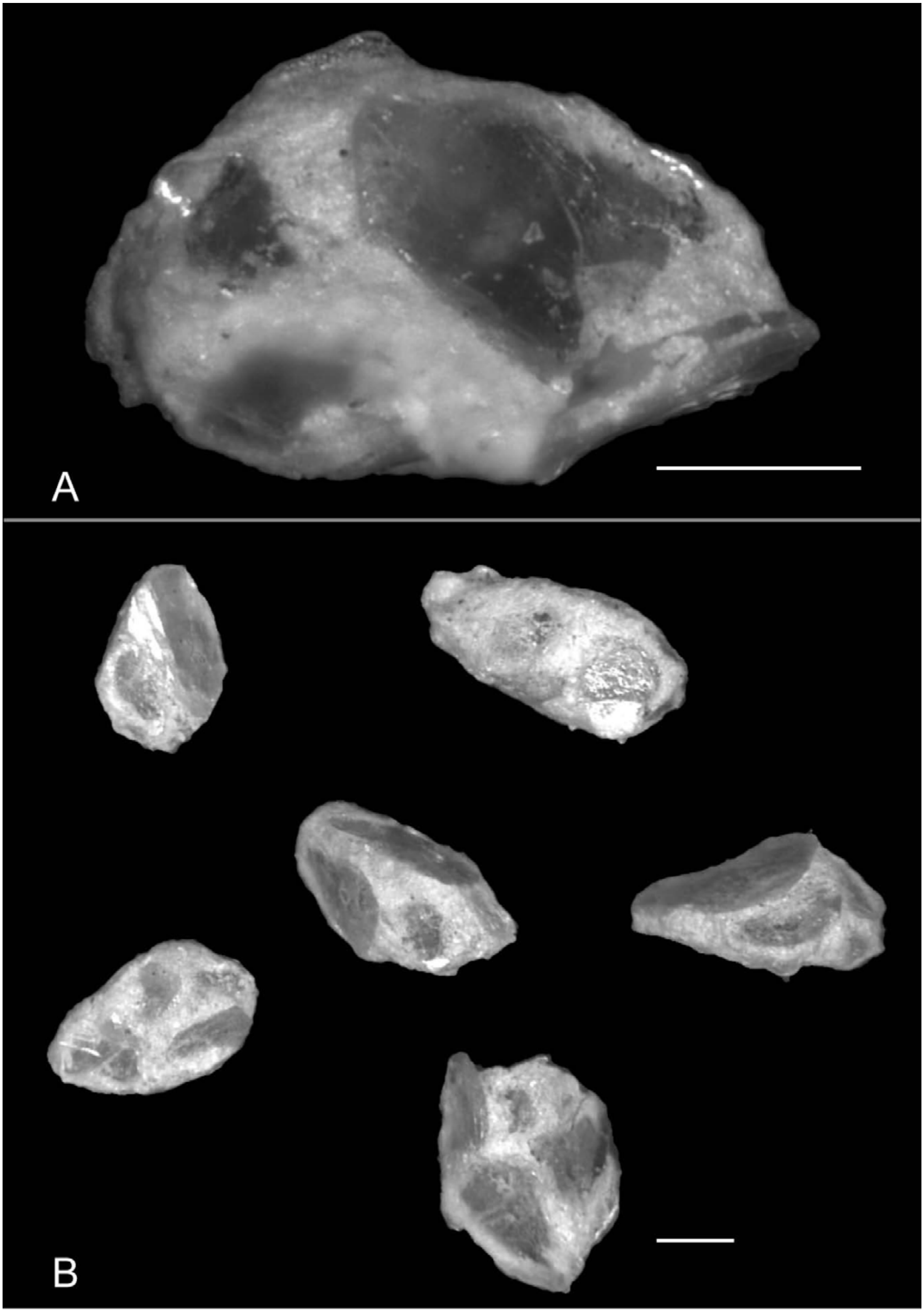
---

PLATE 1

Psammosphaera bowmanni Heron-Allen and Earland, 1912; scale bars = 100µm.
Specimens from Goldseeker Haul 73, Burghead Bay, Firth of Forth, Scotland, housed in the Natural History Museum, London.
Photographs courtesy of Prof. John Murray.

A Registration number. 1957.11.14.93.

B Registration number 1957.11.14.87-92.


A
B

resent different kinds of clay mineral, possibly chlorite and smectite.

This ring-like formation of ‘mortar’, and the cell body that it encloses, are clearly visible through the transluscent plates. In flat specimens, the length and width of the test vary from 200 to 640µm and 150 to 500µm respectively. However, these dimensions are usually those of the mica plates. The size of the test is more accurately reflected by the size of the mortar ring. This ranges from 200 to 260µm long and 160 to 200µm wide. The inner lumen generally occupies over a half (50-70%, usually 53-62%) of the diameter of the mortar ring. In side view, the test is very thin (Pl. 4, Fig. A). Many specimens are only 30-50µm thick but a few are thicker, up to 80µm.

A minority of specimens incorporate three or more mica plates. Sometimes, there are two overlapping plate-like grains on one side of the test with a double ring of white mortar developed between the grains (Fig. 2C,E; 3A). In a few cases, 3-4 plates are arranged to form a more three-dimensional, triangular test (Pl. 2, Fig. A); occasionally, more plates are present, forming a polygonal test (Pl. 2, Fig. B; Pl. 5, Fig. A).

The cell body almost completely fills the space within the mortar ring. In unfixed specimens it is pale cream in colour in reflected light, translucent in transmitted light. The cytoplasm is relatively featureless, except for a single nucleus (Pl. 2, Fig. D) and, in some specimens, various inclusions, including brown, spherical, cyst-like structures, which are presumably an ingested particles (Pl. 2, Fig. F).

Molecular characterization

For each extraction, two clones were sequenced and a total of six sequences were deposited in the EMBL/GenBank under accession numbers FJ646883-646888. No particular structural features (introns, insertions) were observed. The sequenced fragments were 1120 nucleotides and the GC content ranged from 44.5 to 44.8%. The observed divergences between the six sequences of *Capsammina patelliformis,* including variable regions, ranged from 0% to 2.7% (between clones from the same single-cell extraction, divergences ranged from 0% to 0.18%) which is quite low but also not surprising since the analysed samples were from the same 3400-m locality. The maximum likelihood phylogenetic tree (text-fig. 1) showed that these six sequences are monophyletic (with a bootstrap support of 100%) and comprise a clade branching with three crithioninids: *C. delacai, C. granum* and an undescribed specimen of crithioninid morphology. Because the genetic database for crithioninids and for the monothalamous species in general is still poor, it is difficult to evaluate the closeness of the relationship between *C. patelliformis* and species of the genus *Crithionina*. However, the observed divergences between the new species and its closest relatives are 20% (23% including variable regions) for the “Unidet. crithioninid k55”, 20% (26% including variable regions) for *C. granum* and 21% (27% including variable regions) for *C. delacai*. The variation between *C. granum* and *C. delacai* is only 6% (13% including variable regions) and so we consider that these percentages are too high to include the new species in the genus *Crithionina*, assuming that the *C. granum* and *C. delacai* are representative of this genus. Unfortunately, there are currently no sequence data for the type species, *C. mamilla* (the species with this name in Pawlowski et al. 2003, Fig. 1 therein was another species). The phylogenetic tree also shows that another monothalamous species, *Psammosphera* sp., is very distant from *C. patelliformis* based on the partial sequences of SSU.

Relative abundance and vertical distribution in the sediment

The new species occurs in the Nazaré (344-3400m water depth) and Whittard (1389-2436m) canyons. At CD179 station 56848, close to the type locality in the Nazaré canyon, 52 specimens of *Capsammina patelliformis* represented 7.9% of all stained foraminifera in the 0-2cm layer (>150µm fraction). All except one of these specimens were extracted from the 0-0.5cm layer, where they accounted for 43% of the 119 stained foraminifera in the >150µm fraction. At station 56851, 37 specimens represented 67% of the 55 stained foraminifera in the same sieve fraction.

The vertical distribution of *C. patelliformis* was also investigated at the two shallow sites, 64PE236-13 and 64PE236-07

PLATE 2

Capsammina patelliformis gen. et sp. nov.; JC station 127 (3535 m, Nazaré Canyon); light micrographs except for Fig. B; scale bars = 100µm, unless indicated otherwise.

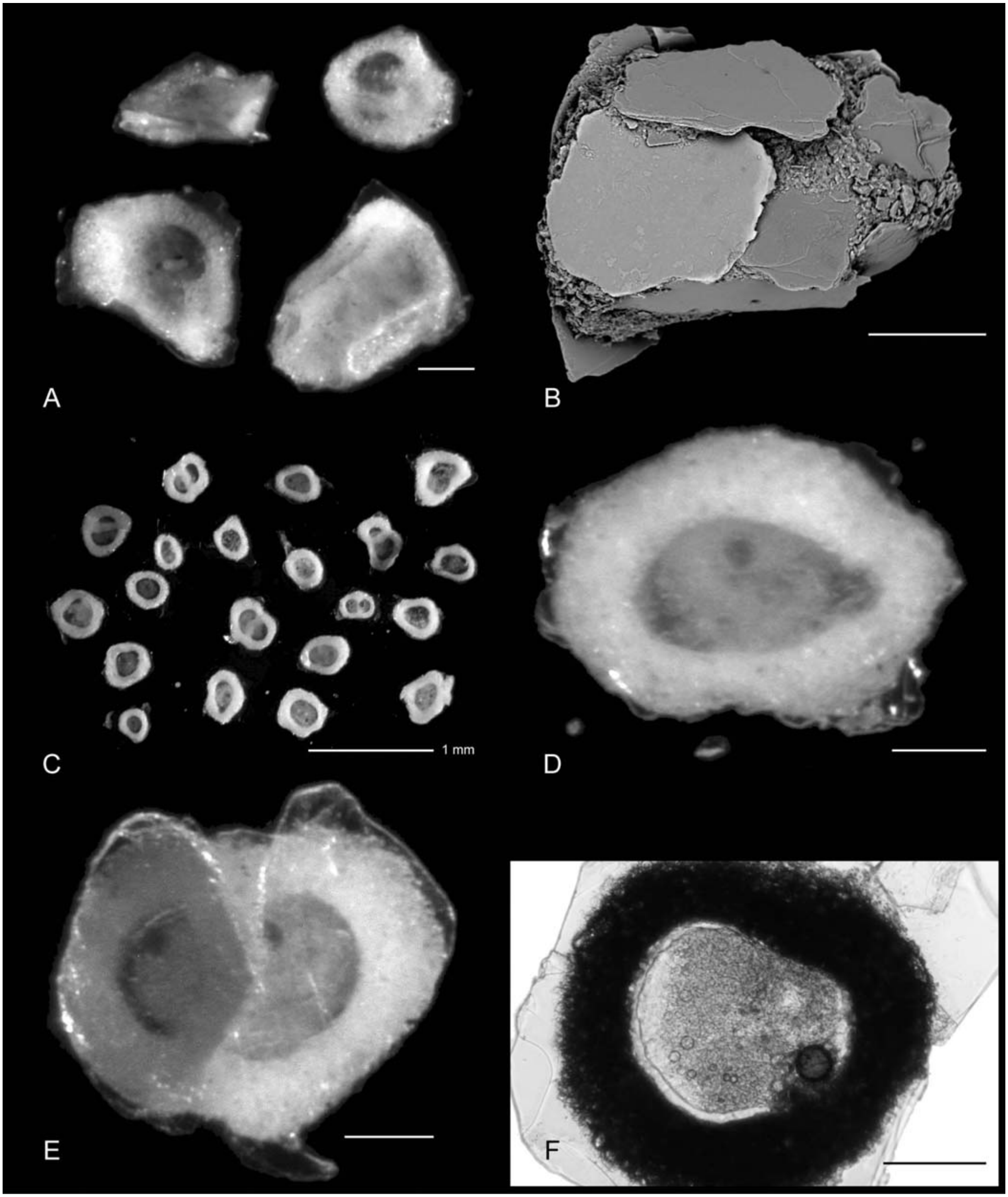
A Four specimens with multifaceted tests; JC station 101.

B SEM photograph of bottom right-hand specimen in Fig. A.

C Holotype and paratypes (reg. nos ZH5210-5229).

D Holotype, reg. no ZH5210, Paratype, reg. no. ZH5211

F Transmitted light photograph showing cell body with inclusions.


A
B
C
1 mm
D
E
F

(927-m and 1160-m water depth, respectively). At 64PE236-13 a total of 18 well-stained specimens were found, of which 12 were located in the top 0.5-cm of sediment, followed by 3, 2 and 1 in the following three 0.5-cm slices of sediment. Only the top 2cm of the core were examined at 64PE236-07. Here, 9 specimens were found in the first 0.5-cm of sediment and 3 specimens between 0.5 and 1.0cm depth.

These observations suggest that *C. patelliformis* is a sediment surface dwelling species and has a shallow microhabitat distribution.

Remarks

The white, finely granular 'mortar' that separates the mica plates in *Capsammina patelliformis* resembles the material that constitutes the test in *Crithionina granum* Schultz 1877 and *C. delacai* Gooday, Bernhard and Bowser 1995. A phylogenetic relationship between these three species is indicated by the fact that they belong to the same clade (Fig. 1). However, the relatively high genetic divergence (20-21%) between *C. patelliformis* and the two *Crithionina* species suggests that they are not closely related.

As far as we are aware, *Capsammina bowmanni* is the only species that resembles *C. patelliformis.* We illustrate some specimens from the type locality in the Moray Firth, Scotland, for comparison with our new species (Pl. 1). They also have a faceted test composed of mica plates separated by fine-grained white agglutinated material. However, the test has an elongate, rounded, pellet or droplet-shaped morphology rather than the strongly flattened form of the new species. Occasional specimens of *C. patelliformis* are more three-dimensional, but they do not approach the shape of the test in *C. bowmanni.* Another difference is that the protoplasm of *C. bowmanni* is described as 'very dark and opaque' in contrast to the light-coloured protoplasm in *C. patelliformis.* The two species have different bathymetric distributions. *Capsammina bowmanni* was described from 55-64m water depth, *C. patelliformis* is most common at 3500m. However, the range of *C. bowmanni* extends down to more than 350m (see below), while that of *C. patelliformis* extends up to ~350m (Table 1). The possibility that *C. patelliformis* represents a deep-water variant of *C. bowmanni* should therefore be borne in mind. Molecular analyses would help to resolve this question.

The abundance of *C. patelliformis* at the organically-enriched, 3400-m site in the Nazaré Canyon suggests that it is an opportunist. Observations by Dr. Thomas Cedhagen (personal communication) suggest that *Capsammina bowmanni* may have similar ecological characteristics. It was apparently absent in the Skagerrak in the 1920-1930s, when Höglund collected material for his 1947 study, but was one of the commonest species between 113 and 354m water depth when Dr Cedhagen sampled in the same area in the late 1990s.

Concluding remarks

The recognition of *Capsammina patelliformis* adds to our knowledge of the diversity of monothalamous agglutinated foraminifera. Modern agglutinated taxa that lack apertures and have spherical or dome-like tests are generally assigned to genera such as *Crithionina, Hemisphaerammina, Iridea* and *Psammosphaera* within the families Psammosphaeridae and Hemisphaeramminidae of morphology-based classifications (Loeblich and Tappan 1987). These 'primitive' taxa form part of the bush-like radiation of foraminifera revealed by recent molecular studies (Pawlowski et al. 2003; Habura et al. 2008). They are represented by a variety of different forms, which are often attached to hard substrates such as stones and shells. These morphotypes tend to grade into each other and are difficult to distinguish clearly based on morphological features (Heron-Allen and Earland 1913). Molecular evidence suggests that they represent several different clades (Pawlowski et al. 2002, 2003). Some basically organic-walled foraminiferans (allogromiids in the "classic" sense) also sometimes create loosely-agglutinated dome structures (Loeblich and Tappan 1987), or encase themselves in cyst-like envelopes (Sabbatini et al. 2007).

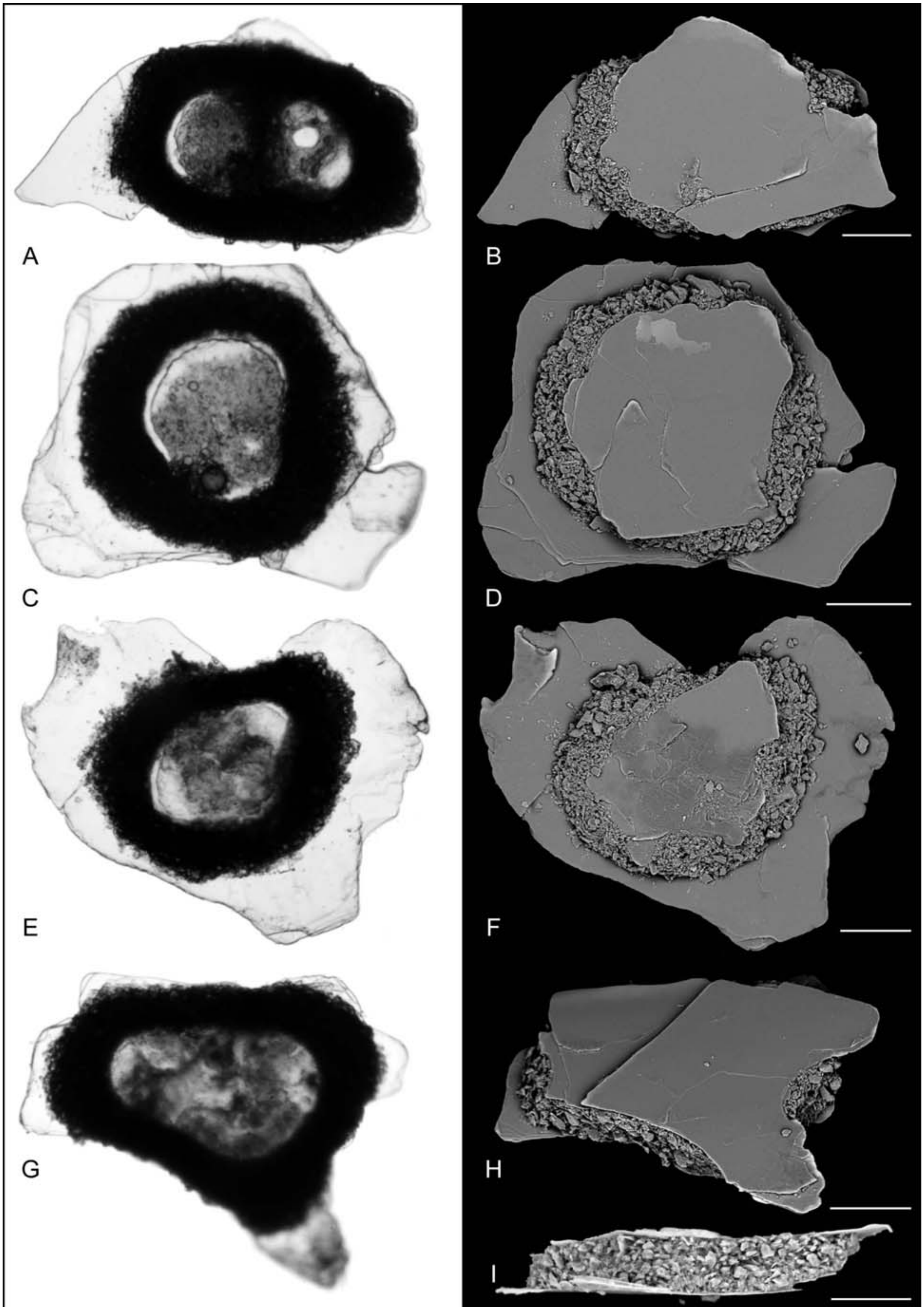
The new genus, however, possesses some characteristic features that distinguish it from other monothalamous agglutinated taxa without apertures. The most distinctive of these is the use of flakes of mica as the dominant test component. Many agglutinated foraminifera construct their tests from particular kinds of particles. Those selected include sponge spicules, globigerina shells, coccoliths and quartz grains. As Heron-Allen and Earland (1912) remark, mica flakes are rarely used, probably because they are difficult to cement together and easily detached. Although these flakes are very common at the type locality for *C. patelliformis*, the fact that they are a consistent feature of the test in this species and in *C. bowmanni,* despite the availability of other suitable test-building particles, suggests that their use is obligate rather than opportunistic.

PLATE 3

Capsammina patelliformis gen. et sp. nov.; JC station 127 (3535m, Nazaré Canyon); scale bars = 100µm

A-F Transmitted light and SEM micrographs of the same three specimens, viewed lying flat.

G-I H is an oblique view and I an edge view of the specimens shown in G.


A
B
C
D
E
F
G
H
I

ACKNOWLEDGMENTS

We thank Prof. John Murray for generously making available his images of *Psammosphaers bowmanni,* reproduced in Plate 1 and Dr Cedhagen for making available his unpublished observations on this species. The paper benefited from the constructive reviews of Drs. Tomas Cedhagen, Andrea Habura and Susan Goldstein. This paper is a contribution to the Oceans 2025 project funded by the Natural Environment Research Council, UK, and the Collaborative Project HERMIONE funded under the European Commission's Framework 7 programme.

REFERENCES

ARZOLA, R.G., WYNN, R.B., LASTRAS, G., MASSON, D.G. and WEAVER, P.P.E., 2008. Sedimentary features and processes in the Nazaré and Setúbal submarine canyons, west Iberian margin. *Marine Geology,* 250: 64-88.

BILLETT, D.S.M., 2006. RRS Charles Darwin Cruise 179, 14 Apr - 17 May 2006. Hotspot ecosystem research in the Setúbal, Lisbon, Cascais and Nazaré canyons on the Portuguese continental margin. *National Oceanography Centre, Southampton, Cruise Report*, 13: 66pp.

DE STIGTER, H.C., BOER, W., DE JESÚS MENDES, P.A., JESUS, C.C., THOMSEN, L., VAN DEN BERG, G.D. and VAN WEERING, T.C.E., 2007. Recent sediment transport and deposition in Nazaré Canyon, Portuguese continental margin. *Marine Geology*, 246: 144–164.

EPPING, E., VAN DER ZEE, C., SOETAERT, K. and HELDER, W., 2002. On the oxidation and burial of organic carbon in sediments of the Iberian margin and Nazaré Canyon (NE Atlantic). *Progress in Oceanography,* 52: 399–431.

GARCÍA, R. and THOMSEN, L., 2008. Bioavailable organic matter in surface sediments of the Nazaré canyon and adjacent slope (Western Iberian Margin). *Journal of Marine Systems,* 74: 44–59

GARCÍA, R., KOHO, K.A., DE STIGTER, H.C., EPPING, E., KONING, E. and THOMSEN, L., 2007. Distribution of meiobenthos in the Nazaré Canyon and adjacent slope (western Iberian Margin) in relation to sedimentary composition. *Marine Ecology Progress Series,* 240: 207–220.

GALTIER, N., GOUY, M. and GAUTIER, C., 1996. SEAVIEW and PHYLO_WIN, two graphic tools for alignment and molecular phylogeny. *Computer Applications in the Biosciences,* 12: 543-548.

GUINDON, S. and GASCUEL, O., 2003. A simple, fast, and accurate algorithm to estimate large phylogenies by maximum likelihood. *Systematic Biology,* 52: 696–704.

HABURA, A, GOLDSTEIN, S.T., BRODERICK, S. and 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.

HERON-ALLEN, E. and EARLAND, A., 1912. On some Foraminifera from the North Sea, etc, dredged by the Fisheries cruiser 'Goldseeker' (International North Sea Investigations – Scotland). I. On some new Astrorhizidae and their shell structure. *Journal of the Royal Microscopical Society,* 1912: 382-389.

HERON-ALLEN, E. and EARLAND, A., 1913. On some Foraminifera from the North Sea, etc, dredged by the Fisheries cruiser 'Goldseeker' (International North Sea Investigations – Scotland). II On the distribution of *Saccammina sphaerica* (M. Sars) and *Psammosphaera fusca* (Schultz) in the North Sea: particularly with reference to the suggested identity of the two species. *Journal of the Royal Microscopical Society,* 1913: 1-26.

HÖGLUND, H., 1947. Foraminifera in the Gullmar Fjord and the Skagerak. *Zool. Bidrag från Uppsala,* 26: 1-328.

KOHO, K.A., KOUWENHOVEN T.J., DE STIGTER H.C. and VAN DER ZWAAN G.J., 2007. Benthic foraminifera in the Nazaré canyon, Portuguese continental margin: sedimentary environments and disturbance. *Marine Micropaleontology*, 66: 27-51.

LOEBLICH, A.R. and TAPPAN, H., 1987. Foraminiferal Genera and their Classification. Van Nostrand Reinhold Company, New York, 2 vols, 970 pp. + 847 pls.

MASSON, D.G., 2009. R.R.S. *James Cook* cruise 36, 19th June -28th July, 2009. The Geobiology of Whittard Submarine Canyon. National Oceanography Centre, Southampton, Cruise Report, 41: 53 pp.

PAWLOWSKI, J., 2000. Introduction to the molecular systematics of foraminifera. *Micropaleontology* 46, (supplement no. 1) 1-12.

PAWLOWSKI, J., FAHNI, J.F., BRYKCZYNSKA, U., HABURA, A. and BOWSER, S.S., 2002. Molecular data reveal high taxonomic diversity of allogromiid Foraminifera in Explorers Cove (McMurdo Sound, Antarctica). *Polar Biology,* 25: 96-105.

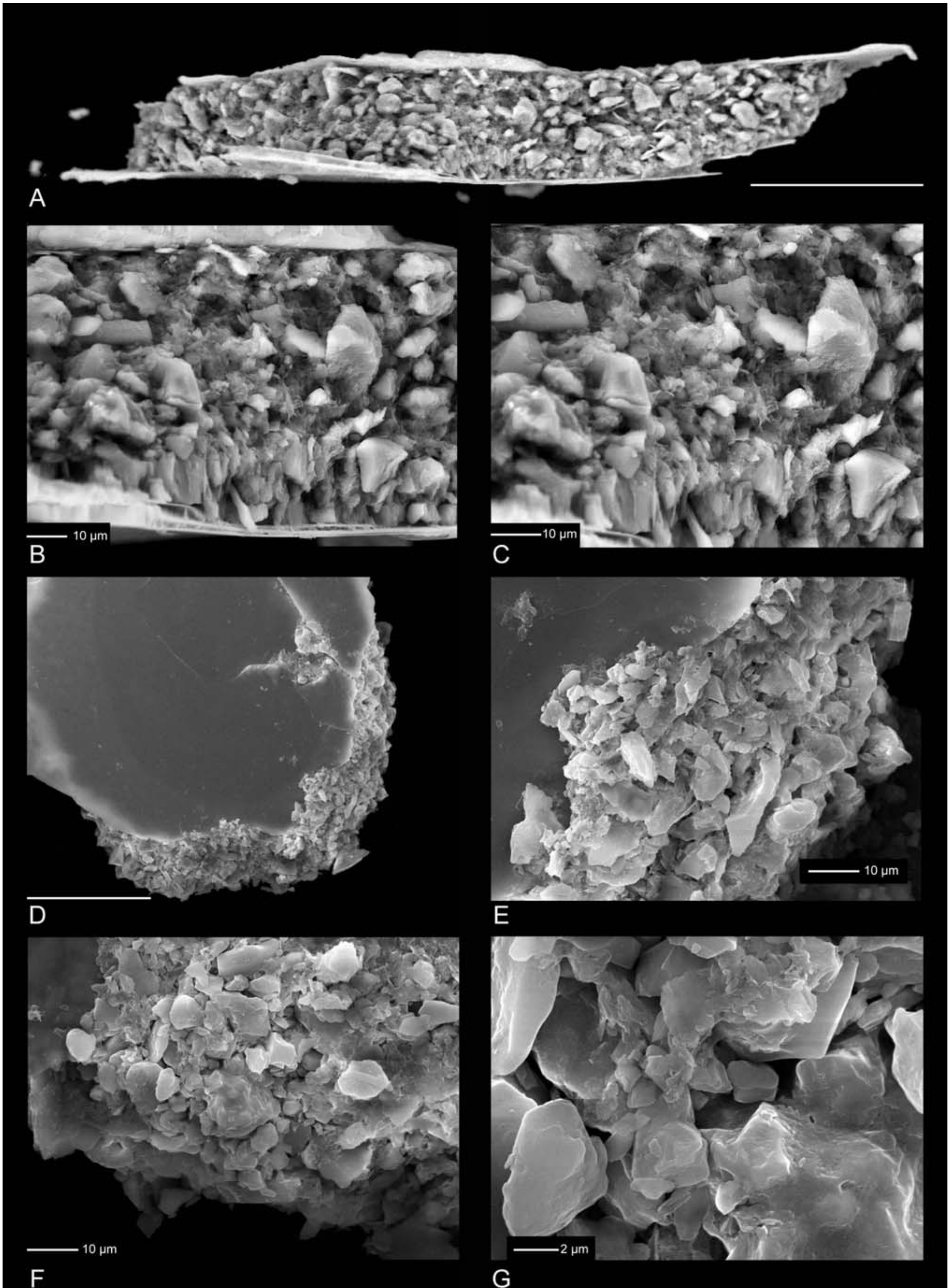
PLATE 4

Capsammina patelliformis gen. et sp. nov.; JC station 127 (3535m, Nazaré Canyon); scanning electron micrographs; scale bars = 100µm except where indicated otherwise.

A-C Edge view of specimen at progressively higher magnifications.

D-E General view and detail of agglutinated 'mortar'.

F-G General view and detail of mortar of second specimen.


A
10 µm
B
10 µm
C
D
10 µm
E
10 µm
F
2 µm
G

PAWLOWSKI, J., HOLZMANN, M., BERNEY, C., FAHRNI, J., GOODAY, A.J., CEDHAGEN, T., HABURA, A. and BOWSER, S.S., 2003. The evolution of early Foraminifera. *Proceedings of the National Academy of Sciences*, 100: 11494-11498.

SABBATINI, A., MORIGI, C., NEGRI, A. and GOODAY, A.J. 2007. Distribution and biodiversity of living benthic foraminifera, including monothalamous taxa, from Tempelfjord, Svalbard. *Journal of Foraminiferal Research,* 37: 93 - 106.

TYLER, P., AMARO, T., ARZOLA, R., CUNHA, R.H., DE STIGTER, H., GOODAY, A., HUVENNE, V., INGELS, I., KIRIAKOULAKIS, K., LASTRAS, G., MASSON, D., OLIVEIRA, A., PATTENDEN, A., VANREUSEL, A., VAN WEERING, T., VITORINO, J., WITTE, U. and WOLFF, G., 2008. Europe’s Grand Canyon: Nazaré Submarine Canyon. *Oceanography,* 22: 46-57.

WEAVER, P.E., 2005. The geobiology of the Nazaré and Setubal Canyons, Portuguese Continental Margin. Cruise report No. 1 RRS *Discovery* cruise D297 27 July - 16 August 2005. National Oceanography Centre, Southampton, 41 pp.

WEAVER, P.P.E. and MASSON, D.G., 2007. RRS *James Cook* Cruise 10, 13 May – 07 July 2007. National Oceanography Centre, Southampton, Cruise Report, 22: 93 pp.

WEAVER, P.P.E., BILLETT, D.S.M., BOETIUS, A. DANOVARO, R., FREIWALD, A. and SIBUET, M., 2004. Hotspot Ecosystem Research on Europe’s Deep-Ocean Margins. *Oceanography,* 17: 132-143.

PLATE 5

Capsammina patelliformis gen. et sp. nov; scanning electron micrographs of specimens from shallower depths in the Nazaré Canyon (64PE236-07 = 1160m; 64PE236-13 = 927m); scale bars = 100μm except where indicated otherwise.

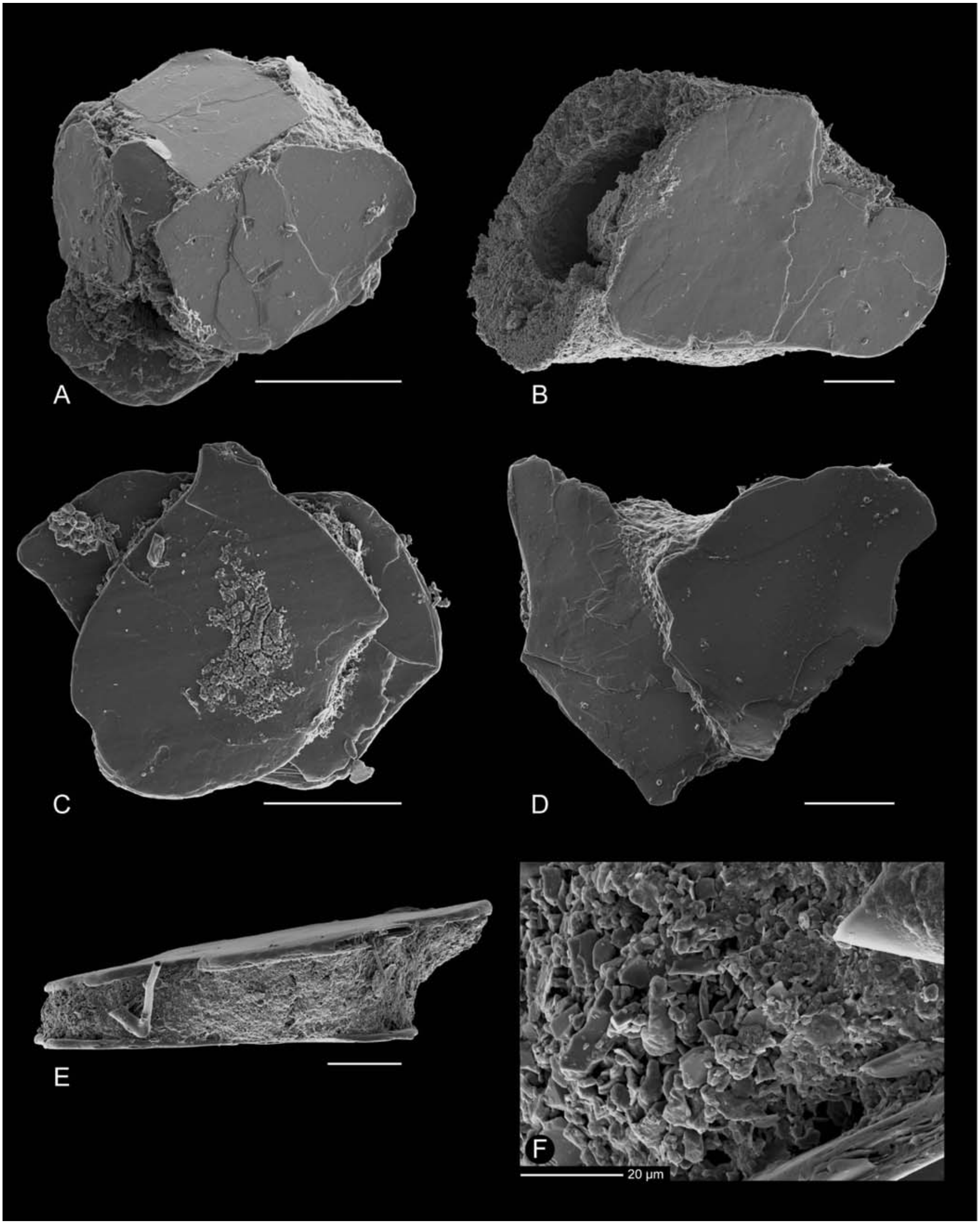
A Specimen with a multifaceted test; station 64PE236-13 (0.0-0.5cm depth in sediment)

B Specimen displaying the ‘mortar’ wall and the interior of the test; station 64PE236-07 (0.0-0.5cm depth in sediment).

C General view; station 64PE236-13 (0.0-0.5cm depth in sediment)

D General view; station 64PE236-07 (0.5-1.0cm depth in sediment)

E-F Edge view and a detail of ‘mortar’; station 64PE236-13 (0.0-0.5cm depth in sediment).


A
B
C
D
E
F
20 µm

This page intentionally blank.