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Xenophyophores (Rhizaria, Foraminifera), including four new species and two new genera, from the western Clarion-Clipperton Zone (abyssal equatorial Pacific)

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Abstract

The Clarion-Clipperton Zone (CCZ) occupies a vast swathe of the Pacific with extensive polymetallic nodule deposits. Eastern and central parts host diverse assemblages of xenophyophores (megafaunal agglutinated foraminifera). Here we describe xenophyophores obtained using a Remotely Operated Vehicle from the western CCZ. Eleven distinct forms include two known species, *Stannophyllum zonarium* Haeckel, 1888 and *Aschemonella monile* Gooday and Holzmann in Gooday et al., 2017b. Another four are described as new species based on morphological and genetic data. In *Abyssalia foliformis* gen. nov., sp. nov. and *Abyssalia sphaerica* sp. nov. the flattened or spherical test comprises a homogeneous framework of sponge spicules. *Psammina tenuis* sp. nov. has a delicate, thin, plate-like test. *Moanammina semicircularis* gen. nov., sp. nov. has a stalked, fan-shaped test and is genetically identical to '*Galatheammina* sp. 6' of Gooday and co-workers from the eastern CCZ. Sequence data revealed a spherical 'mudball', which disintegrated and cannot be formally described, to be a novel xenophyophore. Finally, four morphospecies are represented by dead tests: *Psammina* spp., *Reticulammina* sp., and an unknown genus with a unique test structure. This collection enhances our knowledge of Pacific xenophyophore diversity and provides the first genetic confirmation of wide geographic ranges for abyssal species.

Keywords: Areas of Particular Environmental Interest; Biogeography; Foraminifera; Megafauna; Polymetallic nodules; Seabed mining

Introduction

The first xenophyophores were described, either as foraminifera (Brady 1883; Goës 1892) or sponges (Haeckel 1889), towards the end of the 19th century. Schulze (1907,

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1912) described further species and introduced the name 'Xenophyophora', regarding them as a distinct group (order) of large agglutinated rhizopod protists. However, despite this promising start, xenophyophores were largely forgotten until Ole Tendal's 1972 monograph (Tendal 1972) rescued them from neglect. Since then, appreciation of their importance in deep-sea benthic communities has steadily grown and they are now recognised as a ubiquitous and sometimes dominant component of deep-sea benthic communities (Gooday et al. 2011; Levin and Thomas 1988; Tendal 1996). At the same time, genetic studies have confirmed Brady's and Goës' interpretation of xenophyophores as agglutinated foraminifera within the radiation of monothalamous (single-chambered) taxa (Gooday et al. 2017a; Pawlowski et al. 2003).

The works of Haeckel (1889), Goës (1892) and Schulze (1907) showed that xenophyophores were diverse in the abyssal equatorial Pacific; indeed, early studies described more species from here than from any other part of the deep ocean (Plate VIII in Schulze 1907). In recent years, this area, and specifically the Clarion-Clipperton Zone (CCZ), has acquired considerable potential economic importance because it hosts rich deposits of polymetallic nodules (Petersen et al. 2016). Exploitation of these valuable resources is regulated by the International Seabed Authority (ISA), a body set up under the United Nations Law of the Sea Convention. The ISA issues exploration contracts covering ~75,000 km^2 of seafloor to contractors with interests in seabed mining, on condition that contractors conduct baseline studies of benthic biota within their contract areas. This requirement has resulted in the CCZ becoming the focus of a substantial research effort by a number of different countries and organisations. In addition to the contract areas, the ISA recognises a system of Areas of Particular Environmental Interest (APEIs), areas ~100,000 km^2 in extent that are currently protected from mining (Lodge et al. 2014).

Video surveys conducted as part of this ongoing effort have revealed that xenophyophores are a dominant component of the abyssal plain megafauna within the CCZ (Amon et al. 2016; Kamenskaya et al. 2013; Simon-Lledó et al., 2019). At the same time, morphological and genetic analyses of collected specimens have led to the description of new species and genera (Gooday et al. 2017b, 2017c, 2018; Kamenskaya 2005; Kamenskaya et al. 2015, 2017). However, these studies have been concentrated in the central and eastern parts of the CCZ, mainly the Russian, UK-1 and Ocean Mineral Singapore (OMS) contract areas and APEI-6 (Fig. 1 in Gooday et al. 2017a). Much less is known about xenophyophores from the western CCZ. The only previous records are those of Veillette et al. (2007) who list two types ('Xenophyophorea-like, no agglutinated particles' and 'Xenophyophorea-like, fan-shaped agglutinated') attached to nodules in the western French contract area (09°N, 150°W). The small collection described here was obtained in the three westernmost APEIs (numbers 1, 4 and 7) as part of the DeepCCZ project, which aims to study biodiversity on seamounts and abyssal plains in these areas as well as to explore biodiversity and connectivity across the CCZ. Specimens were obtained using a Remote Operated Vehicle (ROV), which photographed them in their life positions prior to collection. We have two main goals: 1) to describe new and known xenophyophore species based on molecular and genetic data; and 2) to compare these species with those recorded from the central and eastern CCZ.

Material and Methods

Sample collection and shipboard processing

Samples were collected opportunistically during cruise 1808 of the R/V Kilo Moana (14 May to 16 June 2018) on the abyssal plains of APEI-1, APEI-4 and APEI-7 in the western CCZ (Table 1, Fig. 1). All sampling was undertaken by the ROV Lu'ukai. Xenophyophores were first photographed in situ before being recovered, either in a pushcore or by being gently scooped up with the manipulator arm of the ROV and deposited in the biobox.

Samples were removed as soon as possible to the shipboard laboratory following the recovery of the ROV. In the case of xenophyophores collected in pushcores, the top water in the core was discarded and the specimens photographed in air with a Nikon Coolpix S8100 digital camera prior to being removed from the core. All specimens collected in pushcores or the biobox were also photographed in a Petri dish with a Canon EOS 600D (35 and/or 100 mm macro lens). Finally, the xenophyophores were preserved in RNAlater in a suitable wide-mouthed jar and stored in a −20 °C freezer. Following the cruise, the frozen samples in RNAlater were air freighted with freezer packs to the Geneva laboratory (Department of Genetics and Evolution, University of Geneva) for genetic and morphological analyses.

Macro- and micro-photography

In Geneva, key specimens were transferred from RNAlater into LifeGuard (in order to avoid the crystals that form in RNAlater) and photographed using a tripod-mounted Sony ILCA-99 M2 digital camera fitted with a 35 mm lens and processed using Photoshop C6. Other photographs were taken using a Leica M205C motorised stereomicroscope equipped with a Leica DFC 450C camera and an Olympus SZX7 microscope equipped with a Canon 60D SRL digital camera.

DNA extraction, PCR amplification and sequencing

Upon arrival in the laboratory, specimens preserved in RNAlater® solution (Qiagen) were frozen at −20 °C until they could be examined. Care was taken to preserve the specimens as intact as possible and only fragments were dissected in order to obtain pieces of cytoplasm for analysis. DNA was extracted using the

Table 1. Sampling data and species occurrences. All samples were collected by the Remote Operated Vehicle Lu'ukai. The new taxa described here are indicated in bold (*M.* = *Moanammina*).

Date	Area	Event	Dive	Sampling method	Specimen number	Latitude	Longitude	Depth (m)	Species	Specimens
25-May-18	APEI-7	KM1808-25	LK-086	Core 4	034	5.1149	−141.8968	4855.4	*Psammina* sp. B	1 dead
28-May-18	APEI-7	KM1808-36	LK-089	Core 9	079	5.0599	−141.8310	4868.8	*Stann. zonarium*	1 ?dead
28-May-18	APEI-7	KM1808-36	LK-089	Core 16	080	5.0443	−141.8162	4874.2	*Reticulammina* sp.	1 dead
01-Jun-18	APEI-4	KM1808-43	LK-090	Core 12	No number	7.0214	−149.9356	5040.1	*Asch. monile*	3 live frags
01-Jun-18	APEI-4	KM1808-43	LK-090	Core 12	084	7.0214	−149.9356	5040.1	Indeterminate	Dead frags
01-Jun-18	APEI-4	KM1808-43	LK-090	Core 1	085	7.0360	−149.9395	5040.3	Xeno mudball.	1 live
02-Jun-18	APEI-4	KM1808-47	LK-091	Biobox	090	6.9879	−149.9124	4999.7	***M. semicircularis***	1 live
02-Jun-18	APEI-4	KM1808-47	LK-091	Biobox	091	7.0091	−149.9113	5018.4	*Asch. monile*	1 dead frag.
02-Jun-18	APEI-4	KM1808-47	LK-091	Core 11	095	6.9879	−149.9125	4999.5	***Abyssalia sphaerica***	1 live
06-Jun-18	APEI-4	KM1808-61	LK-094	Core 11	171	6.9703	−149.9426	5008.6	*Asch.* aff. *monile*	Dead frags
09-Jun-18	APEI-1	KM1808-66	LK-095	Biobox	184	11.2751	−153.7444	5241	***Psammina tenuis***	Live frags
09-Jun-18	APEI-1	KM1808-66	LK-095	Core 6	192	11.2750	−153.7442	5240.7	***Abyssalia foliformis***	1 live
10-Jun-18	APEI-1	KM1808-70	LK-096	Core 4	207	11.2518	−153.6053	5204.9	*Psammina* sp. C	1 dead

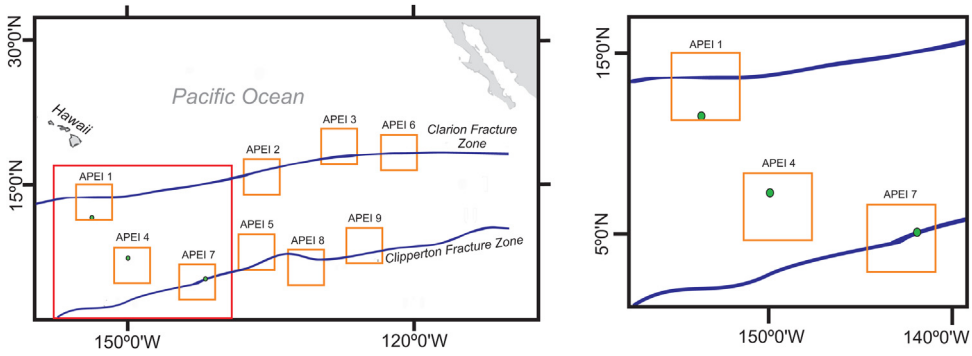

Fig. 1. Location of APEIs 1–9 within the Clarion-Clipperton Zone and detail showing APEIs 1, 4 and 7 with sampling sites represented by green dots. The blue lines indicate the Clarion and the Clipperton Fracture Zones.

DNeasy® Plant Mini Kit (Qiagen). DNA isolate numbers and collection sites are provided in Supplementary Table S1. Semi-nested PCR amplification was carried out with the foraminiferal SSU-specific forward primer s14F3 (5′-ACGCAMGTGTGAAACTTG) at the first amplification step, s14F1 (5′-AAGGGCACCACAAGAACGC) for the reamplification, and the 20r eukaryotic SSU reverse primer (5′GACGGGCGGTGTGTACAA) for both amplification steps.

The amplified PCR products were purified using the High Pure PCR Cleanup Micro Kit (Roche Diagnostics). Sequencing reactions were performed using the BigDye Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems) and analysed in a 3130XL Genetic Analyzer (Applied Biosystems). The sequences obtained were deposited in the EMBL/GenBank database (accession numbers MK748292-MK748302, MK74882-MK74889; Supplementary Table S1).

Phylogenetic analyses

The new sequences were added to an existing database using the Muscle automatic alignment option as implemented in SeaView vs. 4.3.3 (Gouy et al. 2010). The alignment contained 90 sequences with 1564 sites, of which 978 were used for the analyses. Nucleotide frequencies are 0.27 (A), 0.14 (C), 0.18 (G) and 0.41 (T).

A phylogenetic tree was constructed using PhyML 3.0 with automatic model selection by SMS as implemented in ATGC:PhyML (Guindon et al. 2010). The AIC (Akaike Information Criterion) was chosen as selection criterion. A GTR substitution model was selected for the analysis. The initial tree is based on BioNJ. Bootstrap values (BV) are based on 100 replicates.

Terminology and classification

The following special terms are used in morphological descriptions of xenophyophores (Tendal 1972). (1) 'Granellare': the cytoplasm and the organic tube that encloses it. (2) 'Linellae': organic (proteinaceous) threads that ramify the test in species of the genera *Stannoma* and *Stannophyllum*. (3) 'Stercomata': waste pellets, composed largely of clay minerals. (4) 'Stercomare': masses of stercomata enclosed within an organic sheath and retained within the test. (5) 'Xenophyae': the agglutinated particles from which the test is constructed.

The higher-level classification follows Adl et al. (2019). The monothalamids are regarded as a paraphyletic group that occupies a basal position within the Phylum Foraminifera (Pawlowski et al. 2013). The type material is deposited in the Natural History Museum, London.

Results

Rhizaria Cavalier-Smith, 2002
Retaria Cavalier-Smith, 1999
Foraminifera D'Orbigny, 1826
Monothalamea Pawlowski, Holzmann and Tyszka, 2013
Xenophyophoroidea Tendal, 1972
Aschemonella Brady, 1879
Aschemonella monile Gooday and Holzmann in Gooday et al., 2017b (Figs. 2A–E, 3A–F; Supplementary Fig. S1A)

2017 ***Aschemonella monile*** Gooday and Holzmann sp. nov. – Gooday et al., Zool. J. Linn. Soc. 182, 483–492, Figs. 1–8.

Material. DNA sequences and morphology. Three fragments from the same jar as specimen 084 (described below as 'Indeterminate xenophyophore'), collected on 01 June 2018 in APEI-4 during ROV dive LK-090 (core 12), event ID KM1808-43; latitude 7.02137482, longitude −149.9356419, water depth 5040 m.

Morphology only. Specimen 091, one dead fragment collected on 02 June 2018 in APEI-4 during ROV dive LK-091 (BIOBOX), event ID KM1808-47; latitude 7.00915135, longitude −149.91128, water depth 5018 m. The fragment is currently located in the first author's collection at the National Oceanography Centre, Southampton.

Test morphology. The two most complete fragments have different morphologies. One comprises three elongate seg-

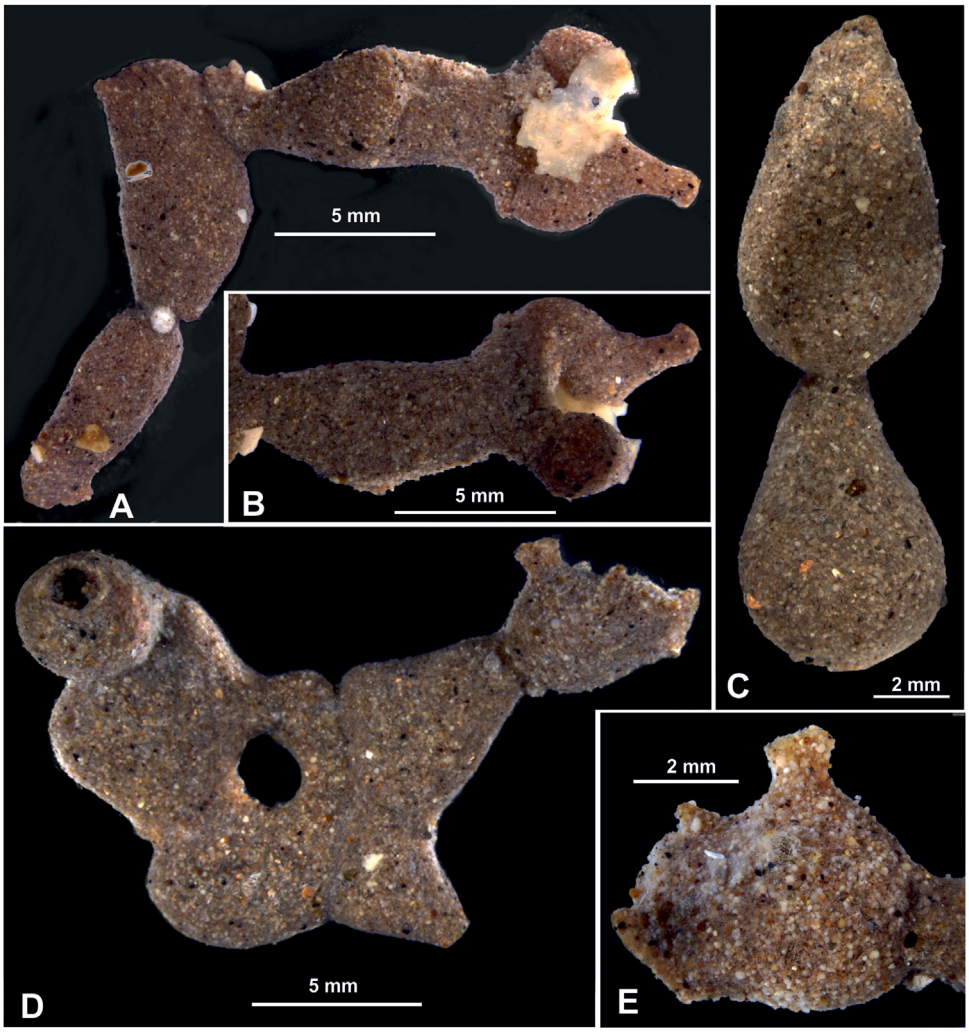

Fig. 2. (A–E) *Aschemonella monile.* Fragments found in jar with specimen 084 (Fig. 17), APEI-4, external features of test. (A) Complete fragment prior to being broken open to extract granellare for sequencing. (B) Opposite side of terminal segment. (C) Fragment with two segments. (D) Atypical fragment organised around an open space. Granellare was extracted from one of the segments of this specimen for sequencing. (E) Opposite side final segment with short tubular processes.

ments. The first two segment are approximately cylindrical and measure 7.3 × 3.0 mm and 8.2 × 4.3 mm (Fig. 2A, B), the third is 15.1 mm long, angled at ~90° with respect to the second segment, and increases in width from about 2 to 3.8 mm to form a cylinder expanding into a bulbous feature with a terminal neck and a lateral branch. The second fragment measures about 20 × 12 mm in overall size (Fig. 2D, E). It comprises four or five poorly defined chambers merged together around a central space. What is probably a terminal chamber with several short tubular-conical projections is developed on one side. A third fragment comprises two droplet-shaped chambers (Fig. 2C). A dead fragment (specimen 091) incorporating several somewhat inflated segments with a short lateral chamber, probably also belongs to *A. monile* (Supplementary Fig. S1A).

Test structure and internal features. The wall is reddish-brown and composed of radiolarians and mineral grains set in a fine-grained matrix. There are no internal xenophyae and the interior contains only granellare and stercomare. The granellare strands branch but do not appear to anastomose (Fig. 3D). The width varies considerably; some sections are more or less cylindrical but elsewhere narrow threads (<100 μm wide) swell to 300 μm or more in width. In one of the two fragments that were broken open, these wider sections give rise to narrower branches and pointed processes that extend into delicate threads (Fig. 3B, C). The stercomare form compact masses, ranging from about 100 μm to >300 μm in size, generally fairly equidimensional but sometimes more elongated (Fig. 3E, F). These masses are enclosed and linked together by a cobweb-like system of delicate organic membranes, so that, with care, fairly large clumps can be extracted intact from the test.

Remarks. This small collection of fragments displays a range of test morphologies. In particular, the segments vary from subcylindrical to droplet-shaped (Fig. 2A–C), or merge to form a circuit around a central space (Fig. 2D). None of

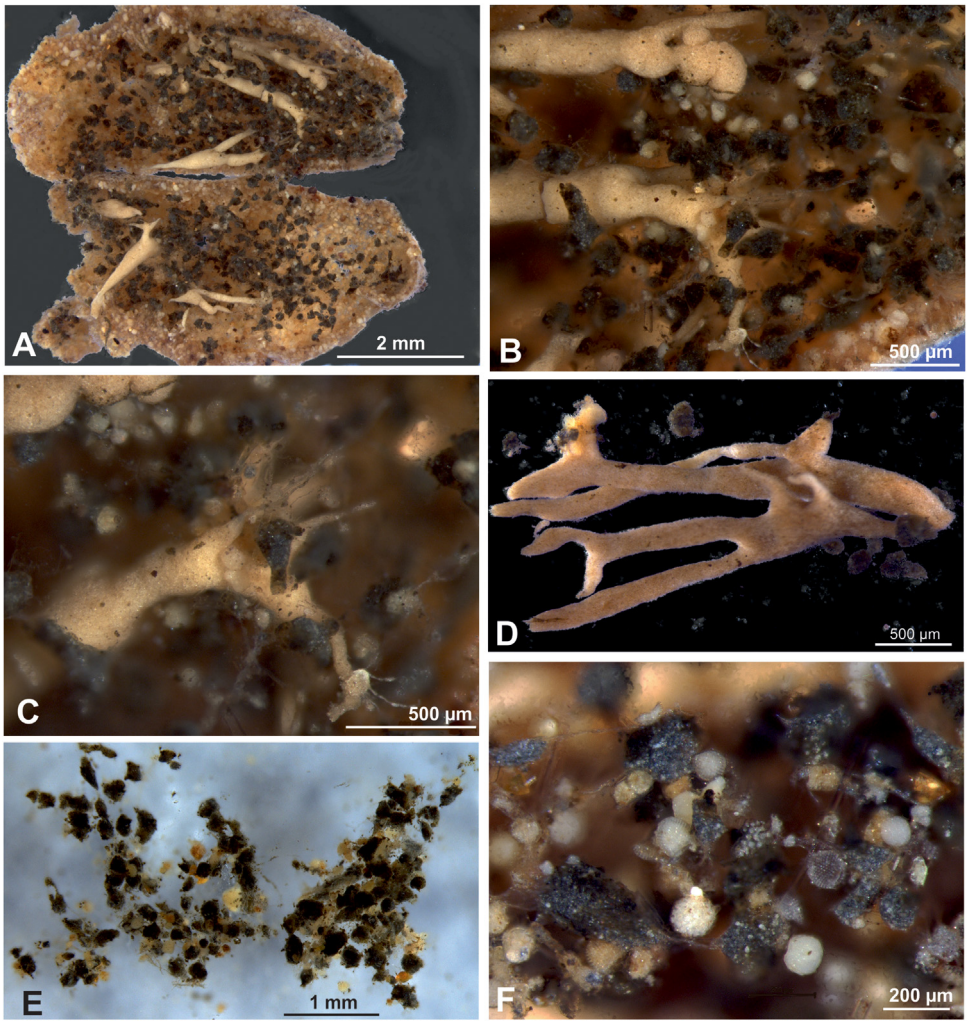

Fig. 3. (A–F) *Aschemonella monile.* Fragments found in jar with specimen 084 (Fig. 17), APEI-4, internal features of the specimen illustrated in Fig. 2A, B. (A) Overview of interior of segment showing granellare and stercomare. (B, C) Details of granellare strands in situ, showing relatively thick branches amongst stercomare masses, extending out into fine threads of cytoplasm. (D) Branched granellare removed from test; the ends of several branches broke during the removal. (E) Globular stercomare masses linked by narrow necks removed from test. (F) Stercomare in situ.

these fragments resemble typical specimens of *Aschemonella monile* from the eastern CCZ (UK-1 and OMS areas), which generally consist of globular segments (Gooday et al. 2017b). The closest correspondence is between the fragment with elongate subcylindrical segments (Fig. 2A) and the delicate form of *A. monile* from the UK-1 area (Fig. 8 in Gooday et al. 2017b). The clusters of tiny pustule-like apertural structures that are a feature of some of the eastern-CCZ specimens are also absent. Instead, likely test apertures are located at the ends of short tubular features (Fig. 2E).

We obtained genetic data (Fig. 4) from two fragments (Fig. 2A, B, D, E). Despite the difference in the morphology and arrangement of the segments in these fragments, they yielded identical DNA sequences. Possibly they are fragments of the same specimen. In any case, the sequence data confirm that they are conspecific with *Aschemonella monile* from the UK-1 and OMS sites.

The organic tube enclosing the cytoplasm is not as obvious in species of *Aschemonella,* including *A. monile* (Gooday and Nott 1982; Gooday et al. 2017b), as it is in some other xenophyophores. Instead, the cytoplasm gives the impression of being naked. However, other studies provide some evidence for a tube. A thin section of the granellare of *A. ramuliformis* Brady, 1884 shows the cytoplasm bounded by an organic wall (Fig. 5 in Hopwood et al. 1997). A scanning electron micrograph of the granellare surface in *A. monile* appears to show a very thin organic sheet covering the cell surface and partly obscuring the underlying barite crystals (Fig. 7D in Gooday et al. 2017b). Whether these delicate structures are equivalent to the fairly robust organic tube present in, for example, *Syringammina* Brady, 1883 (Figs. 6 and 8 in Lewis 1966) and the *Abyssalia* species described below, is an open question that deserves investigation.

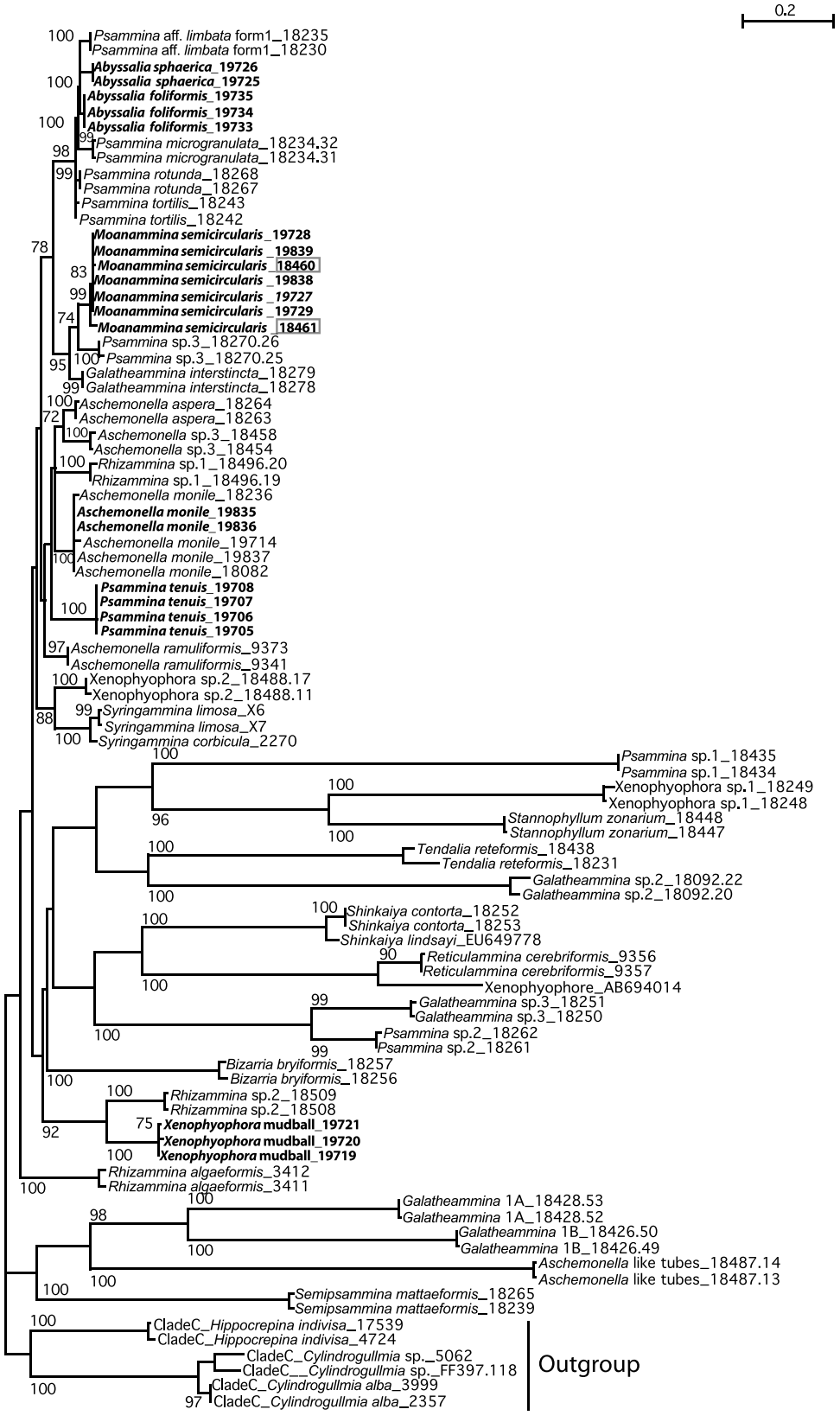

Fig. 4. PhyML phylogenetic tree showing evolutionary relationships of 37 xenophyophore taxa, together with an outgroup represented by six specimens of monothalamid clade C. The numbers are DNA isolate numbers; see Supplementary Table S1 for corresponding GenBank accession numbers. Newly acquired sequences are shown in bold. The two isolate numbers corresponding to the single *Moanammina semicircularis* specimen from the eastern CCZ (OMS area) are boxed. Numbers at nodes indicate bootstrap values (BV's) > 70%.

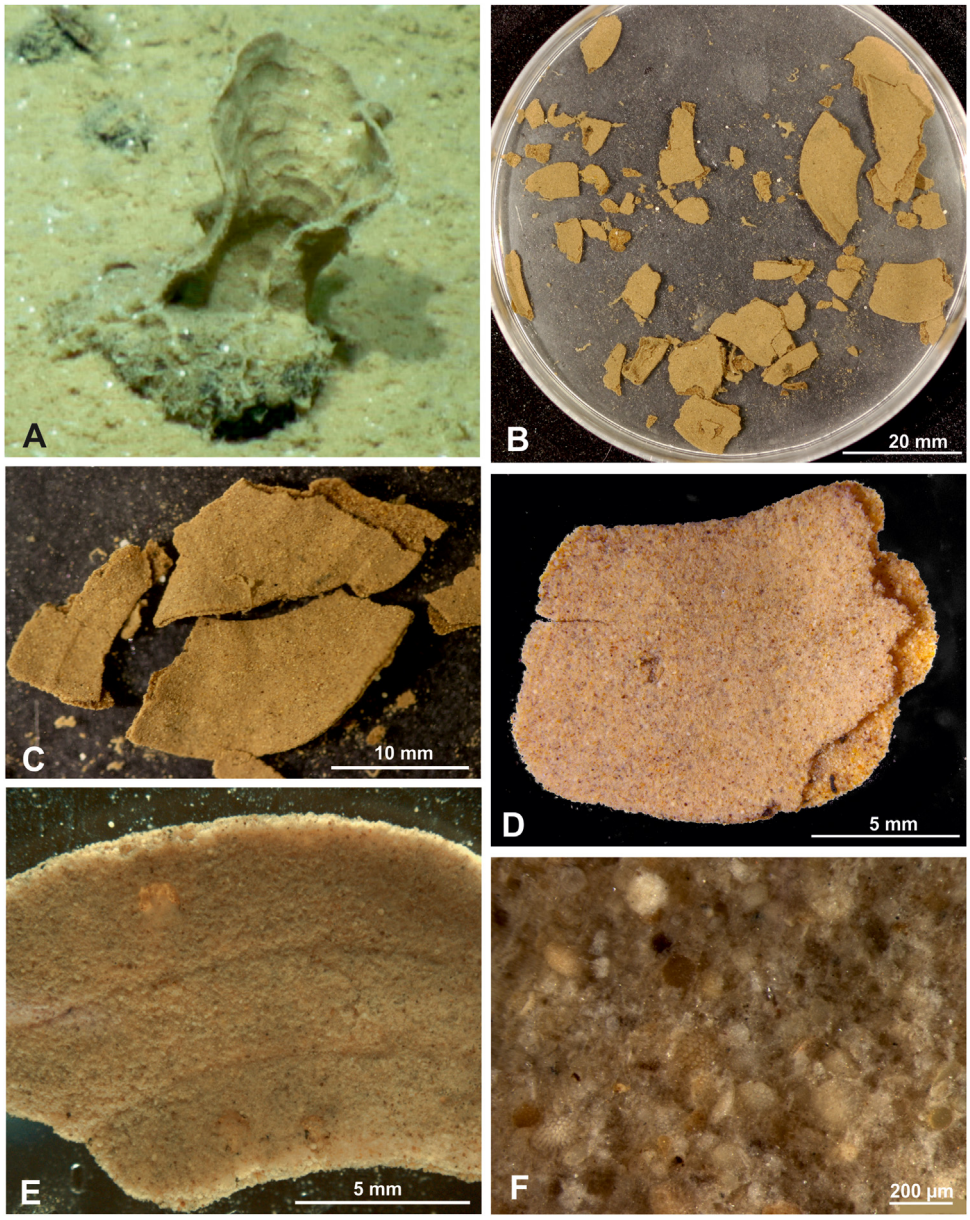

Fig. 5. (A–F) *Psammina tenuis* sp. nov., holotype (NHMUK PM ZF 9914); specimen 184, APEI-1, external features. (A) Specimen on seafloor prior to collection. (B, C) Fragments photographed at sea immediately after collection. (D–F) Laboratory photographs. (D) Fragment; the curved upper and lower edges are fractures developed along 'growth lines'. (E) Fragment with growth lines; the upper curved edge is the original margin, somewhat abraided; the lower curved edge is a fracture developed along a growth line. (F) Detail of test wall showing radiolarians (xenophyae) set in a fine-grained matrix.

Aschemonella* aff. *monile Gooday and Holzmann in Gooday et al., 2017b (Supplementary Fig. S1B–E)

Material. Morphology only. Specimen 171, three dead fragments collected on 06 June 2018 in APEI-4 during ROV dive LK-094 (core 11), event ID KM1808-61; latitude 6.97029592, longitude −49.94264, water depth 5009 m.

Remarks. Three fragments from another sample obtained in APEI-4 have a more complex morphology than those assigned to *A. monile*. They range from 9 to 12 mm in length and comprise irregularly arranged chambers with larger chambers overgrown by smaller ones.

Psammina Haeckel, 1889

Psammina tenuis Gooday and Holzmann sp. nov. (Figs. 5A–F, 6A–G)

Diagnosis. *Psammina* with very thin (0.6–0.8 mm), curved, plate-like test that directly adjoins substrate with no intervening stalk. No clearly defined internal pillars or partitions. Marginal apertures apparently absent. Xenophyae comprise small radiolarian shells in fine-grained matrix. Granellare branches narrow (10–30 µm) and attached to inner surface of wall.

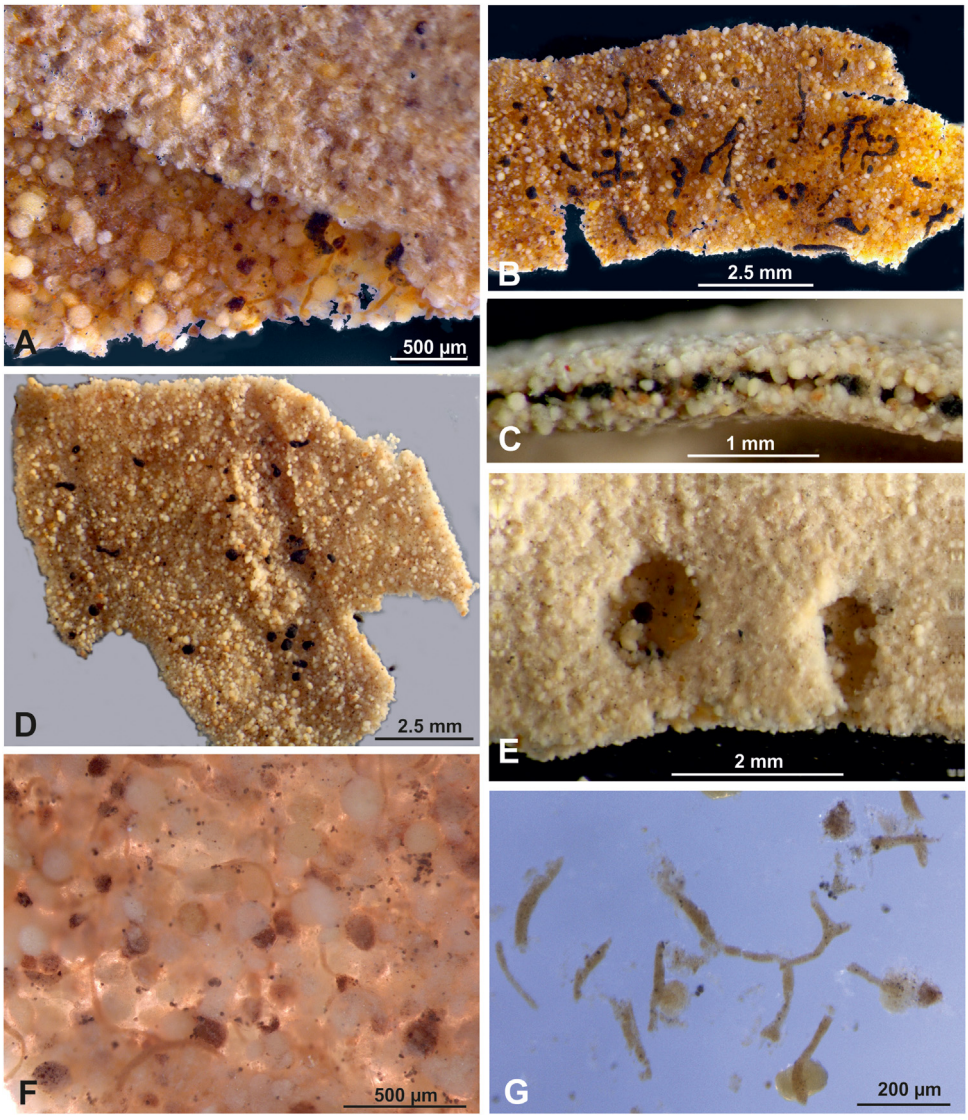

Fig. 6. (A–G) *Psammina tenuis* sp. nov., holotype (NHMUK PM ZF 9914); specimen 184, APEI-1, fragments. (A) Broken edge of test with part of upper wall missing to show inner surface of opposite wall; a few granellare strands are also visible. (B) Inner surface of wall showing stercomare masses attached to the wall. (C) Outer margin of test with dark stercomare visible inside; the margin is probably abraided. (D) Inner surface of wall showing protruding xenophyae (radiolarians) and vague ridges corresponding to 'growth lines' on the exterior. (E) Two holes through one of the test plates, probably caused by predators; the right-hand hole may have become more elongated through damage. (F) Inner surface of wall showing attached strands of granellare weaving between the protruding radiolarians. (G) Fragments of granellare removed from wall.

Zoobank registration. LSID urn:lsid:zoobank.org:pub:98813A22-AA81-4FD9-94FA-3BC3E81819D3.

Etymology. Latin *tenuis* meaning thin, referring to the thin, delicate test.

Type material. Holotype (DNA sequences and morphology): reg. no. NHMUK PM ZF 9914. Specimen 184, fragment collected on 09 June 2018 in APEI-1during ROV dive LK-095 (BIOBOX), event ID KM1808-66; latitude 11.27509352, longitude −153.74441, water depth 5241 m.

Test morphology. In situ images show a plate-like test, approximately 6.5 cm high and about 5 cm wide (not considering the curvature), attached directly to a nodule without any intervening stalk (Fig. 5A). It was strongly curved around a vertical axis, particularly in the lower part. Concentric 'growth lines' were distinctly visible on the surface. The recovered fragments are fragile, pale creamy yellow, up to 21 mm in maximum dimension (Fig. 5B–D) and only 0.6–0.8 mm thick (Fig. 6C). They comprise two walls ('plates') separated by a narrow space. The original outer margin is preserved in some fragments but always appears abraded, so that whether it continues uninterrupted around the rim is not clear. However, it appears uninterrupted in seafloor photographs, with no clear sign of marginal apertures. The curved growth lines visible in the seafloor photograph are

evident on some fragments (Fig. 5E). They are spaced 2.8–4.8 mm apart, and represent lines of weakness along which the fragments tend to break. In several fragments, one of the test plates is penetrated by circular holes (up to 1.2 mm diameter), most likely the work of predators.

Test structure and internal features. The wall is thin (~240–300 μm), pale cream in colour and relatively smooth overall but bumpy on a sub-millimetre scale. The main constituents are small radiolarian shells set in a fine-grained matrix (Figs. 5F, 6A, F). The interior contains some internal xenophyae (radiolarians), either loose or projecting into the space (Fig. 6F). Vague ridges corresponding to external growth lines are sometimes visible (Fig. 6D), but there is no evidence of clearly developed pillars or partitions. The granellare strands are brownish, very narrow (10–30 μm, typically 15–20 μm), and branch but do not appear to anastomose (Fig. 6G). They are attached to the inner surface of the test wall, generally weaving between rather than across the projecting surfaces of radiolarian shells (Fig. 6F). The stercomare is attached loosely to the inner wall surface and forms strings and apparently isolated rounded masses (Fig. 6B). The strings branch occasionally and vary in width along their length, sometimes with wider (130–240 μm) segments or sections separated by narrower necks. The rounded masses are typically between 175 and 320 μm in maximum dimension.

Remarks. *Psammina tenuis* lacks certain features that are considered typical of the genus, notably clearly defined internal pillars or partitions and marginal apertures (Tendal 1972). Nevertheless, we feel justified in assigning it to *Psammina* based on the construction of the test from two well-defined, plate-like walls, separated by a space that is not completely filled by internal xenophyae. The type species, *P. nummulina* Haeckel, 1889, is known from three dredge samples collected in the central and eastern Pacific. Haeckel's original material, apparently now lost, was from Challenger Station 274 (7°25′S, 152°15′W, 5033 m depth). As described by Tendal (1972), based on numerous fragments from two closely spaced localities off Costa Rica (3563–3590 m), *P. nummulina* differs from the new species in a number of features. (1) The test is somewhat thicker (0.6–1.4 mm compared to 0.6–0.8 mm). (2) Apertures ('pores') are developed around the margin. (3) The xenophyae comprise radiolarians, sponge spicule fragments, and mineral grains, apparently without much of the fine-grained material present between the xenophyae (radiolarian tests) in the new species. (4) The granellare branches are thicker (30–60 μm, compared to 10–30 μm in *P. tenuis*). In addition, intact specimens of *P. nummulina* were apparently more or less discoidal in shape and up to 15 mm in diameter (Tendal 1972). There is no evidence that they formed larger curved structures, comparable to the undisturbed test of *P. tenuis* photographed on the seafloor.

Gooday and Tendal (1988) described three largely fragmented *Psammina* species from the NE Atlantic. The most similar species, *P. delicata* Gooday and Tendal, 1988, includes some fragments that are bar-shaped or incorporate an open space, suggesting that its shape when intact is different from that of *P. tenuis*. The test of *P. delicata* is even thinner (0.30–0.60 mm) than that of the new species (0.60–0.80 mm) and the granellare branches are often wider (20–200 μm compared to 10–30 μm) and more prominent, sometimes forming sheet-like masses. *Psammina fusca* Gooday and Tendal, 1988 also includes bar-shaped fragments and uses quartz grains rather than biogenic particles in test construction. The test of *Psammina sabulosa* Gooday and Tendal, 1988 is composed of well-sorted quartz grains, has well-defined marginal apertures, and the two test plates (walls) are separated internally by parallel bars.

Plate-like unstalked *Psammina* species, including *P. tenuis*, probably form a distinct group from the stalked species, typified by *P. limbata* Kamenskaya et al., 2015 (Gooday et al. 2018). *Psammina tenuis* is the only member of this group for which DNA sequences are available. The phylogenetic tree (Fig. 4) suggests that it is not closely related to the stalked species.

Undescribed *Psammina* species

We designate two species as 'B' and 'C' in order to avoid confusion with *Psammina* sp. A of Gooday (1996; see also Table 1 in Gooday et al. 2018). Because the specimens were dead and DNA sequences could not be obtained from them, we leave them undescribed.

***Psammina* sp. B** (Supplementary Fig. S2A–H)

Material. Test morphology only. Specimen 034, fragments of specimen collected on 25 May 2018 in APEI-7 during ROV dive LK-086 (core 4), event ID KM1808-25; latitude 5.11487947, longitude −141.89678, water depth 4885 m. The fragments are currently located in the first author's collection at the National Oceanography Centre, Southampton.

Description. In situ photographs show an oblique lateral view of the test, with a fan-shaped upper part at the end of a relatively long vertical stalk that appears to widen near the base (Fig. S2A). The total height above the sediment surface is about 8 cm. The base of the stalk is buried in the sediment with no obvious attachment to a nodule. Although not evident because of the angle of the photograph, recovered fragments suggest that the lower part of the stalk exposed above the sediment was branched. Some areas of the fan have what appear to be dark contents (presumably decayed stercomare), whereas other parts are translucent and appear empty. The fan displays traces of a concentric structure, shown most clearly as a thin dark band running inside and parallel to part of the outer margin. This feature probably corresponds to accumulations of decayed stercomata, perhaps retained within a compartment of the test.

Except for the broken stalk, the specimen was more or less intact when recovered (Fig. S2B). The fan measured about 63 mm wide and about 38 mm high but was only about 2 mm thick. The slightly damaged lateral and upper margins formed a semicircle; curved embayments on either side of its junction with the stalk, created an 'M-shaped' lower margin with downward pointing lobes at either end. The surface of the fan displayed four or five concentric zones (Fig. S2C). The stalk

itself narrowed unevenly from a width of 9–10 mm near the junction with the fan to 2.5–3.5 mm, before breaking into a brush-like mass of fine branches, which probably formed a root-like structure that anchored the test in the sediment.

Only fragments of the test remained following transport. Thin, delicate meshes of sponge spicules with a scattering of radiolarians form plate-like sheets that are evidently part of the fan wall (Fig. S2D). One fragment, which preserves the two test walls joined together by a short section of the margin (Fig. S2E), is 2.0–2.2 mm thick. The wall itself is very thin (~100 μm) and continues unbroken around the margin. There is no evidence of internal xenophyae. Fragments of the stalk reveal a complex, multi-walled structure. A large piece (width 5.3–6.0 mm) incorporates several (2–3) internal layers and gives rise to a side branch comprising two conjoined tubes (Fig. S2F). Other fragments are narrower, the larger pieces 1.7–3.1 mm and the narrower ones 0.24–0.96 mm wide. Many are flattened and incorporate conjoined or nested tubular elements, sometimes branching away from the main section (Fig. S2F, G). These complex stalk fragments are constructed from longitudinally arranged spicules (Fig. S2H) and also generally include a larger proportion of radiolarians than the plate-like fan fragments. In places, they contain the decayed remains of stercomare strands running parallel to the long axis.

Remarks. This dead specimen is clearly a stalked *Psammina*, resembling *P. limbata* and similar species from the Russian, UK-1 and OMS contract areas in the central and eastern part of the CCZ (Gooday et al. 2018; Kamenskaya et al. 2015). It is most similar to *Psammina* aff. *limbata* form 2 illustrated by Gooday et al. (2018, Fig. 6 therein). However, the shape of the test, particularly the long stalk with a complex structure, and the much higher proportion of spicules from which the test is constructed, distinguishes this specimen from similar species.

***Psammina* sp. C** (Supplementary Fig. S3A–F)

Material. Test morphology only. Specimen 207, fragments of dead specimen collected on 10 June 2018 in APEI-1 during ROV dive LK-096 (core 4), event ID KM1808-70; latitude 11.2518202, longitude −153.6053, water depth 5205 m. The fragments are currently located in the first author's collection at the National Oceanography Centre, Southampton.

Description. In situ photographs show a plate-like test, roughly fan-shaped and attached to a nodule (Fig. S3A). The dark surface of the test is bordered by a very pale translucent margin and the rim is marked by a series of irregular, angular notches, possibly resulting from damage. The specimen suffered some further damage during recovery and shipboard photographs show that one side had been lost during coring (Fig. S3B, C). The remaining part of the test was 56 mm high and 53 mm wide; comparison with the in situ photograph suggests that the width (estimated at ~60 mm) exceeded the height when intact. It formed a flat, dark-brown plate, tapering rapidly into a very short stalk, ~10.5 mm wide at the base, by which it was attached to the nodule.

Only a few dead test fragments remained following transport (Fig. S3D–F). They comprise a fairly dense meshwork of sponge spicules with scattered radiolarians. The interstices of the meshwork are occupied largely by stercomare masses with a reflective sheath. There was no sign of granellare branches.

Remarks. This stalked *Psammina* is similar in shape to *Psammina rotunda* Gooday and Holzmann in Gooday et al., 2018, based on a single specimen from the eastern CCZ. In both cases the test is rounded and attached to the substrate by a short stalk. The main difference is that the test wall comprises a substantial proportion of mineral grains in *P. rotunda* but is composed largely of sponge spicules in *Psammina* sp. C. Whether these two specimens from opposite ends of the CCZ are conspecific is impossible to determine without genetic data.

Reticulammina Tendal, 1972

***Reticulammina* sp.** (Supplementary Figs. S4A–F, S5A–F, S6A–F)

Material. Morphology only. Specimen 080, dead fragments, collected on 28 May 2018 in APEI-7 during ROV dive LK-089 (core 16), event ID KM1808-36; latitude 5.04432241, longitude −141.81617, water depth 4874 m. The fragments are currently located in the first author's collection at the National Oceanography Centre, Southampton.

Description. In situ photographs show an irregularly shaped test partly obscured by possible detrital material (Fig. S4A). The specimen was recovered more or less intact; it measured about 51 mm in diameter and extended about 27 mm above the core surface (Fig. S4B). The reticulated structure emerged more clearly when the test was removed from the core and washed free of adhering material (Fig. S4C). It was brownish, delicate and friable and consisted of fairly broad, rounded, bar-like or flattened branches giving rise to peripheral lobes.

The specimen arrived in Geneva as fragments comprising broad, smoothly rounded, bar-like, flattened and lobate elements, several of which incorporate one or more open spaces (Figs. S4D–F). The xenophyae are mainly radiolarians. They form a rather poorly defined surface layer that is easily abraided and not clearly differentiated from the test interior, which is largely occupied by internal xenophyae (Fig. S5B–D). Parts of the interior are hollowed out in some fragments (Figs. S5E, F), creating voids that are most likely the result of decay rather than being original features. Granellare and stercomare are absent, although greyish material derived from decayed stercomare fill some of the interstices between the internal xenophyae. Parts of the test surface are covered by a yellowish organic film (Figs. S5A, E, F and S6A–C) that can be peeled off in sheet-like fragments (Fig. S6D, E). Thicker, often roughly parallel, poorly defined strands within the film often create a kind of reticulated grain (Fig. S6C). This surface film merges into an organic matrix that permeates the test interior.

Remarks. This single, dead *Reticulammina* specimen resembles xenophyophores from the abyssal NE Atlantic,

assigned to *R. labyrinthica* Tendal, 1972 by Gooday and Tendal (1988) and Gooday (1991, 1996). The most obvious difference is the nature of the xenophyae; radiolarians in the Pacific specimen and planktonic foraminifera in Atlantic specimens. The test shape is also less regular, there is no sign of downwardly projecting bar-like 'roots', and the surface layer of the test is more friable and less well defined. The only other *Reticulammina* species with rounded branches is *R. antarctica* Riemann, Tendal, Gingele, 1993 from 1449 m in the Weddell Sea. This uses sand grains as xenophyae and has a hard, brittle test with a well-defined surface layer (Riemann et al. 1993). Other described species of this genus (*R. lamellata* Tendal, 1972; *R. novazealandica* Tendal, 1972; *R. maini* Tendal and Lewis, 1978) have more or less flattened ('lamellate') branches and bathyal distributions (Araya and Gooday 2018; Tendal 1972, 1975; Tendal and Lewis 1978). Several undescribed, reticulated xenophyophores from east Pacific seamounts also have lamellate branches (Levin and Thomas 1988).

The film of organic material that blankets parts of the test surface and penetrates the interior clearly belongs to the xenophyophore. However, attempts to amplify DNA from it were unsuccessful and so it appears to be some kind of organic matrix rather than cellular material. Fragments examined in a compound microscope contained several roughly spherical structures, a few 10s of microns in diameter with short, blind-ending processes (Fig. S5F). The nature of these structures is unclear.

Moanammina Gooday and Holzmann gen. nov.

Diagnosis. Test flattened, fan-shaped and supported on short basal stalk. Composed largely of radiolarians, forming fairly homogeneous structure and without clearly defined surface layer. Granellare strands brownish, branching frequently, and generally 50–100 μm in diameter. Stercomare not arranged in any obvious pattern.

Zoobank registration. LSID urn:lsid:zoobank.org:act:428B45A0-0FD0-4456-ACE1-61523C0BBA3A.

Type species. *Moanammina semicircularis* Gooday and Holzman sp. nov.

Other species assigned. No other species are currently assigned to this genus.

Etymology. From *Moana* (Hawaiian) meaning 'a body of open water, in particular the sea' and also referring to the R/V Kilo Moana, the ship from which the specimen on which this genus is based was collected, combined with ἄμμος (ámmos, Greek) meaning 'sand', referring to the agglutinated test. Gender feminine.

Remarks. In terms of test morphology, *Moanammina* resembles stalked species assigned to the genus *Psammina*; for example, *P. limbata* (Gooday et al. 2018; Kamenskaya et al. 2015). However, it displays very little differentiation between the surface and internal xenophyae, whereas *Psammina* species are clearly distinguished by having a well-defined test wall and relatively sparse internal xenophyae.

The type species of *Homogammina* Gooday and Tendal, 1988 (*H. lamina* Gooday and Tendal, 1988), described from the NE Atlantic, resembles *Moanammina* in having a typically plate-like test that lacks a more strongly agglutinated surface layer, although there is no evidence that it possesses a fan-like morphology (Gooday and Tendal 1988). Another difference is that the stercomare strands follow a subparallel course in *H. lamina* but display no discernable trend in the new genus. In the two other described species of *Homogammina* (*H. maculosa* Gooday and Tendal, 1988 and *H. crassa* Gooday, 1996), the stercomare strands are not arranged in any particular pattern, but unlike *Moanammina*, both have a generally rounded test morphology and, in the case of *H. maculosa*, a distinctive granellare system in which a few main trunks branch dichotomously into numerous progressively narrower branches (Gooday 1996; Gooday and Tendal, 1988). In the absence of genetic data for any *Homogammina* species, the relationship, if any, between this genus and *Moanammina* is unknown.

Moanammina semicircularis Gooday and Holzmann sp. nov. (Figs. 7A–F, 8A–F)

2017 ***Galatheammina* sp. 6** – Gooday et al. Biol. Conserv., 207: Supplementary Fig. S2c.

Diagnosis. As for genus.

Zoobank registration. LSID urn:lsid:zoobank.org:act:02CEDB46-0AAF-43B7-A671-6D1D73E71E3B.

Etymology. The species-group name refers to the semicircular shape of the upper part of the holotype, as seen in seafloor photographs.

Material. Holotype (DNA sequences and morphology): reg. no. NHMUK PM ZF 9912. Specimen 090, collected on 02 June 2018 in APEI-4 during ROV dive LK-091 (BIOBOX), event ID KM1808-47; latitude 6.98791505, longitude −149.91241, water depth 5000 m. About 10 rounded pieces from the original sample jar are abraided fragments of the holotype.

Test morphology. In situ photographs show a large fan-shaped test attached by a relatively thick basal stalk to a largely buried nodule (Fig. 7A). The test is estimated to be about 9 cm wide and about 8 cm high. The open ends of a tubular structure, probably a polychaete tube, are associated with the top of the stalk and are also visible in shipboard photographs. The specimen was recovered more or less intact (Fig. 7B, C). The marginal zone of the fan, as well as the stalk, had a paler, yellowish tinge than the rest of the test surface, which was brownish. This outer part was very thin (<1 mm) but the test thickened considerably towards the centre. Several faint surface ridges are apparent in shipboard photographs.

Abrasion of the test during transit to Geneva removed the thin, more peripheral parts, leaving just the smoothly rounded central core of the fan and much of the stem (Fig. 7D). This remnant is 33 mm long and 25 mm wide; the stem is about 11 mm wide. It thickens from 2.5–3.0 mm along the edge of the upper part (i.e. the inner part of the original fan) to about 8 mm in the central part and the stem. A low ridge runs along

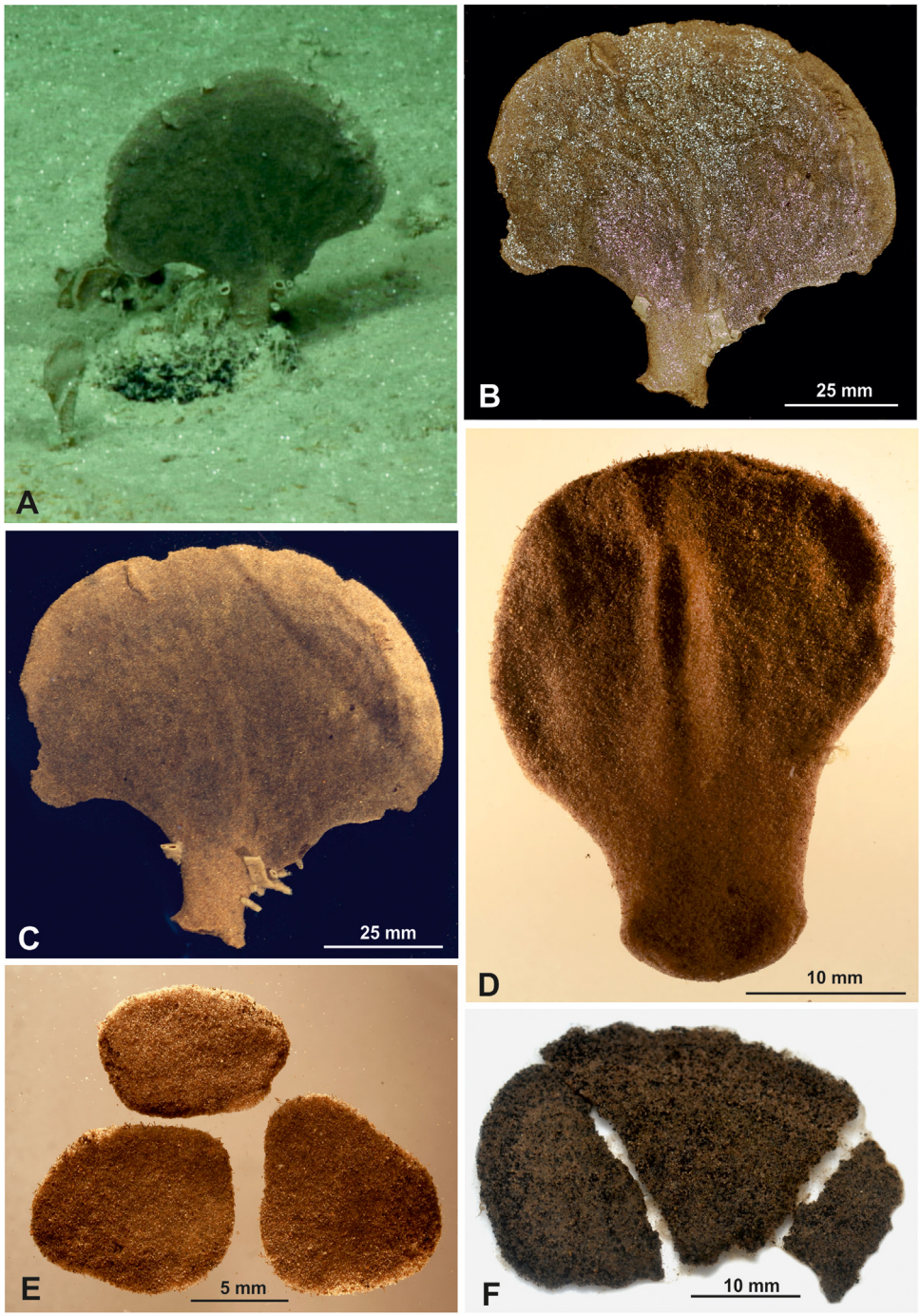

Fig. 7. *Moanammina semicircularis* sp. nov., external features. (A–E) Holotype (NHMUK PM ZF 9912); specimen 090, APEI-4. (A) Specimen on seafloor prior to collection. (B, C) Shipboard photographs of complete test. (B) Damp test photographed in air. (C) Test photographed in water. (D) Main fragment surviving after transport; this represents the abraided core of the fan-shaped test and its basal stalk. (E) Three smaller, rounded fragments. (F) Specimen from ABYSSLINE Cruise AB02, OMS-1 area, Site S07.

part of the axis. The sample jar also contained 10 rounded fragments, 13–18 mm in maximum diameter and 1.7–2.2 mm thick, presumably derived from the more peripheral parts of the test (Fig. 7E).

Test structure and internal features. The test consists largely of radiolarians with subordinate numbers of sponge spicules scattered amongst them; occasional mineral grains are sometimes present (Fig. 8A–C). A poorly defined surface layer is not clearly differentiated from the test interior, which is largely occupied with internal xenophyae (mainly radiolarians), granellare and stercomare. In places, poorly defined voids, containing few xenophyae, create the impression of a vague 'cellular' structure (Fig. 8B, C). The granellare forms branched strands, brownish in colour, that branch frequently

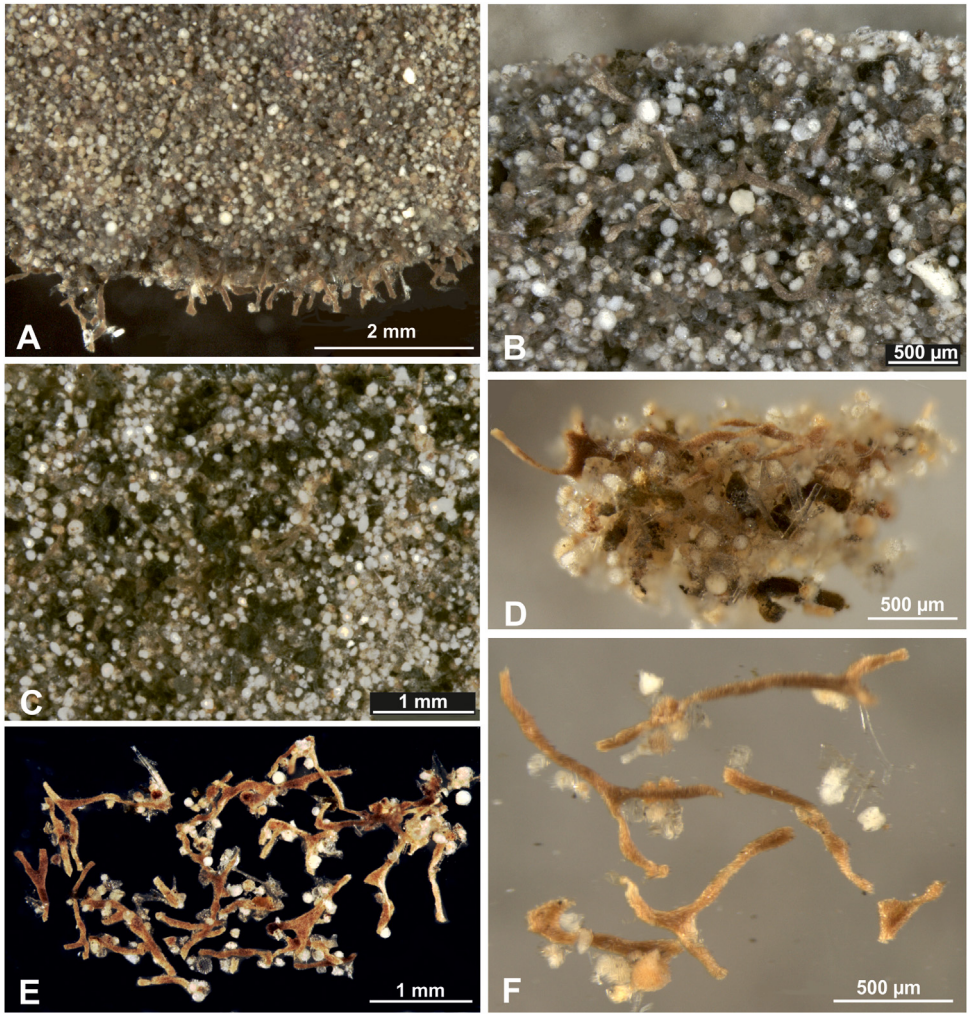

Fig. 8. (A–F) *Moanammina semicircularis* sp. nov., holotype (NHMUK PM ZF 9912); specimen 090, APEI-4, details. (A) Abraided edge of test with protruding granellare strands. (B, C) Abraided surfaces showing vaguely defined cavities and granellare strands. (D) Fragment of test with granellare and stercomare. (E) fragments of granellare with adhering radiolarians. (F) Detail of granellare fragments.

(Fig. 8E, F). They range from 50 to 100 µm diameter, becoming thicker (~140 µm) at branching points. The stercomare forms dark patches on broken surfaces. When the test surface is carefully abraided, the stercomare appears as highly irregularly masses, occasionally isolated or joined together in pairs, but generally forming strings of very variable width and without any obvious trend.

Remarks. The holotype of *Moanammina semicircularis* from APEI-4 is genetically identical to *Galatheammina* sp. 6 (Fig. 4), represented by a single specimen from the OMS area in the eastern CCZ (Fig. 7F). However, the two specimens are morphologically rather different. The test of the holotype consists mainly of radiolarians whereas the *Galatheammina* sp. 6 specimen incorporates a substantial proportion of micronodules. The holotype, or at least the central part, is also much thicker. Unfortunately, since only one specimen is available from each area, and the OMS specimen is incomplete, it is impossible to assess the scale of morphological variation within the species.

The new species shares some morphological features with *Galatheammina interstincta* Gooday and Holzmann in Gooday et al., 2017, notably a plate-like test, composed largely of radiolarian shells and with a more or less homogeneous structure. The two form a well-supported clade (95% BV; Fig. 4) with a species designated *Psammina* sp. 3 by Gooday et al. (2017a), with which they have little in common morphologically. However, *M. semicircularis* and *G. interstincta* are not close enough genetically to be regarded as congeneric.

Abyssalia Gooday and Holzmann gen. nov.

Diagnosis. Test free or attached, flattened or spherical, composed of an undifferentiated three-dimensional meshwork of sponge spicules with no distinct surface layer or internal lumen. Interior structures clearly visible within at least the outer part of this structure. Stercomata form loose aggregations that occupy much of space between spicules, but are easily washed out in preserved specimens. Granellare tube with relatively thick organic wall enclosing cytoplasm and

forming pale yellowish branching system weaving between spicules.

Zoobank registration. LSID urn:lsid:zoobank.org:pub:0B1892D4-65D5-4ED2-9FE5-9F80221DE762.

Etymology. Latin *Abyssalia* meaning abyssal. Gender feminine.

Type species. *Abyssalia foliformis* Gooday and Holzmann sp. nov.

Other species assigned. *Abyssalia sphaerica* Gooday and Holzmann sp. nov.

Remarks. The new genus unites two morphologically distinct species, the type species with a flat, leaf-like test, the other (*Abyssalia sphaerica*) with a spherical test. Nevertheless, they share a number of features, notably the construction of the test as an open, three-dimensional framework of sponge spicules, the relatively thick organic sheath that encloses the cytoplasm, and the loose aggregations of stercomata. Genetic data confirm that the two species are closely related (Fig. 4).

In terms of morphology, *Abyssalia* appears closest to *Psammetta* Schulze, 1906, a genus known mainly from off East Africa in the western Indian Ocean, with one record from near Indonesia (Tendal 1972). *Psammetta* includes four species with spherical or flattened tests that incorporate sponge spicules, exclusively so in *P. erythrocytomorpha* Schulze, 1907. There are two main differences between the genera. First, in the three spherical species (the type species *P. globosa* Schulze, 1906, *P. arenocentrum* Tendal, 1972, and *P. ovale* Tendal, 1972) the test is differentiated into a central core composed of foraminiferal shells or sand grains, and an outer part composed of sponge spicules (Tendal 1972); this contrasts with the homogeneous test of *Abyssalia*. Second, the stercomare form distinct branching masses that can be extracted from the test as coherent structures in *P. erythrocytomorpha* (Plate I figs. 5–7 in Schulze 1907) rather than loose aggregations of stercomata that are easily washed out. It is possible that the two genera will eventually prove to be synonymous, but without genetic data for any described *Psammetta* species, this cannot be tested.

The two *Abyssalia* species form a well-supported clade (98/99% BV) with several stalked, fan-shaped forms currently assigned to the genus *Psammina* (). Further research will be necessary in order to resolve taxonomic relationships within this close but morphologically disparate grouping.

Abyssalia foliformis Gooday and Holzmann sp. nov. (Figs. 9A–D, 10A–H)

Diagnosis. Species of *Abyssalia* with a flattened, somewhat flexible, leaf-like test composed almost entirely of sponge spicules.

Zoobank registration. LSID urn:lsid:zoobank.org:act:BE36D8A8-71BF-4E65-AB07-7A1E3CA84F90.

Etymology. Latin *folium* (leaf) referring to the leaf-like appearance of the test.

Type material. Holotype (DNA sequences and morphology): reg. no. NHMUK PM ZF 9915. Specimen 192, collected on 09 June 2018 in APEI-1 during ROV dive LK-095 (core 6), event ID KM1808-66; latitude 11.2749739, longitude −153.74425, water depth 5241 m.

Test morphology. Seafloor photographs show the test standing more or less upright with its base attached to the surface of a nodule and the upper part slightly angled with respect to the lower part (Fig. 9A). The specimen collapsed from its vertical orientation when removed from the core into air following recovery, reflecting a moderate degree of flexibility (Fig. 9C). The overall length of the test when intact, based on shipboard photographs (Fig. 9B) and the preserved test fragments, was about 43 mm and the maximum width about 25 mm. In side view, the test is distinctly flattened, approximately 4.4 mm thick near the base, somewhat narrower (2.5–3.3 mm) in the upper part.

Test structure and internal features. The test comprises a three-dimensional meshwork of sponge spicules of uniform structure and composition with no distinct surface layer or internal differentiation. No other kinds of particles are present. Outwardly projecting spicules create a somewhat spiky surface.

The open structure of the test allows the internal features to be clearly visible (Fig. 10A–E). The in situ images show a dark interior, reflecting the presence of stercomata, with a faint, narrow, lightish rim (Fig. 9A). The dark interior is also evident in shipboard photographs (Fig. 9B) but the preserved specimen contains only scattered stercomata, although numerous individual stercomata and groups of stercomata were found in the sample bottle, presumably washed out from the spicule mesh. The pale yellow granellare system has a well-developed organic tube and is clearly visible within the largely transparent test, forming a complex, three-dimensional network (Fig. 10C–E). The strands are clearly developed (widths typically 320–430 μm) in the upper lobes of the test, becoming less obvious and narrower (typically 210–270 μm) in the lower part, where many appear to comprise the empty organic tube. The basal part of the test, now detached, is largely devoid of granellare, the only feature of interest being a brownish tube embedded within it (Fig. 10B). The nature of this tube is unclear; possibly it is a structure that the test has grown around.

Remarks. *Abyssalia foliformis* resembles *Psammetta erythrocytomorpha* in being composed exclusively of sponge spicules and having a flattened test. The two species can be distinguished mainly by the test shape: elongate, and leaf-like in *A. foliformis,* circular and biconcave in *P. erythrocytomorpha*. Unlike *P. erythrocytomorpha*, the new species is sessile and has much less coherent stercomare masses.

Abyssalia sphaerica Gooday and Holzmann sp. nov. (Figs. 11A–F, 12A–F)

Diagnosis. Species of *Abyssalia* with a spherical test composed almost entirely of sponge spicules, which project from the surface in all directions.

Zoobank registration. LSID urn:lsid:zoobank.org:act:0E99BE28-03AA-4A66-9B66-01911CF2654B.

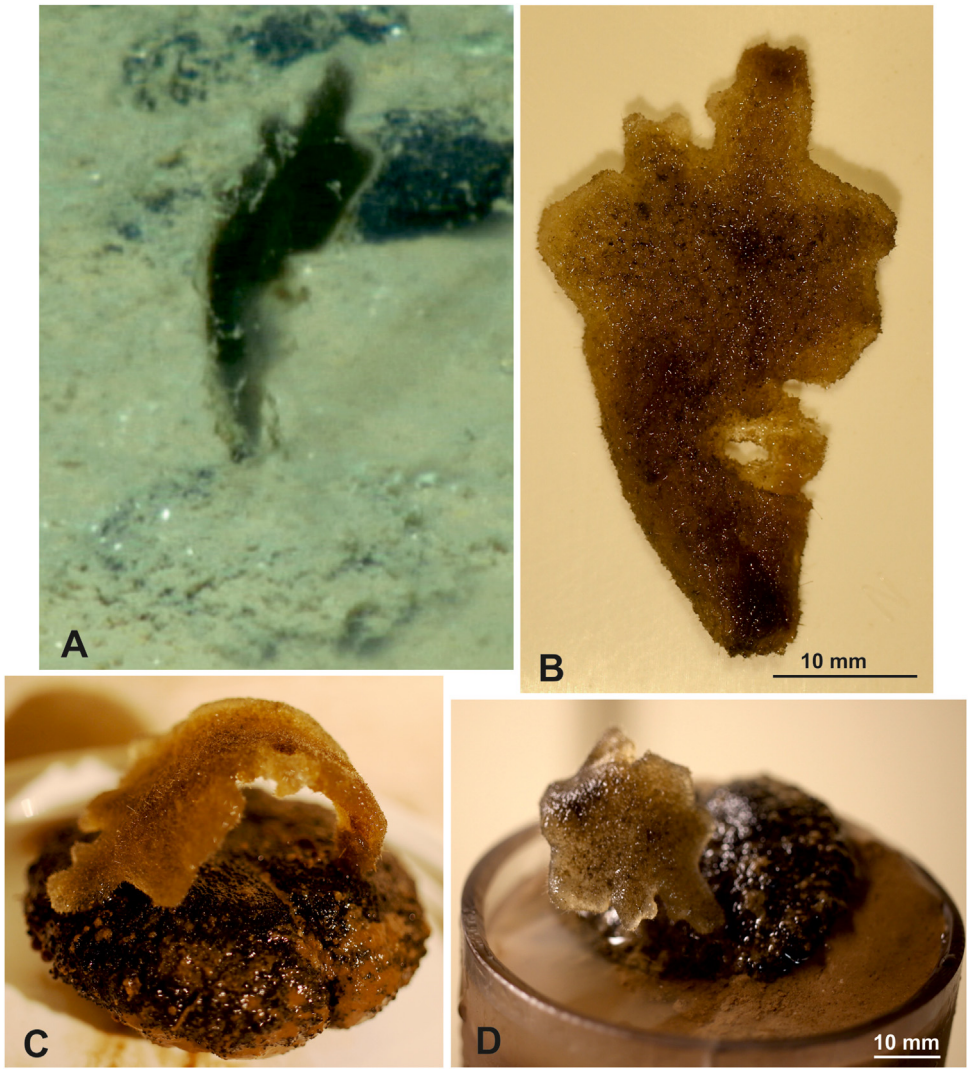

Fig. 9. (A–D) *Abyssalia foliformis* sp. nov., holotype (NHMUK PM ZF 9915); specimen 192, APEI-1, complete test. (A) Specimen on seafloor prior to collection. (B–D) Shipboard photographs showing different views of the complete test before and after removal from the nodule to which it was attached.

Type material. Holotype (DNA sequences and morphology): reg. no. NHMUK PM ZF 9913. Specimen 095, collected on 02 June 2018 in APEI-4 during ROV dive LK-091 (core 11), event ID KM1808-47; latitude 6.9878737, longitude −149.9125, water depth 4999.5 m.

Test morphology. The test forms a perfect sphere, ~22 mm in diameter. Seafloor photographs (Fig. 11A) show almost the entire test exposed on the sediment surface, with a faint pale or transparent outer layer, perhaps formed by projecting spicules, around the dark interior. Two delicate-looking, translucent features (indicated by arrows in Fig. 11A) originate from the lower part of the test. The most obvious one splays out like a fan towards the sediment surface and incorporates several more or less distinct strands. The other has a more rectangular shape. They may represent parts of a pseudopodial system.

Test structure and internal features. The test comprises a complex, three-dimensional framework of sponge spicules. The framework is delicate, but its 3-D architecture imparts a degree of structural resilience that allowed it to survive recovery and transport intact. There is no surface layer of xenophyae, although outwardly projecting spicules create a distinctly 'spiky' surface. The open structure of the test allows internal features to be seen clearly, at least in the outer part (Fig. 11E, F). The composition appears to be homogeneous throughout; when viewed with strong transmitted light there was no sign of an inner core composed of different xenophyae (Fig. 12C). Images taken soon after recovery show a dark interior filled with stercomare (Fig. 11C, D), which was largely washed out of the test during its subsequent transport. By the time the test was examined in Geneva, the remnants of the stercomare comprised small, scattered clusters of stercomata, lodged within the spicule framework and apparently not enclosed in an organic membrane (Fig. 12D).

In reflected light, the pale cream-coloured, branching granellare strands are clearly visible within the test (Fig. 12A,

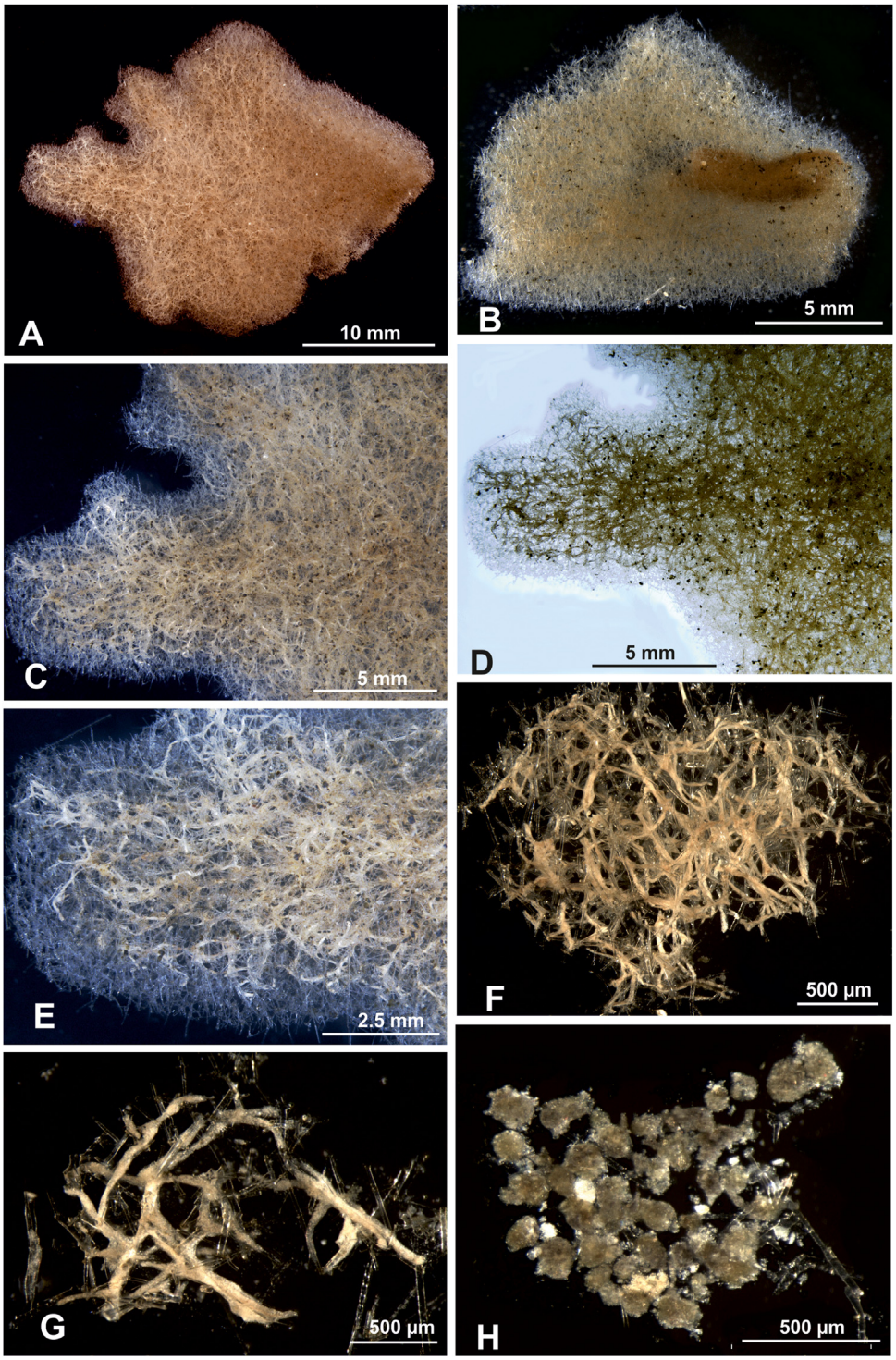

Fig. 10. (A–H) *Abyssalia foliformis* sp. nov., holotype (NHMUK PM ZF 9912); specimen 192, APEI-1, details. (A) Main fragment of the test showing elaborate granellare network, particularly well-developed at the distal (left-hand) end and visible within spicule framework. (B) Smaller fragment that includes the basal part of the test; note the brown tubular structure. (C–E) Different views of the test showing the granellare system visible within it. (F, G) Detached fragments of test with granellare strands adhering to the spicule framework. (H) Collection of separate stercomare fragments from sample jar.

B), where they are closely associated with the spicules. The strands comprise a visually distinct, relatively thick organic tube that encloses the cytoplasm (Fig. 12E, F). They weave between the spicules and are securely anchored to them so that it is impossible to remove pieces without attached spicule fragments. They branch frequently, but do not appear to

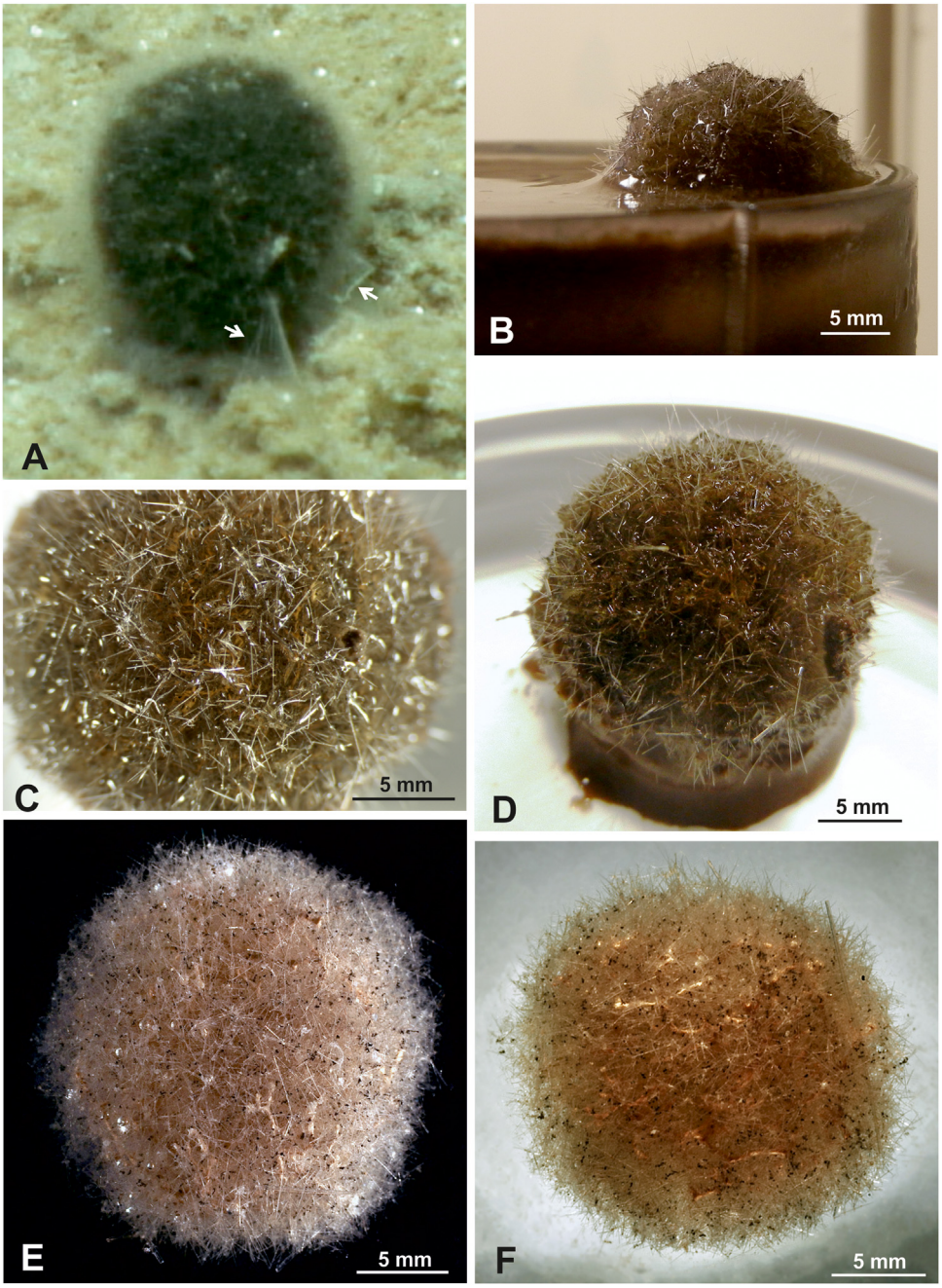

Fig. 11. (A–F) *Abyssalia sphaerica* sp. nov., holotype (NHMUK PM ZF 9913); specimen 095, APEI-4, complete test. (A) Specimen on seafloor prior to collection. The arrows indicate features extending from the lower part of the test that may be bundles of pseudopodia deployed onto the sediment surface. (B) Shipboard photograph of specimen in core tube following recovery. (C, D) Shipboard photograph of specimen removed from core tube. (E, F) Laboratory photographs taken against different backgrounds and with different lightings; the granellare show up better in (F) against the light background.

anastomose. The width is very variable, with wider (typically ~280–360 μm) sections where the strands branch or are attached to spicules, and narrower (typically ~90–160 μm) necks.

Remarks. The spherical test of *Abyssalia sphaerica* distinguishes it from *A. foliformis*. It is similar in size (22 mm) to *Psammetta globosa* (up to 25 mm according to Tendal 1972). In addition to the genus-level differences mentioned above, the granellare branches are considerably wider (up to >300 μm diameter) than those of *P. globosa* (up to 120 μm). These differences also apply in the case of another spherical species *P. arenocentrum*, which, in addition, is much smaller (maximum 9 mm diameter) than *A. sphaerica.*

Stannophyllum Haeckel, 1889

Stannophyllum zonarium Haeckel, 1889 (Figs. 13A–E, 14A–F)

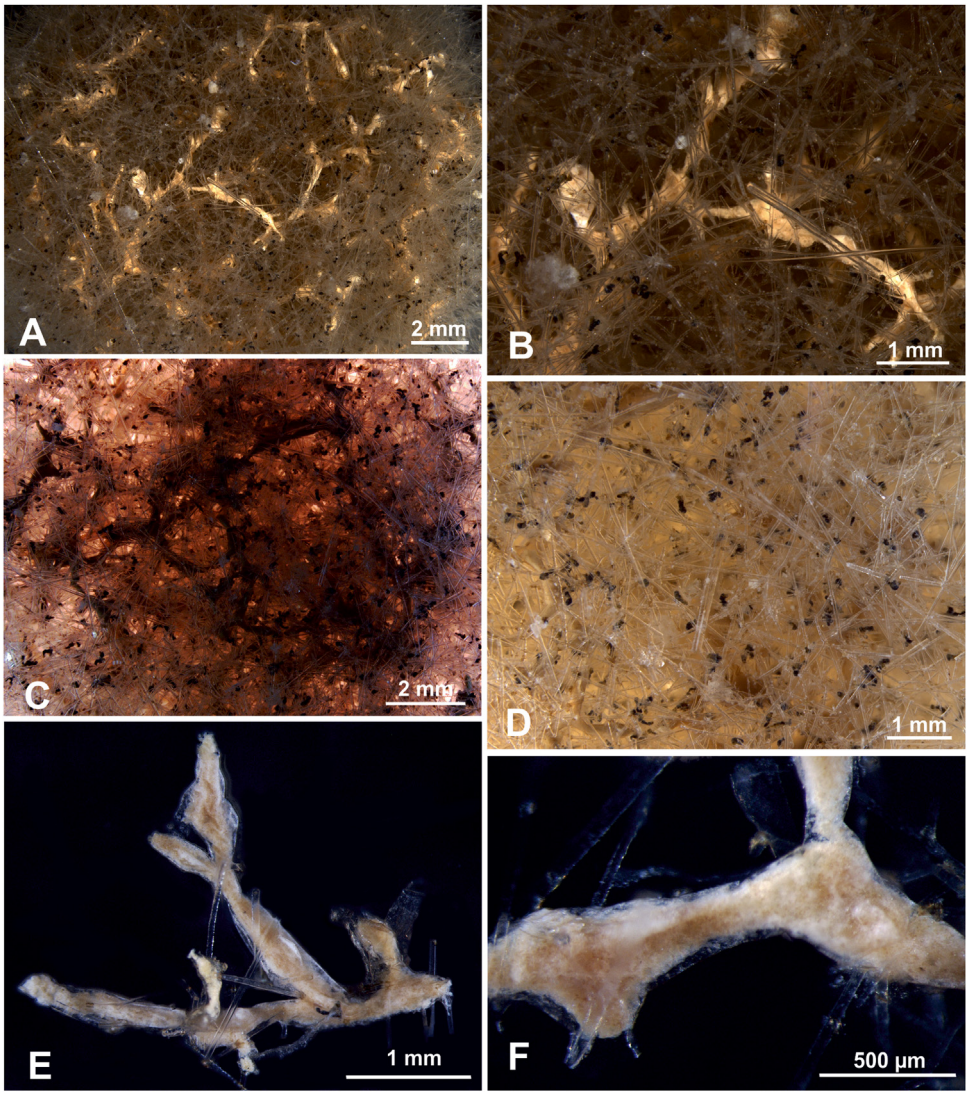

Fig. 12. (A–F) *Abyssalia sphaerica* gen. nov, sp. nov., holotype (NHMUK PM ZF 9913); specimen 095, APEI-4. (A) Granellare strands seen within the spicule framework of the test. (B) Detail of granellare. (C) Back-lit detail of test showing granellare strands as dark shapes. (D) Top-lit view of same area showing scattered remnants of stercomare. (E, F) Fragments of granellare showing cytoplasm enclosed within a transparent organic sheath.

1889 ***Psammophyllum annectens*** **sp. nov.** – Haeckel, Rep. Sci. Res. Voyage of H.M.S. Challenger; Zoology, 82: 52; Pl. IV, figs. 1–4.

1889 ***Stannophyllum zonarium*** **sp. nov.** – Haeckel, Rep. Sci. Res. Voyage of H.M.S. Challenger; Zoology, 82: 62; Pl. I, fig. 1A–C; Pl. II, figs. 1–4.

1892 ***Neusina agassizi*** **sp. nov.** – Goës, Bull. Mus. Comp. Zool. 23: 195; Pl. I, figs. 1–9.

1907 ***Stannophyllum zonarium*** Haeckel, 1889 – Schulze, Bull. Mus. Comp. Zool. Harvard, 51: 152 –154.

1907 ***Stannophyllum zonarium*** Haeckel, 1889 – Schulze, Wiss. Ergeb. Deutschen Tiefsee-Expedition Dampfer "Valdivia" 1898–1899, 11: 37–41; Pl. V. figs 1–12; Pl. VI, figs 1–2.

1972 ***Stannophyllum zonarium*** Haeckel, 1889 – Tendal, Galathea Rep., 12: 45–51; Text-figs. 9–11; Pl. 8, fig. E; Pl. 9, figs. A–D; Pl. 15, fig. D; Pl. 16, fig. C; Pl. 17, figs. F–G.

1973 ***Stannophyllum zonarium*** Haeckel, 1889 – Tendal, Akad. Nauk USSR, 12: 27; Pl. 1, figs. 1–2.

1974 ***Stannophyllum zonarium*** Haeckel, 1889 – Hedley and Rudall, Cell Tissue Res. 150: 107–111; Figs. 1–5.

1985 ***Stannophyllum zonarium*** Haeckel, 1889 – Tendal, Galathea Rep. 16: 95–97; Pl. 13, fig. A.

1992 ***Stannophyllum zonarium*** Haeckel, 1889 – Levin and Gooday, Kluwer Academic Publishers: 97.

1996 *Stannophyllum zonarium* Haeckel, 1889 – Tendal, Galathea Rep. 17: 92.

Diagnosis (adapted from Tendal 1972, p. 46 therein). *Stannophyllum* having flaccid test with distinct concentric

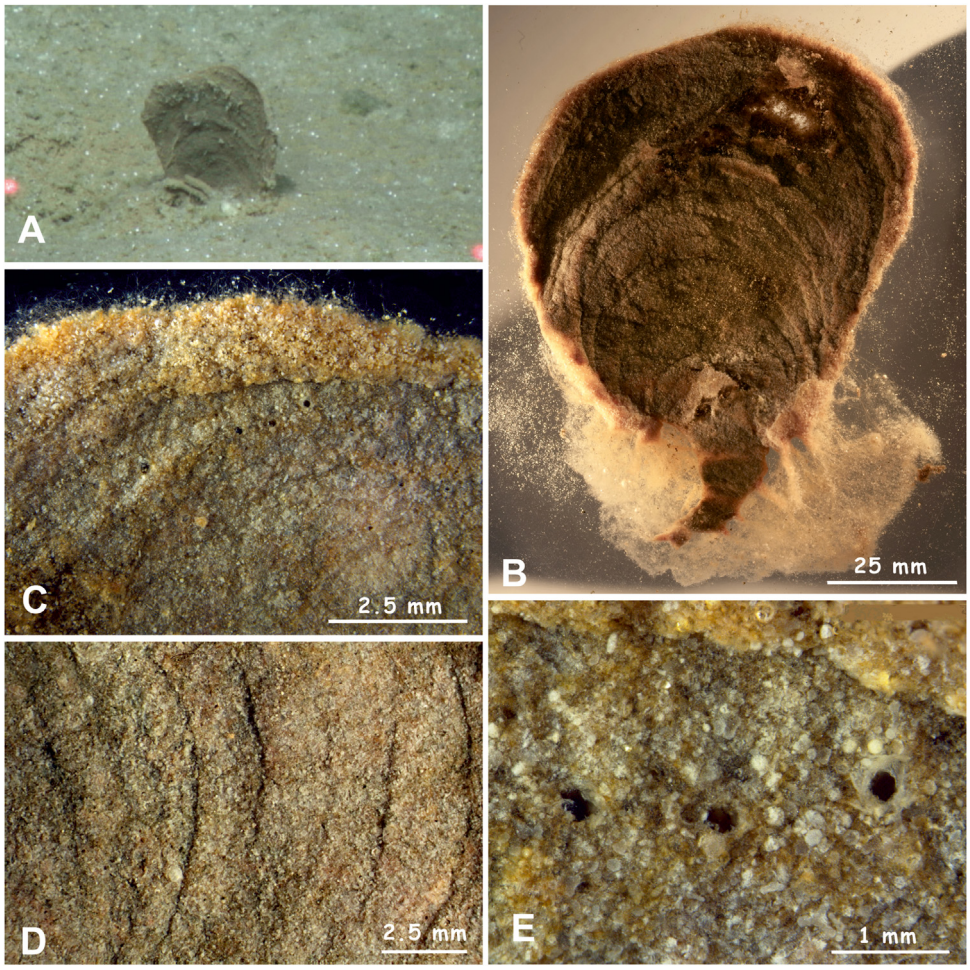

Fig. 13. (A–E) *Stannophyllum zonarium* Haeckel, 1889, specimen 079, APEI-7, external features. (A) Specimen on seafloor prior to collection (the two red laser points are 15 cm apart). (B) Test photographed in laboratory with pale mass of tangled linellae arising from lower part; it was somewhat damaged by excavations to look for granellare material for genetic analysis. (C) Detail of surface with yellowish, slightly raised margin. (D) Detail of surface showing 'growth lines'. (E) Surface with a row of three pores.

surface zonation. Linellae well developed, forming felt-like component of test wall and sometimes bundles arising from the margin. Xenophyae mainly radiolarian shells.

Material. Morphology only. Specimen 079 (intact), collected on 28 May 2018 in APEI-7 during ROV dive LK-0089 (core 9), event ID KM1808-36; latitude 5.05993953, longitude −141.83105, water depth 4869 m. The specimen is currently located in the first author's collection at the National Oceanography Centre, Southampton.

Test morphology. The seafloor image shows a roughly rectangular plate-like test rising from the seafloor and not obviously attached to a substrate (Fig. 13A). One side appears to be curved towards the camera. The surface exhibits rather vague, somewhat irregular, concentric traces as well as a scattering of small features that may be attached organisms. Two tubular structures, possibly worm tubes, are associated with the test at its base.

Viewed in the laboratory, the preserved test is greyish brown, flaccid, and ~55 mm long. The upper part is asymmetrically oval with a smoothly curved margin that occupies 43 mm of the length and is about 42 mm across at its widest point (Fig. 13B). The lower (more proximal) part of the test merges at the base into a short, curved, stalk-like feature tapering from about 10 mm to about 2 mm. This, and the lower part of the main test, were clearly buried below the sediment surface in the image taken with the ROV. The test rim appears orange-brown in contrast to the greyish-brown colour of the remaining surface; in places, it is somewhat raised above the general level of the surface (Fig. 13C). Low-angled lighting reveals more or less concentric step-like features, spaced 1.5–3.1 mm apart (Fig. 13D), corresponding to the concentric traces visible in the seafloor photograph. Small, round holes, 200–360 μm in diameter, are scattered across the test surface, sometimes in rows of three (Fig. 13E). Short, delicate, thin-walled translucent tubes extending up from these openings suggest that they are original features.

Test structure and internal features. The wall is composed of radiolarian shells and fine-grained material and ramified by a felt-like meshwork of linellae. A narrow fringe of linellae is present around the margin (Fig. 14A, B) but

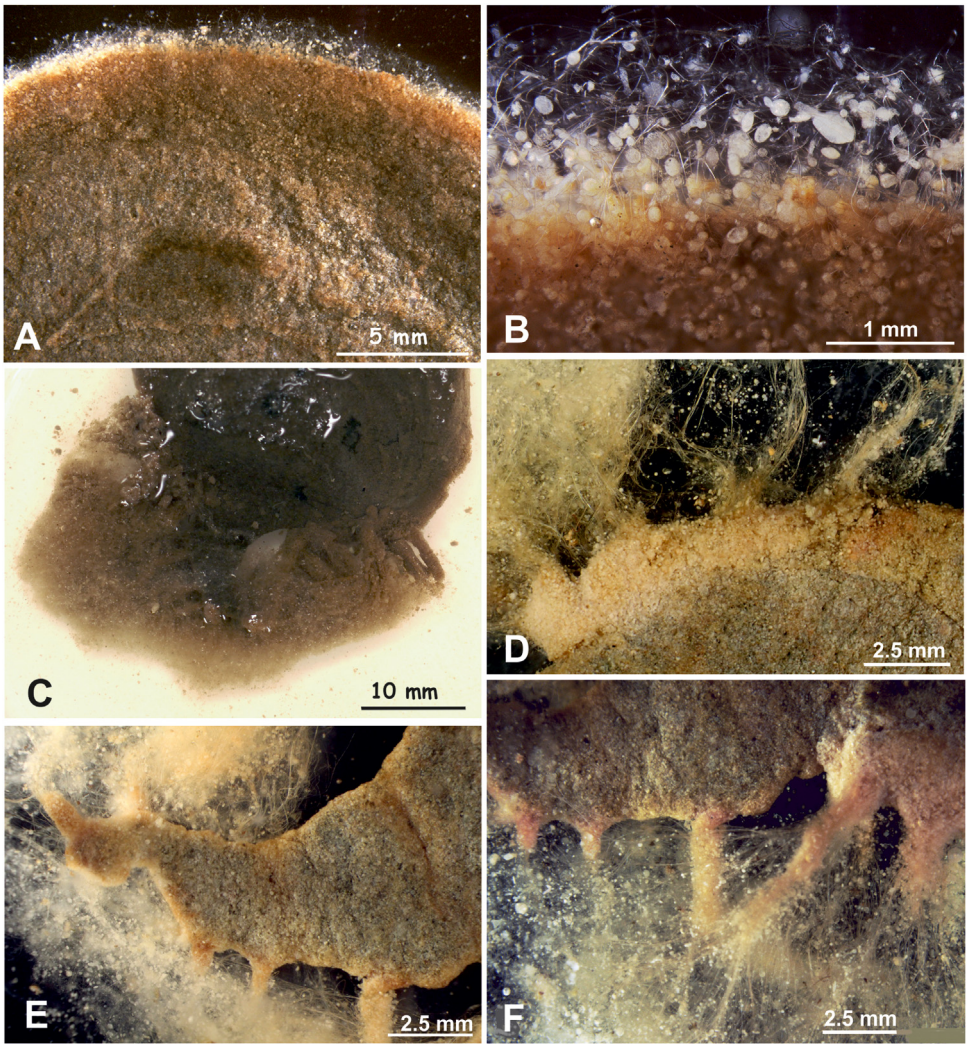

Fig. 14. (A–F) *Stannophyllum zonarium* Haeckel, 1889, specimen 079, APEI-7, linellae and associated structures. (A) Margin of test with fringe of projecting linellae. (B) Detail of linellae. (C) Shipboard photograph of freshly collected test showing mass of linellae and long cylindrical projections. (D) Bundles of linellae. (E) Basal stalk with projections giving rise to bundles of linellae. (F) Transition between the stalk and the base of the upper part of the test showing projections and linellae bundles. Note the overlap between E and F.

these proteinaceous threads are profusely developed as tangled masses only in the lower third of the test (Fig. 14C). On one side, the linellae are concentrated in about five bundles spaced along the margin (Fig. 14D). On the other side, five or six prominent cylindrical projections of different lengths along the lower part of the main test and the side of the basal 'stalk' merge into dense bundles of linellae that expand into tangled masses (Fig. 14E, F). Two other bundles of linellae arise from projections near the end of the stalk.

Several exploratory excavations of the test revealed a clearly developed system of granellae branches only in the proximal part of the test, just above the stalk. The branches were between 40 and 125 μm in diameter and pale cream in colour. They branched and in a few places appeared to anastomose. Attempts to amplify DNA from these fragments were unsuccessful. The stercomare was not well exposed in the excavated regions. Where visible it formed masses of irregular width.

Remarks. Tendal's (1972) detailed description of *Stannophyllum zonarium*, based mainly on a collection of 100 specimens from Galathea Station 716 in the Eastern Pacific off Costa Rica, is largely consistent with our observations. The length (55 mm) of the DeepCCZ specimen falls towards the middle of the range (30–75 mm, ignoring two outliers with lengths of 110 and 120 mm) given by Tendal (1972, Fig. 10 therein) for intact specimens from St. 716, whereas the width (42 mm) lies at the lower end of the range (25–110 mm). It resembles Tendal's 'Growth form A', in which the length of the test is similar to the width and a stalk is typically developed.

Many of the test features described by Tendal (1972) are present in our specimen. He mentions that the test wall is

punctuated by 'pores', sometimes arranged in rows, recalling those illustrated in Fig. 13E. He also describes 'tubes' and 'tufts' arising from the margins of the test. The 'tubes' probably correspond to the marginal projections described above and the 'tufts' to the bundles of linellae that they give rise to. Tendal discusses different ideas about the function of these features. He finds no support for the view of Goës (1892) that they serve to anchor the test in the sediment. A photograph showing a seafloor feature interpreted as a possible flat-lying *Stannophyllum* test was published by Lemche et al. (1976, Plate 5a therein). However, the fact that our specimen was positioned vertically with the lower part, where linellae are profusely developed, buried in the sediment, tends to support the interpretation of Goës. As mentioned above, our specimen is relatively small. Whether larger individuals are also able to maintain a vertical orientation is unclear.

Xenophyophore mudball (Fig. 15A–D, 16A–F)

Material. DNA sequences and some morphology. Specimen 085, collected on 01 June 2018 in APEI-4 during ROV dive LK-0090 (core 1), event ID KM1808-43; latitude 7.03599787, longitude −149.93947, water depth 5040 m. Test is largely disintegrated but tiny fragments remain that show some aspects of morphology

Description. Seafloor images show the spherical test completely exposed on the seafloor (Fig. 15A), although it sunk into the sediment during recovery (Fig. 15B). The surface was fairly smooth and devoid of obvious features apart from a few irregular lumps, possibly of detritus, similar to material visible on the surrounding substrate. The test appears dark brown in shipboard photographs, with a smooth surface except for several step-like features (Fig. 15C, D) that suggest a layered internal structure. It was about 36 mm in diameter.

The test started to disintegrate as soon as it was put into RNAlater and by the time it reached Geneva only some tiny fragments remained. Most are plate-like with small, cell-like compartments on one side (Fig. 16A–C). The compartments are ∼300–900 μm in diameter (mean 609 ± 155 SD μm, $n = 21$), delimited by low partitions, and tend to be roughly polygonal. These fragments suggest that the test consisted of compartmentalised layers. A single fragment comprises parts of two compartments sandwiched between an upper and a lower plate and separated by a vertical partition (Fig. 16D). This probably represents a section through a test layer. It is ∼640 μm thick.

The fragments are very delicate and composed largely of loosely agglutinated radiolarian tests with some scattered dark mineral grains. The stercomare forms approximately spherical masses, 110–250 μm (mean 166 ± 35 SD μm, $n = 53$) in diameter (Fig. 16E). Most of these were found loose in the sample jar as single entities, but some were joined together in pairs, triplets, or occasionally in four masses, linked by thin necks. It seems likely that the stercomare formed delicate, chain-like formations in the undamaged test but broke up into isolated masses when the test itself disintegrated. However, some of the compartments contained single stercomata masses, apparently in their original location (Fig. 16C). Fragments of granellare were also found in the sample jar. They are brownish in colour, 30–65 μm in width and wider at branching points. One fragment comprises branches that formed three or four complete circuits (anastomoses), two of them enclosing a stercomare mass (Fig. 16F).

Remarks. *Psammetta globosa* and *Abyssalia sphaerica* have spherical tests similar to the xenophyophore mudball. However, both have tests composed of sponge spicules rather than fine sediment particles, and their internal structure is very different. In particular, there is no sign in *Psammetta globosa* and *Abyssalia sphaerica* of the tiny compartments, apparently arranged in layers, which characterise the mudball. The only genus with which it shares some features is the monotypic *Cerelpemma* Laubenfels, 1936, known only from a few specimens collected in dredge samples by H.M.S. Challenger in the central Pacific (4438–5353 m depth) (Haeckel 1889; Tendal 1972). The single species, *Cerelpemma radiolarium* (Haeckel, 1889), has a 'rounded, subsphaerical, clavate or turbinate' test composed exclusively of radiolarians of friable consistency. The radiolarians are 'cemented into numerous thin layers' each comprising a single layer of particles, with each layer being separated by a space that is 'approximately the same thickness as the layers themselves' (p. 34 in Tendal 1972). This description is reminiscent of our specimen although there is no mention of the layers being divided into compartments. Also, the illustrations of Haeckel (1889; Pl. VII, fig. 4A, B therein), who describes the test as being 'turbinate' (shaped like an inverted cone), show a mushroom-shaped structure, quite different from our spherical 'mudball'. *Cerelpemma* is too poorly known for any judgement to be made regarding its relationship, if any, to our 'mudball'.

Unfortunately, this remarkable species cannot be formally described since the almost total disintegration of the delicate test makes it impossible to designate the unique specimen as a holotype. It forms a well-supported (92% BV) clade with *Rhizammina* sp. 2 (Fig. 4), an undescribed, branched, tubular species with a completely different test morphology.

Indeterminate xenophyophore (Figs. 17A–G, 18A–F)

Material. Morphology only. Specimen 084, dead fragments, collected 01 June 2018 in APEI-4 during ROV dive LK-090, event ID KM1808-43; latitude 7.021367°, −149.93564°, water depth 5040 m. Fragments of the specimen are currently located in the first author's collection at the National Oceanography Centre, Southampton.

Description. Seafloor images show an upright test, about 56 mm high and 50 mm wide with at least five short, relatively wide, more or less horizontal branches (up to ∼18 mm long and 7–8 mm wide) arising from a central axis (Fig. 17A). Much of the visible surface has a dense ornamentation that appears to be finely reticulated. The test is draped with patches of paler material, also present on the surrounding surface and presumably some sort of detritus. The specimen was damaged during recovery from the seafloor. Shipboard images show a complex morphology with a num-

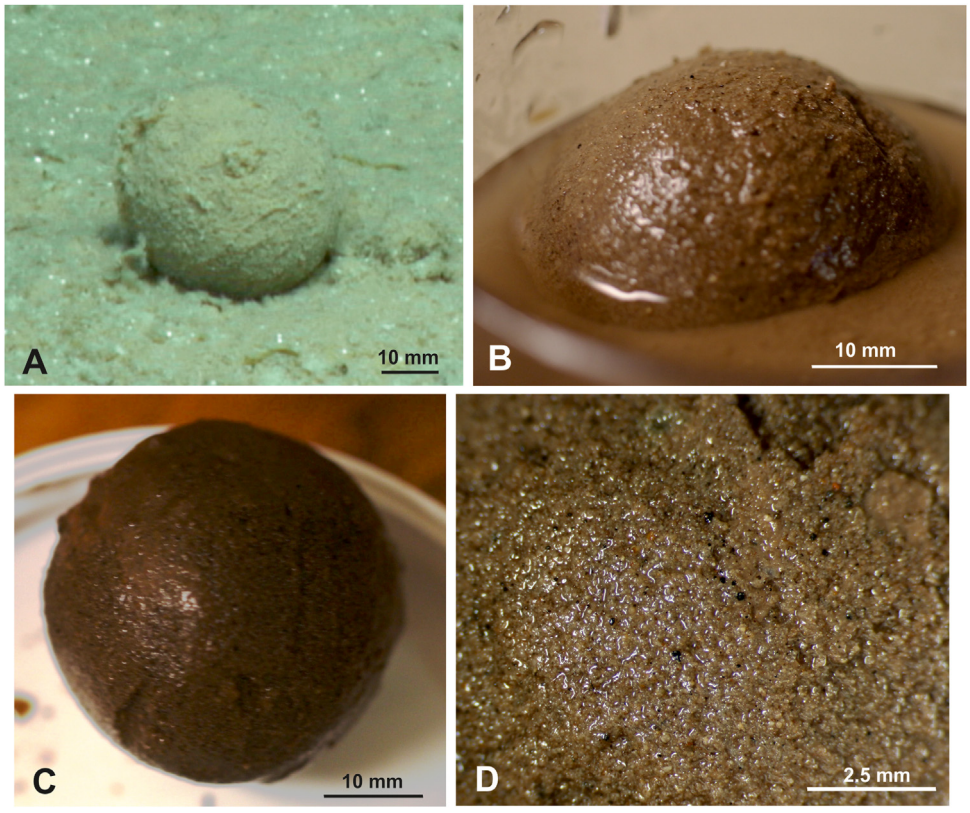

Fig. 15. (A–D) Xenophyophore mudball, specimen 085, APEI-4, external features of intact test. (A) Specimen on seafloor prior to collection. (B) Shipboard photograph of specimen in core tube following recovery. (C) Shipboard photograph of specimen removed from core tube. (D) Detail of surface (scale approximate).

ber of branches (at least 6 or 7) orientated in different directions and with circular or somewhat flattened cross sections (Fig. 17B–D). Unbroken surfaces are covered in small, raised lumps ('pustules'), sometimes merging into more linear features (Fig. 17E). These correspond with the surface ornamentation seen in the in situ images. A specimen of *Aschemonella monile* (described above) was lodged between the branches of test and also visible on the seafloor (Fig. 17A, C).

Only fragments of the test were available for detailed examination. The interior consists of delicate tubular elements, 390–560 μm (usually 430–480 μm) in diameter, fused together rather loosely into a more or less coherent mass (Fig. 18B, E, F). The tubes may adjoin each other, but there is often some open space between them. The structure is very delicate and some parts can be easily disaggregated by gentle brushing with a fine brush. This mass of tubes is bounded by a rather poorly-defined surface layer. Over most of the surface, the pustules are much less evident than in the shipboard photographs. Where clearly developed, they form small rounded domes (500–750 μm in diameter), sometimes merging into more elongate features (Fig. 18A, C, D). Small bumps, undulations and depressions, sometimes with a vague linear grain, are more common in the preserved material (Fig. 17F, G). These features are clearly surface expressions of the underlying tubular structures.

The surface layer consists of radiolarians set in a fine-grained matrix (Fig. 17G), while the internal tubular elements are loosely agglutinated and composed largely of radiolarians. Much of the test appears to be dead. The tubes often contain dark accumulations of loose stercomata. In two places, several unbranched reddish strands (width 20–40 μm), presumably part of a granellare system, were visible within tubules. Attempts to amplify DNA from these strands were unsuccessful.

Remarks. The test structure of this remarkable specimen, which comprises a mass of tubular elements that are fused together to a variable extent and enclosed within a surface layer of xenophyae, is unlike that of any other known xenophyophore. The tubes are rather similar those of *Rhizammina* Brady, 1879, although more delicate and without a clearly developed organic layer.

Molecular characterisation

The obtained partial SSU rDNA sequences correspond to the barcoding region of foraminifera (Pawlowski and Holzmann 2014) and were aligned to 73 other monothalamid sequences. Six monothalamid sequences of Clade C (*Hippocrepina indivisa*, *Cylindrogullmia* spp.) were chosen as the outgroup. Xenophyophores are divided in three clades

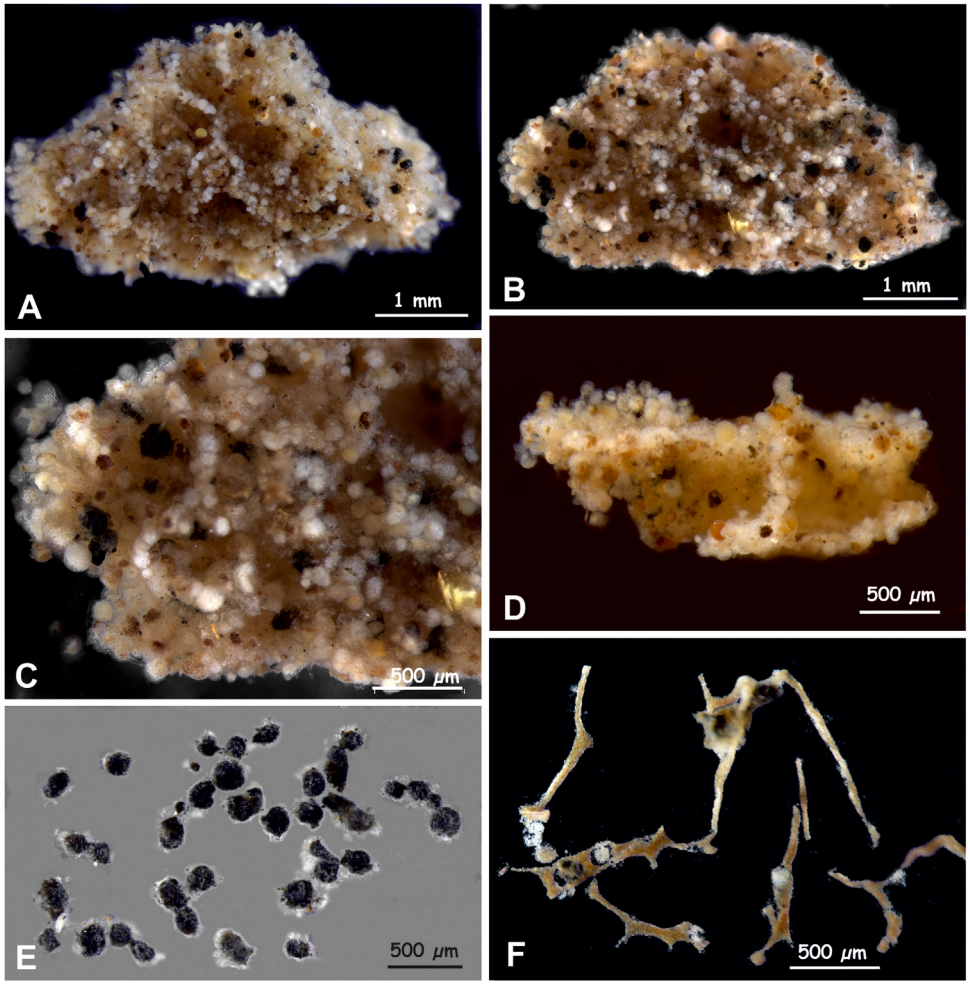

Fig. 16. (A–F) Xenophyophore mudball, specimen 085, APEI-4, fragments of test. (A, B) Fragments showing compartments. (C) Detail of fragment shown in B; note spherical stercomare mass in some compartments. (D) side view of two incomplete compartments with partition between them. (E) Spherical stercomare masses found loose in sample jar; note that some are joined in short chains. (F) Granellare fragments.

but none of these is supported by bootstrap values (Fig. 4). One clade contains three of the species described above (*Abyssalia sphaerica*, *A. foliformis* and *Moanammina semicircularis*) as well as *Galatheammina interstincta*, *Psammina* spp, *Aschemonella* spp, *Rhizammina* sp., *Syringammina* spp. and an unidentified xenophyophore. A second clade contains the xenophyophore mudball, *Psammina* spp., *Stannophyllum zonarium*, *Tendalia reteformis*, *Galatheammina* spp., *Reticulammina cerebriformis*, *Shinkaya* spp., *Bizarria bryiformis*, *Rhizammina* spp. and an unidentified xenophyophore. The third clade comprises *Galatheammina* spp., *Semipsammina mattaeformis* and an *Aschemonella*-like form.

Discussion

This small collection of xenophyophores from abyssal plains in the western CCZ includes 11 morphological species, only two of which could be assigned to known species (*Aschemonella monile* and *Stannophyllum zonarium*). Previous studies in the UK-1 and OMS contract areas and APEI-6 in the eastern CCZ have documented some 45 species (Gooday et al. 2017a, 2018), with a further 10 known from the Russian area (Kamenskaya 2005; Kamenskaya et al. 2015, 2017). This new material therefore increases the number of xenophyophore species recorded from the CCZ alone to around 55, of which 17 have been formally described. Additional species were described in earlier works from parts of the abyssal equatorial Pacific outside the CCZ (Goës 1892; Haeckel 1889; Schulze 1907; Tendal 1972, 1996), while Levin and Thomas (1988) and Levin (1994) illustrate undescribed species from bathyal seamounts to the east of the CCZ (102°W to 109°W). Clearly, the equatorial Pacific is a region of high xenophyophore diversity (Tendal 1996; see Supplementary Table 3 in Gooday et al. 2017a for a summary of previous records).

Our species encompass a wide range of test morphologies and display some previously unknown features. Two were particularly notable. The relatively featureless 'Xenophyophore mudball' quickly disintegrated, but enough

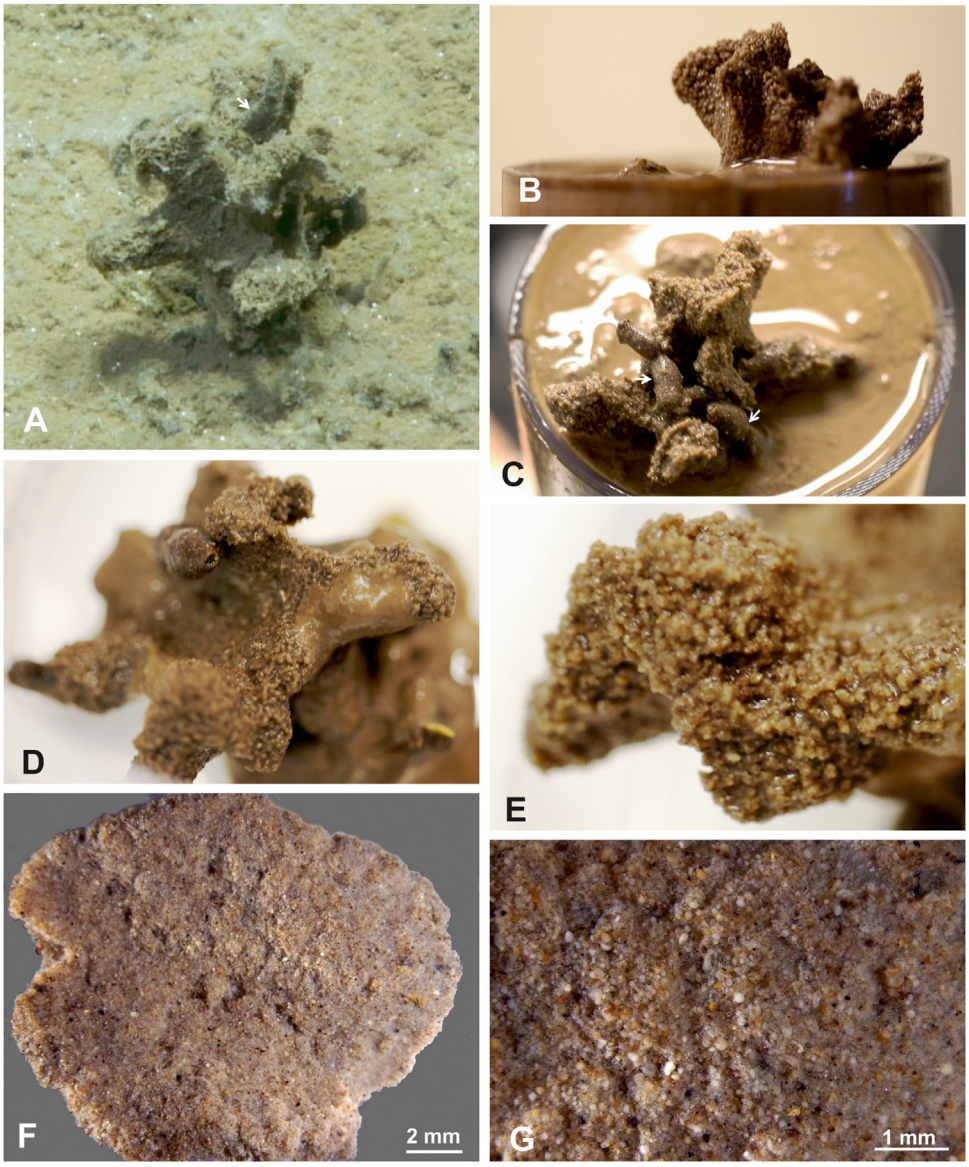

Fig. 17. (A–G) Indeterminate dead xenophyophore, specimen 084, APEI-4. (A) Specimen on seafloor prior to collection. (B, C) Shipboard photographs of the specimen in core tube following recovery. (D) Shipboard photograph of the specimen removed from core tube. (E) Detail showing well-developed surface 'pustules'. (F) Laboratory photograph of external surface of test fragment. (G) Detail of uneven surface. The arrows in A and C indicates an associated test of *Aschemonella monile,* probably the pieces illustrated in Fig. 2A, C.

fragments remained to show that the internal structure comprised tiny compartments, probably arranged in layers. Despite this unique test structure, genetic data confirmed that the specimen was a xenophyophore. The indeterminate xenophyophore from sample 084 (Figs. 17 and 18) had an irregularly shaped test formed from a mass of loosely fused tubular elements, another novel kind of test structure. This specimen was dead and its identification as a xenophyophore could not be confirmed genetically, but the size and morphology of the test, and the *Rhizammina*-like appearance of the tubular elements, makes it likely to belong to this group. These two species therefore expand the already wide diversity of test structures recognised among the xenophyophores.

Relatively little is known about biogeographic patterns among xenophyophores. Many species appear to have restricted distributions. Of the 78 that have been formally described, 56 are known only from one area (e.g., off east Africa, the Porcupine Abyssal Plain, the eastern CCZ) and 27 from a single site. In most cases, these species are rare and almost half (13) of those confined to a single site are singletons. Such species must be chronically undersampled, making it impossible to draw any conclusions regarding their distributions. A few xenophyophore species, however, appear to have broad ranges. *Aschemonella ramuliformis* and *A. scabra* are both widely reported in different oceans (Brady 1884; Cushman 1920). *Syringammina fragilissima* (Tendal

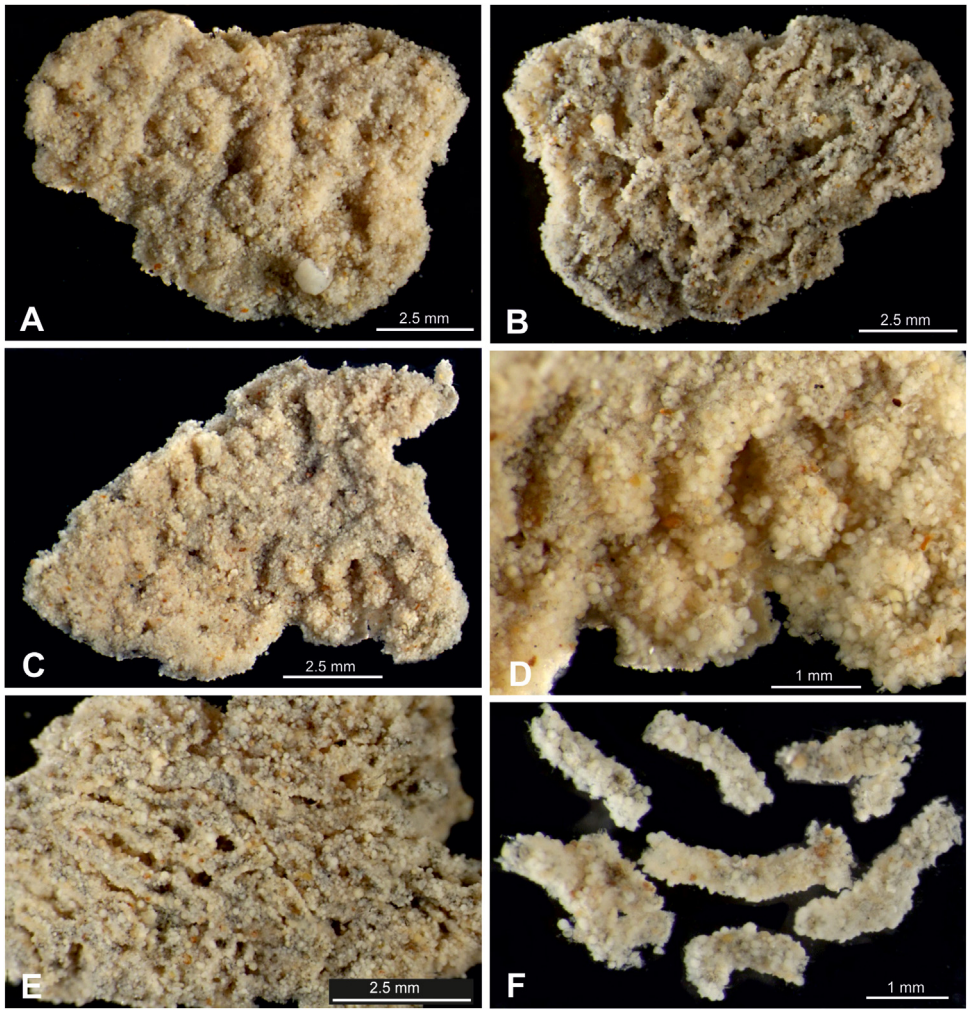

Fig. 18. (A–F) Indeterminate dead xenophyophore, specimen 084, APEI-4. (A) External surface of test fragment. (B) Underside of the same fragment showing construction from tightly packed tubular structures. (C, D) External surface of test fragments with clearly developed dome-like pustules. (E) Underside of fragment showing tubular construction. (F) A collection of tubules detached from the test.

1972, 1975) and *Reticulammina labyrinthica* (Gooday 1991, 1996; Gooday and Tendal 1988) are reported from the New Zealand area and the NE Atlantic, *R. lamellata* from the New Zealand area and the northern Chilean margin (Araya and Gooday 2018), and *Stannoma dendroides* and *Stannophyllum globigerinum* from the Indian Ocean (off eastern Africa) and the Pacific (Tendal 1972).

These wide ranges depend on morphological similarities between specimens from distant locations. In the present study, specimens of *Aschemonella* from APEI-4 were found to be genetically identical to *Aschemonella monile* from the UK-1 and OMS areas, 3800 km to the east, while *Moanammina semicircularis*, also from APEI-4, was genetically identical to *Galatheammina* sp. 6 from the OMS area. This study therefore provides the first genetic confirmation that some abyssal xenophyophores have ranges spanning thousands of kilometres. In the case of *A. monile*, this is not entirely unexpected. Based on test morphology, this species was already known to be common in the CCZ and to occur in the UK-1, OMS and Russian contract areas, as well as APEI-6 (Gooday et al. 2017a, 2017b). *Moanammina semicircularis*, however, is represented by only one specimen in the OMS area and one in APEI-4. Their rather different morphologies would made it difficult to recognise them as the same species in the absence of genetic data. The APEI-4 specimens of *A. monile* are also not typical. This morphological plasticity of xenophyophore tests, and their tendency to fragment, complicates the already difficult task of establishing species ranges for this group of megafaunal protists, as well as the challenge of determining their taxonomic diversity in photographic surveys of the seafloor.

Author contributions

The manuscript and most of the figures were prepared by AJG with contributions from JMD; the genetic and phylogenetic analyses (including Fig. 4) were done by MH and

JP; the specimens were collected and photographed at sea by JMD, and the sampling expedition was led by CRS, who also conceived the overall DeepCCZ project. All authors read and approved the final manuscript.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.ejop.2020.125715.

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