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Five new species and two new genera of xenophyophores (Foraminifera: Rhizaria) from part of the abyssal equatorial Pacific licensed for polymetallic nodule exploration

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Based on a combination of morphological and molecular data, we describe five new species and two new genera of xenophyophores from the Clarion–Clipperton Zone (abyssal eastern Pacific), an area with commercially valuable seafloor deposits of polymetallic nodules. ***Bizarria bryiformis* gen. et sp. nov.** displays unusual features, notably an organic-walled test, largely devoid of agglutinated particles, comprising interconnected branches growing upwards from the nodule substrate; the bases of the branches contain dark masses of waste material (stercomare) and pale strands of cytoplasm (granellare), the whitish, tuft-like extremities contain sediment particles. ***Tendalia reteformis* gen. et sp. nov.** forms a delicate network of agglutinated tubes. ***Shinkaiya contorta* sp. nov.** is characterized by a contorted, partly reticulated plate-like test while the simpler plate-like test of ***Galatheammina interstincta* sp. nov.** combines characters typical of *Galatheammina* and *Psammina*. In ***Semipsammina mattaeformis* sp. nov.**, a thin, delicate test with one or more tubular extensions forms a flat canopy over the mat-like stercomare encrusting the nodule substrate. *Tendalia reteformis* and *S. contorta* are free-living; the other species are sessile on nodules. Together, they illustrate the considerable morphological diversity of xenophyophores in a region where they dominate the megafauna, and highlight some major taxonomic challenges posed by these giant monothalamous foraminifera.

ADDITIONAL KEYWORDS: abyssal megafauna – Clarion–Clipperton Zone – deep-sea benthos – deep-sea mining – new species and genera – protist.

INTRODUCTION

Xenophyophores are large agglutinated protists confined to deep-sea habitats (Tendal, 1972). They live on and in soft sediments and on hard substrates from upper bathyal to extreme hadal depths (Tendal, 1996; Gallo *et al.*, 2013) and are abundant in abyssal plain settings (Amon *et al.*, 2016). The first species were described towards the end of the 19th century (Brady, 1883; Haeckel, 1889; Goës, 1892). They were variously assigned to the foraminifera, sponges or to a distinct protistan group allied to the mycetozoans or labyrinthulids (Tendal, 1972). Until fairly recently xenophyophores were generally regarded as representing a distinct subclass of 'rhizopods', but during the past

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decade or so an increasing number of molecular analyses have clearly demonstrated that they are monothalamous ('single chambered') foraminifera (Pawlowski *et al.*, 2003; Lecroq *et al.*, 2009; Gooday, Aranda da Silva & Pawlowski, 2011; Gooday *et al.*, 2017a). Two main groups, the stannomids and the psamminids, established as families in Schulze (1907a) and orders in Tendal (1972), have been recognized based on morphological criteria. However, this division is not supported by recent molecular analyses (Gooday *et al.*, 2017a).

Xenophyophores have been obtained during various oceanographic expeditions in the Pacific Ocean (Tendal, 1972; supplementary material in Gooday *et al.*, 2017a). Particularly notable for the present study are the collections from the central and eastern equatorial Pacific made during the *Challenger* (1872–1876) Expedition and several *Albatross* (1891, 1899–1900) campaigns. The *Challenger* material formed the basis for the important publication of Haeckel (1889) and the *Albatross* material was studied by Goës (1892) and Schulze (1907b), while Schulze included all of this early Pacific material in his synoptic 1907a 'Deutsche Tiefsee-Expeditie' report. Additional xenophyophores were collected in the eastern Pacific during the 1958 *Vema* Expedition and the 1964 Magdalena Bay Expedition (Tendal, 1972). Although these eastern Pacific collections were dominated by stannomid xenophyophores (Tendal, 1972), particularly species of *Stannophyllum*, they also provided the basis for the description of two psamminid genera, *Cerelasma* and *Psammina*, by Haeckel (1889).

Since the publication of Tendal's (1972) landmark monograph, several papers have described xenophyophore species from the abyssal eastern equatorial Pacific. Tendal (1980) established a new species of *Stannophyllum* collected during the French *Coriolis* Expedition in the eastern Clarion–Clipperton Zone (CCZ). Kamenskaya (2005) described a new genus and species, *Spiculammina delicata* Kamenskaya, 2005, from an area further west. Based on material from the same general area (130–135°W, 13–14°N), Kamenskaya et al. (2015, 2016) described six new species belonging to the psamminid genera *Aschemonella*, *Cerelasma*, *Psammina* and *Semipsammina* and the stannomid genus *Stannophyllum*. In addition to these taxonomic works, Levin *et al.* (1986) and Levin & Thomas (1988) analysed the diversity and distribution of xenophyophores on east Pacific seamounts and the association of metazoan meiofauna and macrofauna with their tests, Kamenskaya (1987) summarized the contribution of xenophyophores to benthic wet-weight biomass in the eastern and SW Pacific, and Kamenskaya, Melnik & Gooday (2013) presented data on the diversity and density of xenophyophores in the Russian exploration area (central CCZ) based on seafloor photographs and box core collections.

Here, we describe five new species of xenophyophore, two of them representing new genera, from the CCZ, a region of the eastern equatorial Pacific where polymetallic nodules are abundant on the seafloor. Samples were obtained during two research cruises (AB01, AB02) at sites within a 76 000 km^2 area ('UK-1') that has been licensed for seabed exploration to UK Seabed Resources Ltd (UKSRL) by the International Seabed Authority (ISA), and within an adjacent area ('OMS') licensed to Ocean Mineral Singapore (Fig. 1). The work was undertaken as part of ABYSSLINE, a biological baseline study funded by UKSRL that encompasses both of these exploration areas. In describing this new material we have employed a combination of molecular and morphological approaches. Previous publications originating from the ABYSSLINE project have included xenophyophores in a survey of megafauna seafloor photographs obtained in the UK-1 area during the AB01 cruise (Amon *et al.*, 2016), presented an overview of xenophyophore assemblages in samples collected during both cruises (Gooday *et al.*, 2017a), and established two new species of the genus *Aschemonella* (Gooday *et al.*, 2017b).

MATERIALS AND METHODS

Sample collection

The new xenophyophores were collected at 8 sites in the CCZ during the AB01 (R/V *Melville* cruise MV1313; 3–27 October 2013) and AB02 (R/V *Thomas G Thompson* cruise TN319; 12 February to 25 March 2015) cruises (Table 1). The AB01 cruise sampled in 'Stratum A', a 30 × 30 km square centred around 13°49′N, 116°36′W in the northern part of the UK-1 area, while the AB02 cruise sampled in UK-1 'Stratum B', centred around 12°28.9′N, 116°36.3′W in the SW part of the UK-1 area, and in the OMS 'Stratum', centred around 12°8.2′N, 117°17.7′W in the southern part of the OMS claim area. Specimens

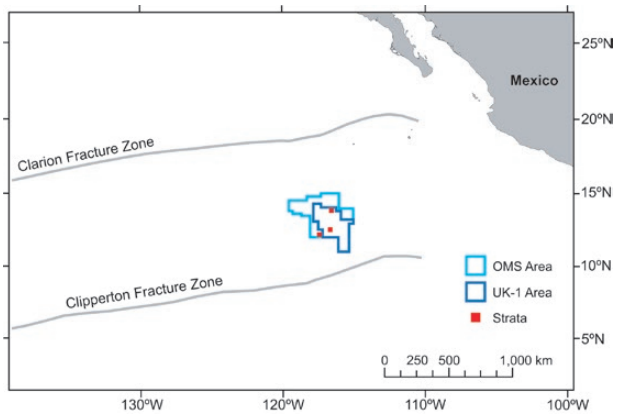

Figure 1. Location of UK-1 and OMS exploration license areas in the eastern Clarion–Clipperton Zone.

Table 1. Station data for samples yielding analysed xenophyophores

Cruise	Site	Deployment	Latitude N	Longitude W	Depth (m)	Species
AB01	B	MC02	13°50.792′	116°37.590′	4079	*Tendalia reteformis*
AB01	J	MC11	13°54.104′	116°35.402′	4166	*Tendalia reteformis*
AB01	I	BC10	13°45.001′	116°30.799′	4036	*Galatheammina interstincta*
AB02	U02	MC02	12°22.024′	116°31.020′	4150	*Semipsammina mattaeformis*, *Tendalia reteformis*
AB02	U05	MC04	12°22.264′	116°36.818′	4163	*Semipsammina mattaeformis*
AB02	U04	MC05	12°37.741′	116°43.424′	4236	*Shinkaiya contorta*
AB02	U09	MC14	12°27.125′	116°30.736′	4199	*Semipsammina mattaeformis*, *Tendalia reteformis*
AB02	S08	MC22	12°11.417′	117°22.284′	4182	*Tendalia reteformis*
AB02	S04	BC10	12°00.567′	117°10.687′	4144	*Bizarria bryriformis*
AB02	U12	BC18	12°25.195′	116°37.477′	4136	*Galatheammina interstincta*

BC, box corer; MC, Megacorer.

were recovered using either an USNEL box core or an OSIL Bowers and Connelly Megacorer equipped with 10 cm diameter core tubes. A few were collected using a Brenke epibenthic sledge. The majority of the specimens described here originated from the second cruise.

Photography

Xenophyophore tests were first photographed on the surfaces of cores before being placed in a bowl of chilled seawater on ice and removed to the ship's laboratory, where they were extensively photographed using either a Canon 60D SRL digital camera attached to an Olympus SZX7 microscope, or a hand-held Nikon D3100 SLR digital camera fitted with Nikon 62 mm macro lens. Parts of specimens, dissected fragments of cytoplasm, or in a few cases entire specimens, were preserved in RNAlater solution (Qiagen) for later molecular analyses. Others were fixed in 4% borax-buffered formalin for morphological analysis. Additional photographs were taken in land-based laboratories using either the same system that was used on the ship (Southampton) or a Leica M205 C motorized stereomicroscope equipped with a Leica DFC 450 C camera (Geneva).

Fragments of selected specimens were examined using a Carl Zeiss LEO 1450VP scanning electron microscope (SEM). Most samples were mounted on SEM stubs and sputter coated with 20 nm of gold, although four were left uncoated and imaged in the variable pressure (VP) mode. All imaging was undertaken with a backscatter detector, at 8–10 kV, a nominal probe current of 350–500 pA, and a working distance (WD) of 13–19 mm. X-ray microanalysis in the SEM was undertaken using an Oxford Instruments X-Act Silicon Drift Detector (operating conditions, 20 kV, probe current 1 nA, 15 mm WD), to determine the composition of agglutinated and other particles associated with the xenophyophore tests.

DNA extraction, PCR amplification, cloning and sequencing

Specimens and fragments of xenophyophores preserved in RNAlater solution (Qiagen) were dissected and pieces of cytoplasm removed for analysis. DNA was extracted using the DNeasy Plant Mini Kit (Qiagen). DNA isolate numbers and collection sites are given in (Table 2). 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 Purification Kit (Roche Diagnostics) cloned with the TOPO TA Cloning Kit (Invitrogen) following the manufacturer's instructions and transformed into competent *Escherichia coli*. Sequencing reactions were performed using the BigDye Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems) and analysed on a 3130XL Genetic Analyzer (Applied Biosystems). The newly obtained xenophyophore sequences were deposited in the EMBL/GenBank database (accession numbers LT854188–LT854219).

Phylogenetic analysis

The new sequences were added to an existing database using the Muscle automatic alignment option as implemented in Seaview version 4.3.3. (Gouy, Guindon & Gascuel, 2010). Sequence length varied from 720 to 1026 base pairs (*Semipsammina mattaeformis* sp. nov. and *Syringammina corbicula* Richardson, 2001, respectively), and 58 taxa were used for the analysis. The GC content ranges from 34.3% (*Tendalia reteformis* gen. et sp. nov.) to 45.2% (*S. mattaeformis*).

Table 2. Sequencing details

DNA isolate	Species	Sampling area	Accession numbers
18256	*Bizarria bryiformis*	OMS Stratum, eastern CCZ	LT854206, LT854207, LT854208
18257	*Bizarria bryiformis*	OMS Stratum, eastern CCZ	LT854209, LT854210, LT854211
18258	*Bizarria bryiformis*	OMS Stratum, eastern CCZ	LT854212, LT854213, LT854214
18259	*Bizarria bryiformis*	OMS Stratum, eastern CCZ	LT576126, LT854215, LT854216
18260	*Bizarria bryiformis*	OMS Stratum, eastern CCZ	LT854217, LT854218, LT854219
18278	*Galatheammina interstincta*	UK-1 Stratum B, eastern CCZ	LT576131, LT854191, LT854192
18279	*Galatheammina interstincta*	UK-1 Stratum B, eastern CCZ	LT854193, LT854194
18460	*Galatheammina* sp. 6	OMS Stratum, eastern CCZ	LT576137
18234	*Psammina limbata*	OMS Stratum, eastern CCZ	LT576129
18270	*Psammina* sp. 3	UK-1 Stratum B, eastern CCZ	LT576130
18239	*Semipsammina mattaeformis*	UK-1 Stratum B, eastern CCZ	LT576127, LT854195, LT854196
18265	*Semipsammina mattaeformis*	UK-1 Stratum B, eastern CCZ	LT854197, LT854198
18436	*Semipsammina mattaeformis*	UK-1 Stratum B, eastern CCZ	LT854199
18231	*Tendalia reteformis*	OMS Stratum, eastern CCZ	LT576120, LT854200
18438	*Tendalia reteformis*	OMS Stratum, eastern CCZ	LT854201, LT854202
18439	*Tendalia reteformis*	OMS Stratum, eastern CCZ	LT854203, LT854204, LT854205
2270	*Syringammina corbicula*	Atlantic Ocean, off Cape Verde	AJ514856
18252	*Shinkaiya contorta*	UK-1 Stratum B, eastern CCZ	LT576124
18253	*Shinkaiya contorta*	UK-1 Stratum B, eastern CCZ	LT854188, LT854189, LT854190
Not specified	*Shinkaiya lindsayi*	Japan Trench off Sanriku	EU649778
9356	*Reticulammina cerebriformis*	Portugal, Nazaré Canyon	LT839028
9357	*Reticulammina cerebriformis*	Portugal, Nazaré Canyon	LT839029
9361	*Reticulammina cerebriformis*	Portugal, Nazaré Canyon	LT839030
9362	*Reticulammina cerebriformis*	Portugal, Nazaré Canyon	LT839031
9363	*Reticulammina cerebriformis*	Portugal, Nazaré Canyon	LT839032
9364	*Reticulammina cerebriformis*	Portugal, Nazaré Canyon	LT839033
9365	*Reticulammina cerebriformis*	Portugal, Nazaré Canyon	LT839034
Not specified	Xenophyophore	Japan, Izu–Ogasawara	AB694014
3541	*Saccammina sphaerica*	Weddell Sea	LT796824
2882	*Gloiogullmia* sp.	Svalbard	LT796823
4724	*Hippocrepina indivisa*	Svalbard	LT796825
5174	*Leptammina* sp.	Weddell Sea	LT796826
4026	*Bowseria arctowskii*	Antarctica	FR875094
3929	*Psammosphaera* sp.	Antarctica	LT796822
1916	Allogromiid	Antarctica	AJ307745
1212	Allogromiid	Antarctica	AJ307744

CCZ, Clarion–Clipperton Zone; OMS, Ocean Mineral Singapore exploration license area; UK-1, United Kingdom 1 exploration license area.

A phylogenetic tree was constructed using PhyML 3.0 with automatic model selection as implemented in ATGC:PhyML (Guindon *et al.*, 2010). A GTR substitution model was selected for the analysis. Bootstrap values (BV) are based on 100 replicates.

Terminology

For consistency with earlier literature, we apply the following special terms for morphological features traditionally used when describing xenophyophores (Tendal, 1972).

Granellare: The cell body and the organic tube system that encloses it (the organic tube is rarely clearly visible in the species described here).

Stercomare: Accumulations of waste pellets (stercomata) enclosed within an organic membrane.

Xenophyae: The agglutinated particles that make up the test. We use this term interchangeably with others such as 'grain' and 'particle'.

The type material is deposited in the Natural History Museum, London, under registration numbers NHMUK PM PF74513–74528.

SYSTEMATICS

PROTISTA
SUPERGROUP RHIZARIA CAVALIER-SMITH, 2002
FORAMINIFERA D'ORBIGNY, 1826

'MONOTHALAMIDS'

GENUS *SHINKAIYA* LECROQ, GOODAY, TSUCHIYA, PAWLOWSKI, 2009

Diagnosis: Test up to 80 mm diameter, fragile, approximately dome-shaped or cylindrical in shape, forming tightly or loosely meshed reticulated structure comprising either bar-shaped elements (~0.5 cm in diameter) separated by open spaces or fairly thick (1.3–2.0 mm) plate-like elements with variably developed 'growth lines'. Test wall relatively thick, weakly cemented with smooth outer surface, and composed of fine sediment with some larger particles. Variable numbers of internal xenophyae, mainly radiolarian tests, present (modified after Lecroq *et al.*, 2009).

SHINKAIYA CONTORTA GOODAY & HOLZMANN **SP. NOV.** (Fig. 2A–F)

urn:lsid:zoobank.org:act:337149E8-C03B-42C4-BE08-38EB7F07C02E

Galatheammina sp. 4, Gooday *et al.*, 2017a, Supplementary Figure 1b therein

Diagnosis: Test free, 46 mm diameter, comprising more or less strongly curved, fairly thick, plate-like elements that merge in places to form a complex, partly reticulated structure; plates display variably developed growth lines and have undulating outer margins sometimes extending into lobate processes. Wall fine-grained, incorporating some larger particles (mainly radiolarians), with outer layer (270–500 µm thick) distinct from the much darker test interior

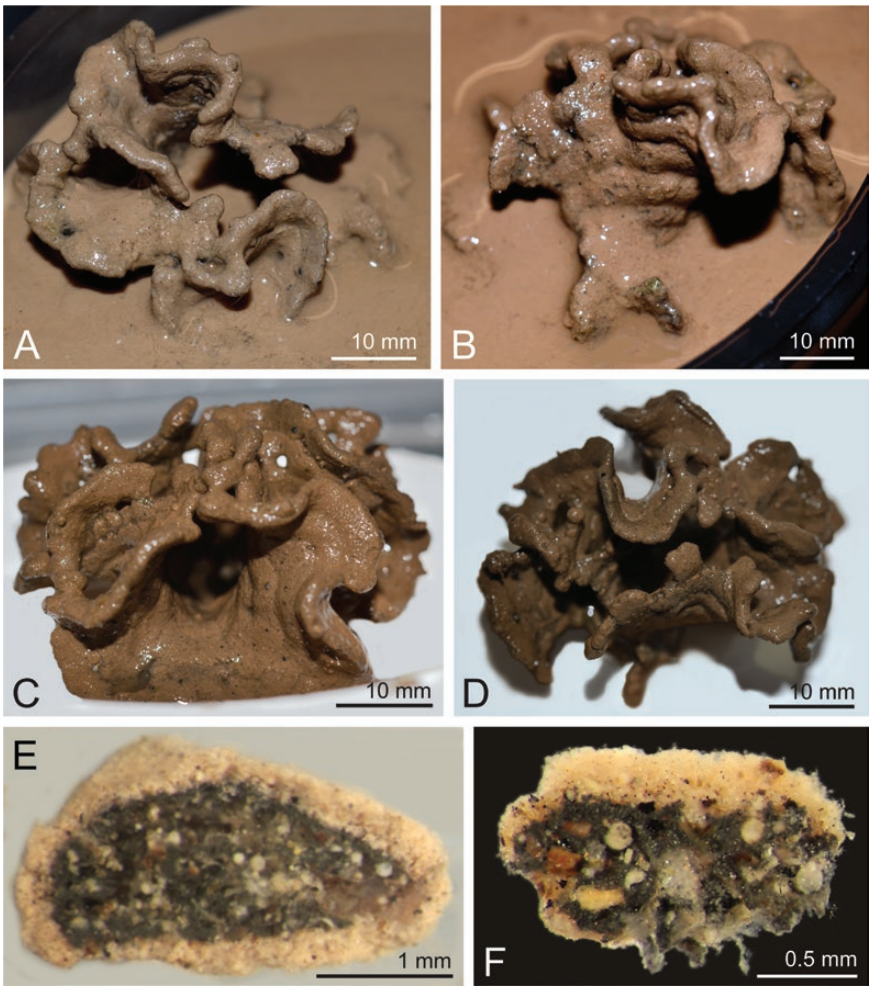

Figure 2. ***Shinkaiya contorta*** **sp. nov.**; AB02 cruise, Station U04 (Megacorer #05); holotype, reg. no. NHMUK PM PF74513. A, B, shipboard photographs showing two views of the test, as originally seen on the core surface. A, view of test from above. B, oblique view showing clearly developed 'growth lines'. C, D, laboratory photographs. C, side view. D, top view. E, shipboard photograph showing broken cross section of test fragment. F, shipboard photograph of test fragments.

occupied mainly by voluminous stercomare masses and radiolarians.

Etymology: Latin: *contorta* referring to the contorted appearance of the test.

Type specimen: The unique holotype was collected in a megacore (deployment MC05) from Station U04 during the AB02 cruise (12°37.741′N, 116°43.424′W, 4236 m). Registration number NHMUK PM PF74513.

Description

Test morphology: The test forms a relatively large and complex structure, light brownish in overall colour and measuring about 46 by 40 mm. The basic morphology is plate-like, but incorporating some bar-shaped elements as well (Fig. 2A–D). The plate-like parts are punctuated by occasional open spaces. They are more or less strongly curved and form several complete circuits to create a partly reticulated structure that includes a funnel-like feature. The plate-like sections are generally ~1.3–2.0 mm thick with smoothly undulating, rounded margins, sometimes produced into lobate extensions. In places, the plates are traversed by concentric 'growth lines' (Fig. 2B, C).

Wall structure: The test has a distinct outer layer (Fig. 2E), which is soft, weakly cemented and generally 270–500 µm thick. The outer surface is more or less smooth and composed of fine-grained material with scattered larger grains, mainly radiolarians, that sometimes protrude from the surface, but also incorporating occasional micronodules and other particles. There are no obvious openings in the wall.

Test interior: The interior is largely occupied by masses of stercomare that weave around the scattered internal xenophyae (Fig. 2E, F). The stercomare is organized as a tightly anastomosing system of irregular strands, typically measuring 50–100 µm diameter, that merge into larger masses up to 200 µm or more in size (Fig. 2F). These formations are enclosed by a reflective organic membrane and consist of accumulations of very dark (almost black) stercomata, 5–12 µm in diameter. The granellare strings are relatively sparse and inconspicuous in the single available specimen; they are pale in colour and 50–70 µm in diameter. Barite crystals were not observed in the few fragments of granellare examined under a compound microscope.

Remarks

Gooday *et al.* (2017a) referred to this species to the genus *Galatheammina*. We transfer it to *Shinkaiya* based on its close genetic affinity with the genotype, *Shinkaiya lindsayi* Lecroq, Gooday, Tsuchiya & Pawlowski 2009, described from a single specimen collected near the Japan Trench at 5435 m depth (Lecroq *et al.*, 2009). The two species are supported by a BV value of 100% (Fig. 3) and share a relatively soft and basically fine-grained test wall, but the test is dominated by bar-shaped elements in *S. lindsayi* compared with plate-like elements in *S. contorta*. Internal xenophyae are also more numerous in the new species.

Shinkaiya contorta presents something of a taxonomic conundrum since, in terms of test morphology, it is more similar to *Reticulammina cerebreformis* Gooday, Aranda da Silva & Pawlowski, 2011 from abyssal depths in the Nazaré Canyon (NE Atlantic) than to *S. lindsayi*. In both cases the test comprises reticulated plates with a similar thickness (1–3 mm), structure and friable consistency (Gooday *et al.*, 2011). The main difference is that the test is less tightly reticulated in *S. contorta* than in *R. cerebriformis* and the wall is thicker (270–500 µm compared to 60–100 µm). The two genera branch as sister groups supported by a strong BV (85%) which confirms the shared origin of their morphological similarities.

Two other species assigned to *Reticulammina* have tests made up of plate-like elements that are reticulated to a greater or lesser extent, as in *S. contorta*. In *R. lamellata* Tendal, 1972 from 1253 m off New Zealand, the test has a more clearly reticulated structure with a thinner (200 µm) surface layer than *S. contorta* and, unlike the new species, is composed exclusively of sand grains. *Reticulammina plicata* Gooday, 1996, described from a single specimen collected on the Cape Verde Abyssal Plain (4613 m depth), has a much smaller, more neatly rounded test than *S. contorta* (~18 mm maximum dimension compared to 46 mm) and the plate-like elements are considerably thinner (0.34–0.42 mm compared with 1.4–2.0 mm). A variety of undescribed xenophyophores with similar morphologies have been photographed on the seafloor in different parts of the CCZ (Kamenskaya *et al.*, 2013; Amon *et al.*, 2016). The Protista section of the Atlas of Megafaunal Morphotypes of the Clarion–Clipperton Fracture Zone includes examples of these morphotypes (Gooday & Kamenskaya, 2013, www.ccfzatlas.com, last accessed 11 November 2017). Levin & Thomas (1988: fig. 2a–e, g) used a submersible to collect some reticulated specimens of this type, which they identified as *Reticulammina* spp., at bathyal depths (1741–1952 m) on two seamounts located southeast of the CCZ (around 10°N, 104°30′W). They recovered similar morphotypes at 1957 and 2776 m, respectively, on Green and NW Bonanza Seamounts, located to the north of the CCZ (Levin & Thomas, 1988: fig. 1a, c; some of the same images were published in Levin, 1991: fig. 2; 1994: fig. 1).

There are no molecular data for *R. lamellata* and *R. plicata*, or for *R. labyrinthica* Tendal, 1972, the type species of the genus *Reticulammina*, making it difficult to establish the boundary between this genus and *Shinkaiya*. Hori *et al.* (2013) published sequence data

Figure 3. PhyML phylogenetic tree showing evolutionary relationships of *Tendalia reteformis*, *Shinkaiya contorta*, *Reticulammina cerebriformis*, *Semipsammina mattaeformis*, *Bizarria bryiformis* and *Galatheammina interstincta* together with eight species of monothalamid Clades A, B and C. The tree is rooted in Clade A. Numbers at nodes indicate bootstrap values.

for an unidentified xenophyophore obtained during an Remote Operated Vehicle (ROV) dive at 7111 m on the Isu–Ogasawara Trench slope. This specimen groups closely with *R. cerebriformis* with 100% BV (Fig. 3). Detailed photographs showing its test morphology are not available, but images taken by the ROV show a

number of specimens on the seafloor that appear to have fairly complex plate-like tests that are reticulated, at least to some extent. This provides additional evidence that xenophyophores with folded, reticulated, plate-like morphologies do not represent a single genetically coherent grouping.

Distribution: Currently known only from Stratum B of the UK-1 exploration license area.

GENUS *GALATHEAMMINA* TENDAL, 1972

Diagnosis: Body lumpy, branched or flattened, sometimes with basal root-like structures. More or less firmly cemented xenophyae form outer test layer. Interior consists of loose accumulation of xenophyae with granellare and stercomare (modified after Tendal, 1972 and Gooday, 1991).

GALATHEAMMINA INTERSTINCTA GOODAY & HOLZMANN SP. NOV.
(Figs 4–6)

urn:lsid:zoobank.org:act:E9678049-7339-4FE2-BD1C-D755E4C3892B

Galatheammina sp. 5. Gooday *et al.*, 2017a, Figure 2c, f; Supplementary Figure 2d therein

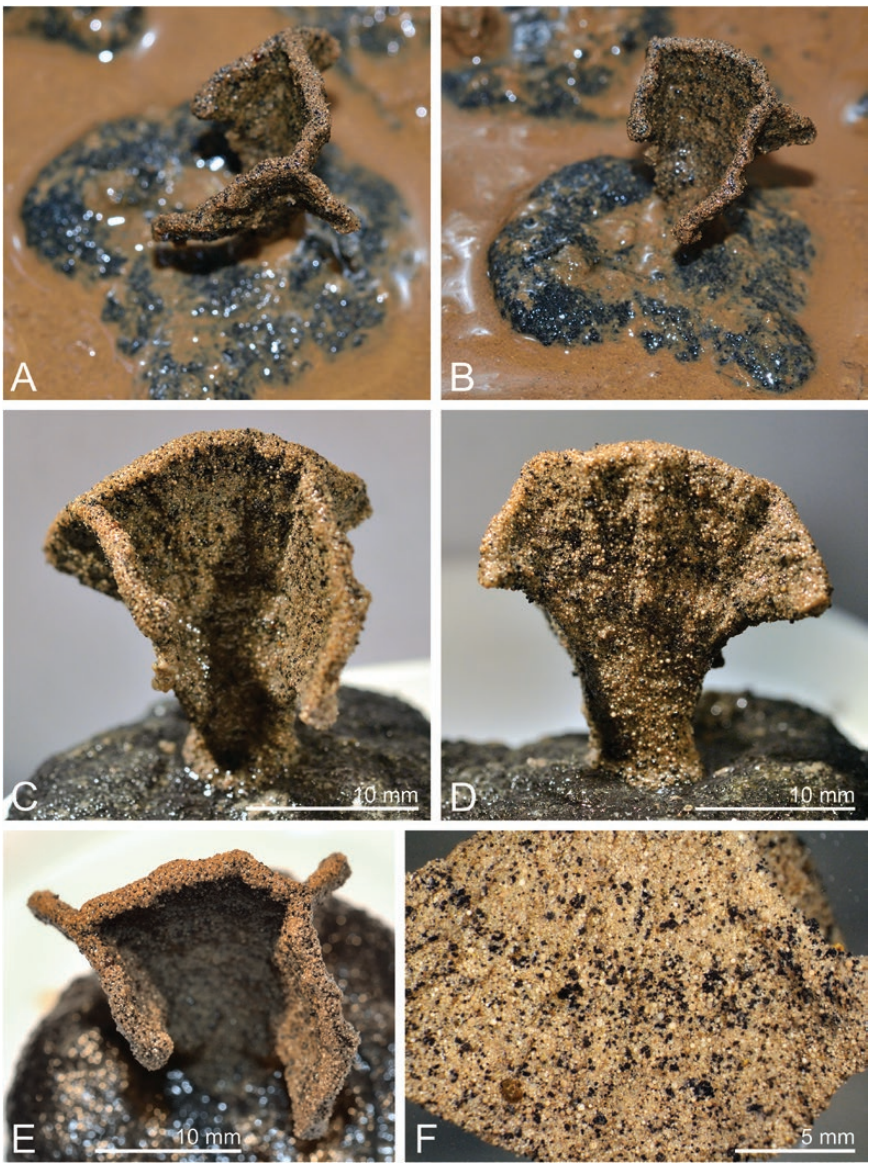

Figure 4. ***Galatheammina interstincta*** **sp. nov.**; AB02 cruise, Station U12 (box corer #18); holotype, reg. no. NHMUK PM PF74514; shipboard photographs. A, B, two views of the test attached to a nodule, as originally seen on the core surface. C, D, opposite sides of the test. E, view of test from above. F, surface of test showing characteristic speckled appearance.

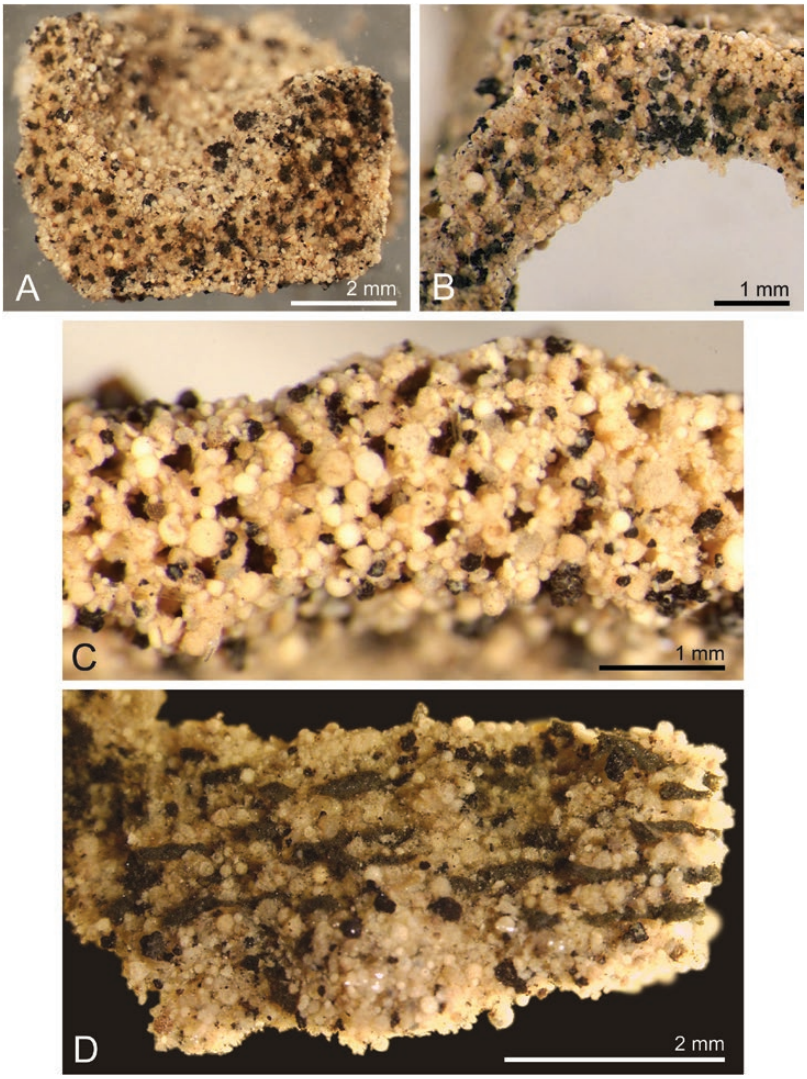

Figure 5. ***Galatheammina interstincta*** **sp. nov.**; AB02 cruise, Station U12 (box corer #18); holotype, reg. no. NHMUK PM PF74514. A, B, shipboard photographs showing broken test surfaces with cross sections of stercomare strands visible as more or less circular black patches. Some of the more irregularly shaped black patches are micronodules. C, laboratory photograph of intact upper margin of the test showing numerous 'pores' (apertures). D, laboratory photograph of longitudinal surface of fractured test showing parallel-trending stercomare strands.

Diagnosis: Test attached, with short basal stalk giving rise to plate-like upper part with one or more side plates. Orange-brown test wall speckled with dark particles (micronodules). Fairly firmly cemented outer layer of xenophyae only weakly differentiated from test interior, which is dominated by internal xenophyae. Distinct stercomare strands run parallel to main axis of growth throughout interior, appearing as distinct spots on broken cross sections of test. Granellare strands relatively sparsely developed.

Etymology: Latin *interstincta*, meaning spotted or speckled, referring to the speckled appearance of the agglutinated test surface, as well as the spotty appearance of the stercomare strands when seen in cross section in broken test surfaces.

Material: The holotype was collected in a box core (BC18) from Station U12 during the AB02 cruise (12°25.195′N, 116°37.477′W, 4136 m). Registration number NHMUK PM PF74514. Part of the test was broken off and used for molecular analyses. A second specimen was collected in a box core (BC10) at Station I during the AB01 cruise (13°45.001′N, 116°30.799′W, 4036 m).

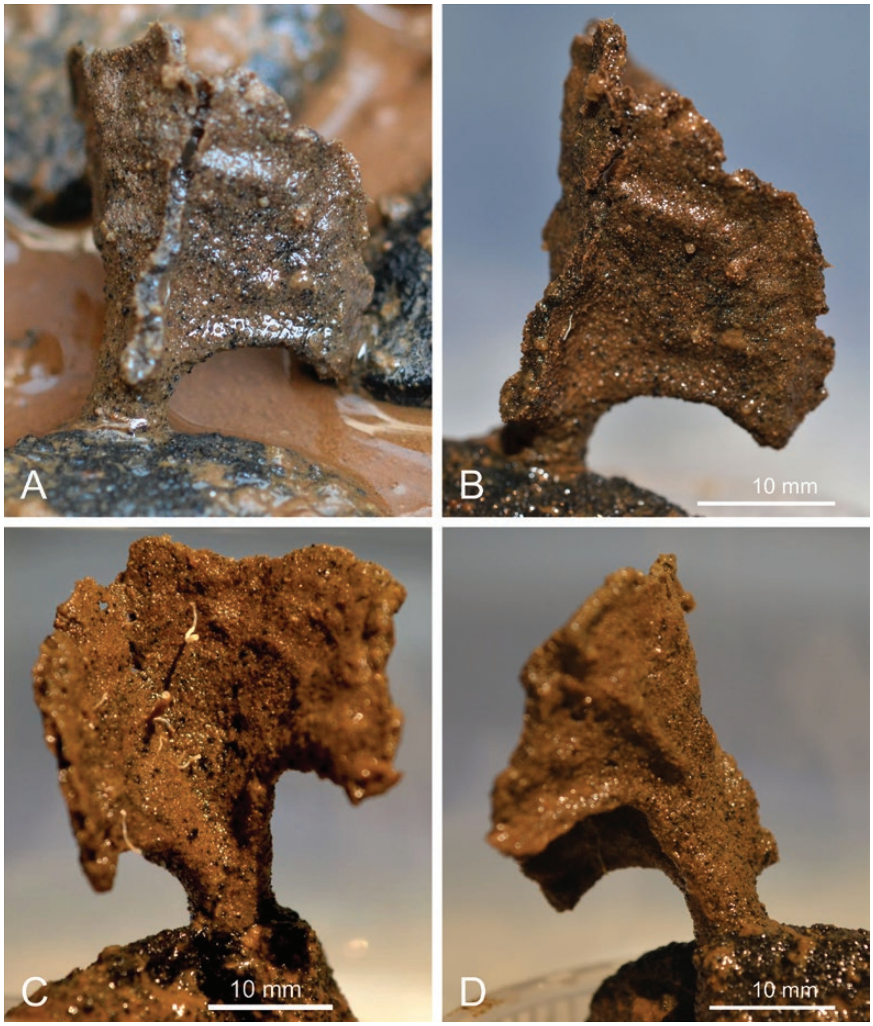

Figure 6. ***Galatheammina interstincta*** **sp. nov.**; AB01 cruise, Station I (box corer #10), shipboard photographs. A, views of the convex side of the test, as originally seen on the core surface; note the broken base of what was probably a side plate. B–D, different views of the test.

Description of holotype

Test morphology: The test was ~22 mm high when intact. It was attached to the nodule surface by a stalk, ~8 mm long and ~6.5 mm wide, that merged into the upper part of the test, which is organized as a series of plates. A gently curved central plate, ~14.3 mm long, arises directly from the stalk. At either end of this central plate are two relatively long side plates, one ~15 mm long and the other ~9.5 mm long, that extend outwards at more or less 90° to the central plate so that the test describes three sides of a somewhat distorted rectangle when viewed from above (Fig. 4A, E). Two shorter plates, both ~4 mm long when viewed from above and triangular in shape when viewed from the side (Fig. 4D, E), extend at an angle of about 45° from the opposite side of the central plate. An abraded ridge, possibly a plate in the early stages of growth, extends down the same side (Fig. 4D). The plates are 1.4–2.0 mm (typically 1.5–1.8 mm) thick. The maximum width of the test, measured along the central plate and including the two short side plates, is 21.5 mm. When complete, the test had a box-like appearance when viewed from above and from the side with the longer side plates (Fig. 4C, E), and a fan-like appearance when viewed from the opposite side (Fig. 4D).

Wall structure: The test is friable and composed of a mixture of light and dark particles (mainly radiolarians and micronodules, respectively) that impart a distinctive speckled appearance to the surface (Fig. 4F). Fine-grained material is largely absent. The outer test layer is rather indistinct and not clearly differentiated from the test interior (Fig. 5A, B). The undamaged margin of the test is gently rounded and punctuated by numerous pore-like features, irregularly rounded openings in the

agglutinated surface measuring 120–230 µm (typically 150–230 µm) in diameter (Fig. 5C). The interior of the test is occupied mainly by internal xenophyae (radiolarians and scattered micronodules) and stercomare.

Stercomare and granellare: The stercomare forms strings, 90–250 µm wide, which run more or less parallel to each other and to the direction of growth of the test. They are seen most clearly on broken longitudinal sections of the test (Fig. 5D), and appear as dark spots on broken surfaces at right angles to the direction of growth (Fig. 5A). These dark spots correspond in size and number to the pores on unbroken margins. The granellare threads are not clearly visible on broken surfaces. They are pale yellowish, 25–75 µm wide and sometimes branch.

AB01 specimen (Fig. 6)

The test is attached to a nodule and measures ~31 mm in overall height and ~34 mm in maximum width. It comprises a relatively short, thick stalk, ~9 mm long and ~6–9 mm wide, that merges into the upper plate-like part. The plate is roughly fan-shaped, 1.4–1.9 mm thick and strongly curved through ~90° about a vertical axis. The margin is damaged and somewhat irregular. The broken base of what was probably a secondary plate extends down most of the height of the test on the outer (convex) side of the main plate; this feature is visible in a photograph of the test on the sediment surface taken immediately after recovery of the box core (Fig. 6A).

The test comprises a mixture of radiolarians and micronodules. The outer layer is more clearly differentiated from the test interior than in the holotype and comprises a mixture of internal xenophyae and fine-grained greyish material, presumably the decayed remains of the stercomare. The specimen was obviously dead when collected.

Remarks

As in the case of some other xenophyophores with a plate-like morphology, the generic placement of this species is problematic. An unusual feature of *Galatheammina interstincta* is the more or less parallel arrangement of the stercomare strands. Schulze (1907b: Pl. 6, figs 1–2) illustrates a general alignment of stercomare strands in *Stannophyllum zonarium* Haeckel, 1889, apparently corresponding to the direction of growth, and in *Psammina nummulina* Haeckel, 1889 the stercomare are described as 'radially extending, sometimes anastomosing masses' (Tendal, 1972: 32; perhaps based on Haeckel, 1889: Pl. 7, fig. 3). However, in neither of these species do the stercomare strands run parallel. The openings on the test margin, which appear to correspond to the stercomare strands, can be compared to the 'large pores' present along the margin of *Psammina* species (Tendal, 1972: 32). On the other hand, the internal xenophyae are not arranged into the pillar-like features mentioned in diagnoses of *Psammina* (Haeckel, 1889; Tendal, 1972). The test structure is more suggestive of *Galatheammina*, although a surface layer of xenophyae that is clearly distinguishable from the test interior is developed only in the specimen from the AB01 cruise. In the holotype, the test has a more homogeneous appearance in broken sections. In our phylogenetic tree (Fig. 3), *G. interstincta* branches as sister to *Galatheammina* sp. 6 and *Psammina* sp. 3, with *Psammina limbata* and *S. corbicula* Richardson, 2001 at their base. The mixed clade, consisting of different *Galatheammina* and *Psammina* species together with *S. corbicula*, is supported by a moderate BV of 77%. For consistency with Gooday *et al.* (2017a), we retain this species in *Galatheammina.* It is possible that the collection of more specimens will lead to the establishment of a new genus to accommodate it.

Distribution: Currently known from Strata A and B of the UK-1 exploration license area.

GENUS *SEMIPSAMMINA* TENDAL, 1975

Diagnosis: Test attached, consisting of one layer of agglutinated particles covering the stercomare and granellare, which lie directly adjacent to the substrate (modified from Tendal, 1975).

SEMIPSAMMINA MATTAEFORMIS GOODAY & HOLZMANN **SP. NOV.** (Figs 7–9)

urn:lsid:zoobank.org:act:71CC9582-4A49-47E8-B51F-F8D589EADB2D

Semipsammina sp. nov. 1. Gooday *et al.*, 2017a, Supplementary Figure 1f therein

Diagnosis: Test attached, up to 2 cm maximum dimension, forming rounded plate-like or more complex reticulated structure covering stercomare that lie directly on substrate. Tubular extensions of test or more complex excrescences typically developed. Test wall thin, delicate, flexible, with rather lumpy upper surface; composed mainly of fine-grained material. Stercomare mat-like, comprising convoluted and closely packed masses, generally 100–200 µm in width, that appear to merge and anastomose, or in places are aligned to run more or less parallel. Obvious granellare strands not observed, but sparse whitish material may represent cytoplasm.

Etymology: Latin: *matta*, *mattae*, mat of rushes; referring to the mat-like appearance of the stercomare.

Type material: The holotype (registration number NHMUK PM PF74515) and two paratypes (registration

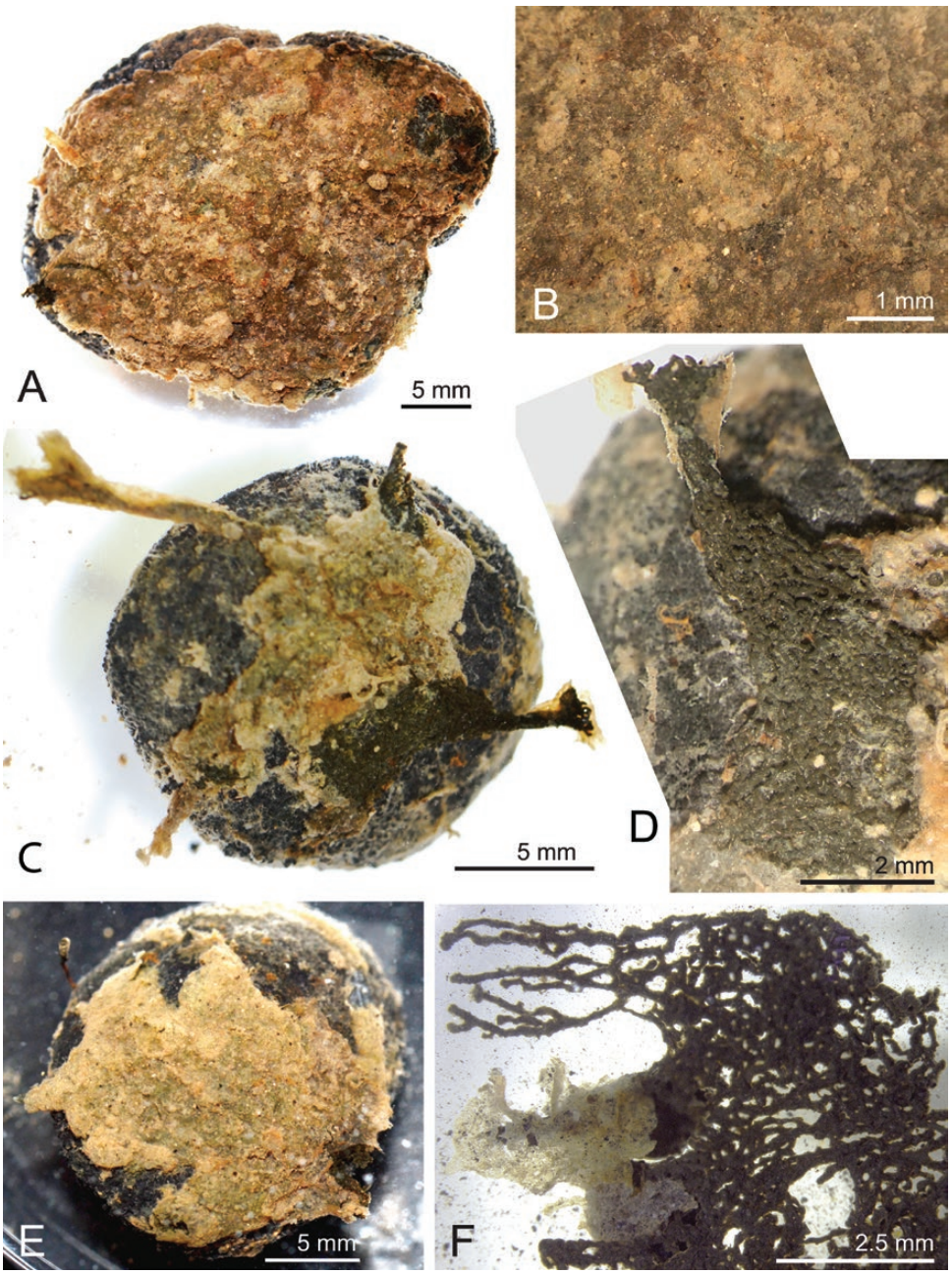

Figure 7. ***Semipsammina mattaeformis*** **sp. nov.**, shipboard photographs except where indicated; AB02 cruise, Station U09 (Megacorer deployment #14). A, B, holotype, reg. no. NHMUK PM PF74515. A, complete individual attached to nodule. B, detail of test surface. C, paratype, reg. no. NHMUK PM PF74516; note the four relatively long tubular extensions, each housing stercomare strands. D, detail showing exposed stercomare and extension. E, entire specimen that was preserved in RNAlater for molecular analysis. F, stercomare and fragment of test (laboratory photograph).

numbers NHMUK PM PF74516 and 74517) were collected in a megacore (deployment MC14) at Station U09 (12°27.125′N, 116°30.736′W, 4199 m) during the AB02 cruise. The test of the second paratype has been largely removed to expose the underlying structures.

Other material: One additional specimen from Station U09, one specimen from Station U02 (Megacorer deployment MC02) and two specimens from Station U05 (Megacorer deployment MC04).

Description

Test morphology: The test is pale brown or somewhat greenish in overall colour and forms a low canopy over the stercomare system. The holotype measures

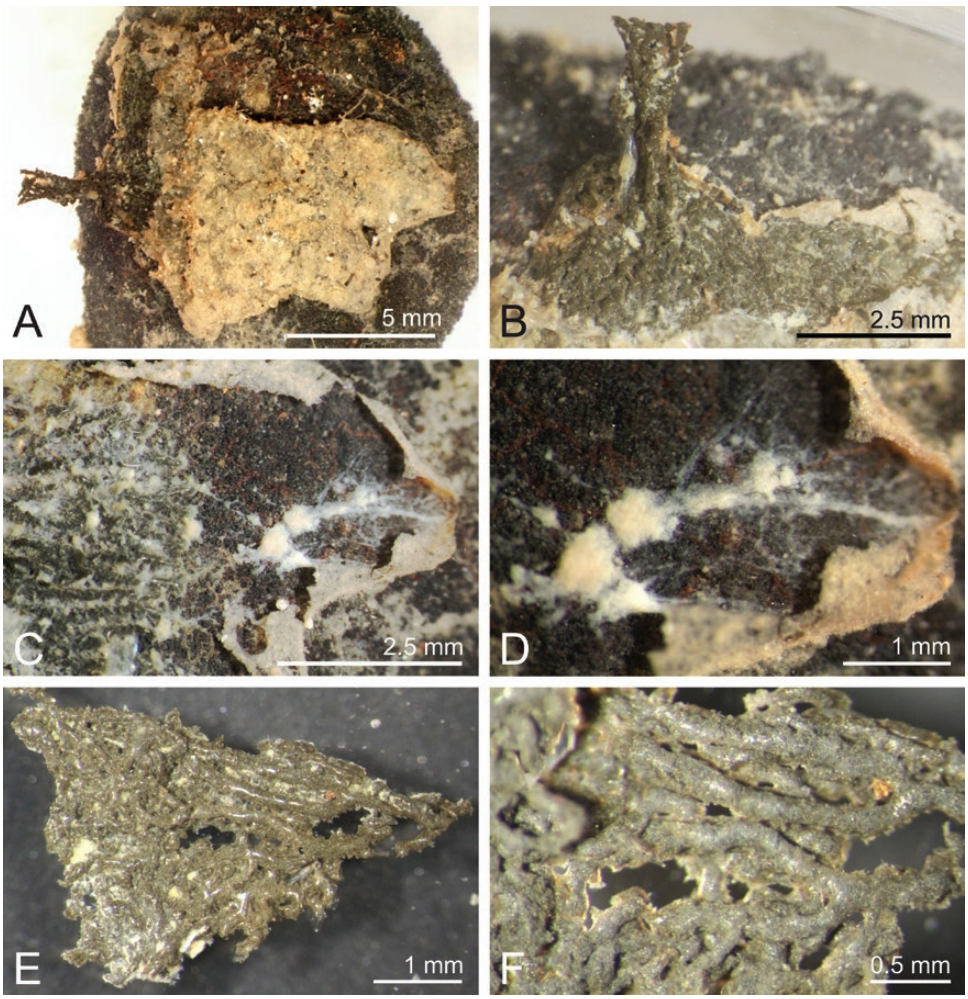

Figure 8. ***Semipsammina mattaeformis*** **sp. nov.**, shipboard photographs; AB02 cruise, Station U09 (Megacorer deployment #14); paratype, reg. no. NHMUK PM PF74517. A, more or less intact specimen. B, detail of stercomare and extension exposed at the edge of the test. C, opposite end with test removed to expose parallel stercomare strands and white material interpreted as cytoplasm. D, detail of white material; note fine threads arising from white masses. E, detached part of stercomare. F, detail. Because the test and part of the stercomare have been removed, the preserved specimen consists of the remains of the stercomare system attached to the nodule surface.

~33 × 30 mm and the two paratypes measure 13.3 × 10 mm and 12.2 × 8.2 mm (Figs 7A–D, 8A). A fourth specimen, preserved in RNAlater for molecular analyses, measured 18.6 × 14.4 mm (Fig. 7E, F). All have, or had, a more or less irregular but basically rounded outline with angular or lobate sections. A fifth unregistered specimen from the type locality has an elongate test, 19.1 mm long and between 1.5 and 5.1 mm wide. All available specimens have tubular extensions of the main test. One of the paratypes (registration number NHMUK PM PF74516; Fig. 7C, D) has four extensions, situated approximately at right angles to each other; the longest is 9.4 mm in length and bifurcates at the end while the second longest is 6.2 mm in length.

Other specimens exhibit more complex morphologies. One from Station U05 has a highly irregular structure that includes flat tunnel and mat-like elements extending around a deep hollow in the nodule surface as well as being draped over different faces of the nodule (Fig. 9A). It measures ~20 mm in maximum extent (excluding the tubular extension). Extending upwards from the surface are a number of complex but basically tubular excrescences of varying size, most of them branching to some extent. In addition, a relatively long tubular extension, which bifurcates at the end and has a short proximal side branch, extends out from one side of the test. A second specimen from the same sample forms an irregularly reticulated structure extending over an area of

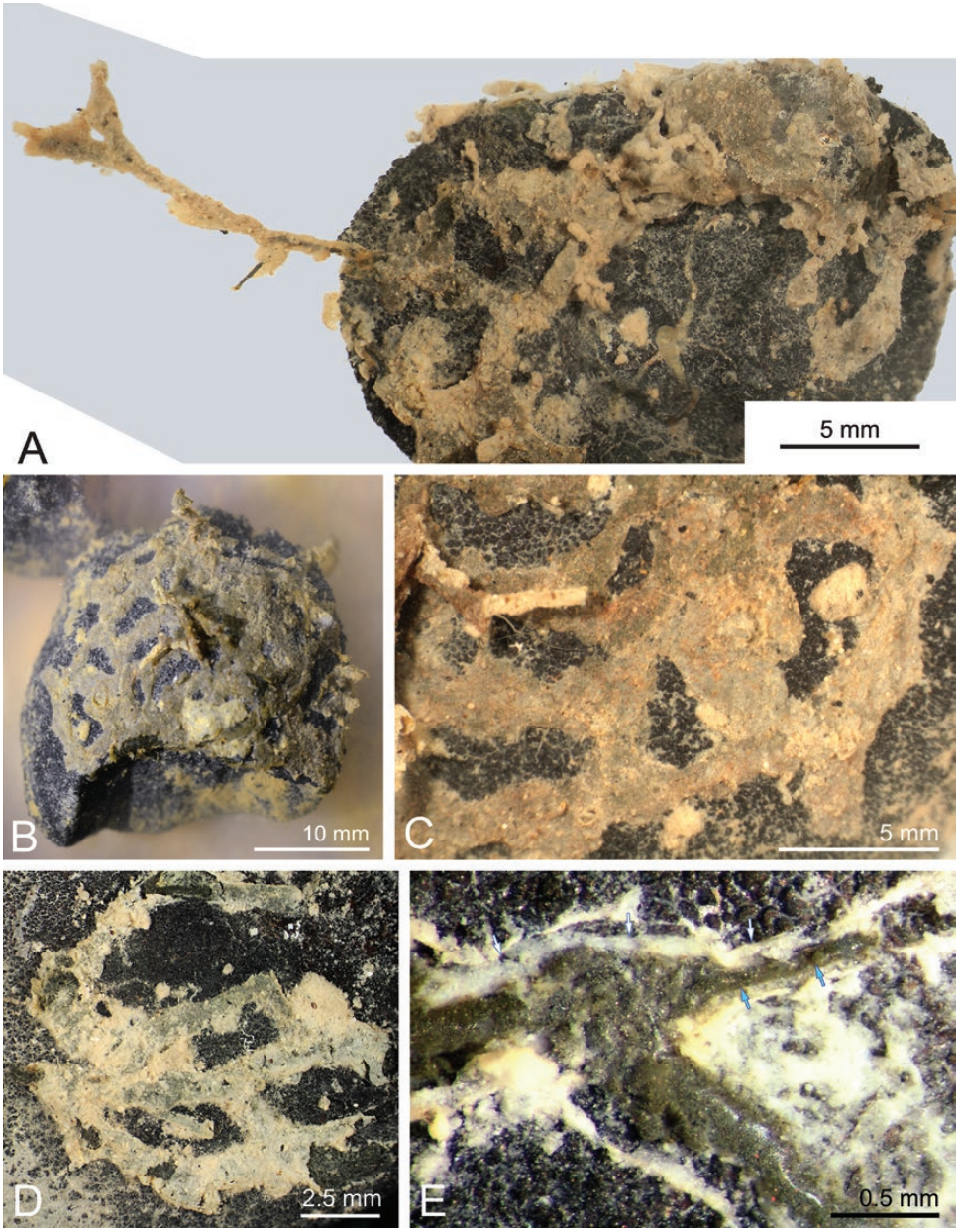

Figure 9. ***Semipsammina mattaeformis*** **sp. nov.**, shipboard photographs except where indicated. A, AB02 cruise, Station U09 (Megacorer deployment #14); complex specimen with long tubular extension and various excrescences. B, Station U09; specimen with reticulated test. C, detail, showing tubular structure (upper right). D, AB02 cruise, Station U02 (Megacorer deployment #02); specimen with reticulated test. E, part of the same specimen (upper part in Fig. D) with the test removed to expose stercomare and strand of white cytoplasm (white arrows). The blue arrows indicate a tubular section of the test occupied by a single stercomare strand.

~27 mm by 20 mm and covering much of the surface of a small nodule (Fig. 9B). Several tubular structures arise from the surface. The largest of these involves two separate tubes, one with a side branch, that fuse together into a single structure (Fig. 9C). Finally, the specimen from Station U02 forms a flat, mat-like structure, covering an area measuring 11 × 7 mm and encompassing two large open spaces delimited by several flat, tunnel-like elements (Fig. 9D). A separate flat, bifurcated tunnel-like branch extends across the nodule surface for a distance of at least 4 mm at ~45° to the main part of the test. The bases of two additional branches are directed upwards, away from the nodule surface.

Wall structure: The wall is very thin, delicate, flexible, easily torn or detached, and often slightly transluscent so that the underlying stercomare are dimly visible through it. The surface is rather uneven (Fig. 7B) and consists of a very fine-grained matrix consisting of tiny mineral grains in which are embedded larger particles including diatom frustules, radiolarian tests, short spicule fragments and black nodule fragments. In one case the wall incorporates a large fragment of a siliceous lattice, part of a hexactinellid sponge skeleton. A patchy deposit of fine-grained, light-brown sediment sometimes covers part of the test surface.

Test interior: There are no internal xenophyae. The stercomare, covered by a reflective organic sheath, lies directly against the nodule substrate and may have a slightly greenish tinge (Figs 7D, 8B, C, E, F). Over at least some of its extent, the stercomare forms a dense, mat-like formation comprising closely packed, convoluted masses, generally 100–200 µm in width, that appear to merge and anastomose, but sometimes are aligned to run more or less parallel (Fig. 8C). Elsewhere, the masses are less closely packed and form a more open system of anastomosing branches (again generally 100–200 µm width) (Fig. 7F). The tubular extensions of the test are typically occupied by fairly rigid masses of twisted stercomare branches (Figs 7D, 8B), although a single strand is sometimes present (Fig. 9E). The stercomata are dark, 8–18 µm (mean 13.1 ± 2.5 µm, n = 58) in diameter, and embedded in a matrix of more diffuse material that includes much paler stercomata-like bodies.

Clearly defined granellare branches are generally not evident in the available specimens. However, white material that was likely cytoplasm was observed occasionally. In one of the paratypes from Station U09, it forms several fairly coherent white masses (~500 µm diameter) that are linked together and lie directly adjacent to the nodule surface between the stercomare and the edge of the test (Fig. 8C, D). Several diffuse white strands, and a web of finer strands, run forward from these masses towards the margin of the test, while 1–2 fine strands link them in the other direction to the stercomare. In the U02 specimen, a rather poorly defined strand (50–70 µm wide) of white cytoplasm runs alongside the stercomare along one of the tubular test sections (Fig. 9E). An area of poorly defined patches and strands of similar material occupies an area between two stercomare branches. There was no evidence in either specimen that the presumed cytoplasm was enclosed within an organic tube system and granellae (barite crystals) were not observed.

Remarks

Semipsammina fixa Tendal, 1975, the type species of the genus, was described from two specimens and some fragments attached to plant remains (turtle grass) collected at depths around 6000 m in the Puerto Rico Trench. According to the original description (Tendal, 1975), it has a number of features in common with the new species. The test is fragile with a fine-grained matrix and forms a single upper 'plate' with the stercomare lying directly adjacent to the substrate. The stercomare are not illustrated but are described as 'dark, rounded, irregular, flattened masses' subdivided into parts 'with each part being covered by a membrane but so tightly placed against each other that they appear as a large coherent mass'. This description is reminiscent of the appearance of the stercomare in *S. mattaeformis* sp. nov. One clear difference between the two species is the presence of well-developed granellare strands in *S. fixa* compared to the absence of obvious granellare strands in the new species. Assuming that the white material illustrated in Figure 8C and D is cytoplasm, then its diffuse appearance is different from that observed in other xenophyophores. If small patches of similar whitish material lying against the stercomare masses in other parts of the same specimen are also cytoplasm, then there may be a close association of the cytoplasm and stercomare in this species. Lecroq *et al.* (2009) observed cytoplasm 'around the margins' of the stercomare in transmission electron microscope images of the xenophyophore *S. lindsayi*, although in this case the cytoplasm occurred within the organic envelope of the stercomare, rather than outside it.

Mullineaux (1987) records, but does not describe, two unnamed species of *Semipsammina* on polymetallic nodules collected to the south of the CCZ (5°N, 125°W, 4500 m depth). The only other described species of the genus, *S. licheniformis* Kamenskaya, Gooday & Tendal, 2015, is currently known from a single specimen collected in the central part of the CCZ (13.26°N, 134.42°W, 4777 m depth). It differs in a number of respects from the new species. The test is larger (maximum dimension 6.1 cm), the test wall is composed mainly of radiolarian skeletons with subordinate numbers of sponge spicules, micronodules and occasional diatoms, branching granellare strands are clearly developed, and the stercomare masses are less closely packed (Kamenskaya *et al.*, 2015).

The mat-like stercomare in *S. mattaeformis* are quite similar to a xenophyophore, illustrated by Levin & Thomas (1988: fig. 1e), found attached to a hard substrate ('glass chip') collected during a submersible dive on the caldera rim of Green Seamount in the eastern Pacific (20°29′N, 109°16′W, 1850 m). Levin and Thomas describe it as a 'small (1.5 cm), flat, naked xenophyophore (lacking an agglutinated test), whose stercome-filled tubules confer a brain-like appearance'. The apparent total absence of a test distinguishes this organism from our new species, although a relationship between the two is possible.

The complex excrescences developed in one of the specimens of *S. mattaeformis* from Station U05 are reminiscent of similar structures in *Nazareammina tenera* Gooday, Aranda da Silva and Pawlowski, 2011 from the lower Nazaré Canyon on the Portuguese margin (NE Atlantic) (Gooday *et al.*, 2011). Both species have delicate, fragile tests and, in places, a parallel arrangement of stercomare strings. However, they differ in a number of respects, notably life habit (attached vs. unattached), the nature of the agglutinated particles that make up the test, the presence of obvious granellare strands only in *N. tenera*, and of dense, mat-like stercomare only in *S. mattaeformis*. Unfortunately, sequence data were not obtained from *N. tenera*, and so the phylogenetic relationship between the two species is unknown.

Distribution: Currently known from three sites within Stratum B of the UK-1 exploration license area.

TENDALIA GOODAY & HOLZMANN GEN. NOV.

urn:lsid:zoobank.org:act:D45EFBB7-4629-449C-8326-FA476C7B14B8

Diagnosis: Test free, forming network of fragile agglutinated tubes lying in single plane with open spaces typically 3–5 mm in maximum dimension. Xenophyae comprising mainly radiolarian and diatom fragments on test exterior with smaller mineral grains forming relatively smooth inner surface without ridges. No internal xenophyae. Test interior occupied by 1–2 stercomare branches and a single pale granellare strand.

Etymology: Named in honour of Ole Secher Tendal, whose landmark 1972 monograph and subsequent publications rescued xenophyophores from obscurity and led directly to our present appreciation of their importance in deep-sea benthic communities.

Remarks: Tubular pieces of the test of *Tendalia* resemble fragments of the genus *Syringammina*, which Tendal (1972: 34) described as being 'made of numerous radiating tubes that are connected by side branches'. The new genus is very fragile and known only from fragments in which the tubes lie in a single plane. Since the fragments originate from two cores and were only discovered when the sediment was sieved, complete tests probably form a single layer that spreads across the sediment, probably just below the surface. *Syringammina*, on the other hand, has a large (often 5 cm or more in diameter) three-dimensional, typically dome-shaped test that is often clearly visible on the sediment surface in seafloor photographs (Tendal & Lewis, 1978; Bett, 2001). There are no molecular data for the type species (*S. fragilissima* Brady, 1881), but DNA sequences obtained from *S. corbicula* (Pawlowski *et al.*, 2003), which is morphologically similar to *S. fragilissima*, suggest that *Syringammina* and *Tendalia* are not closely related (Fig. 3).

Tendalia fragments could be confused with those of *Occultammina*, a genus represented by a single described species (Tendal, Swinbanks & Shirayama, 1982) and several records of undescribed species, including from the eastern CCZ (Gooday *et al.*, 2017a). The main morphological differences are that *Occultammina* tubes branch but unlike those of *Tendalia* they do not anastomose, and they possess distinct inner and outer test layers (the former thicker than the latter) as well as several ridges running longitudinally along the inner surface of the wall (Tendal *et al.*, 1982; Gooday *et al.*, 2017a: fig. S7e–g). Although different kinds of agglutinated grains are visible on the inner and outer surfaces of the test in the new genus, they are not differentiated into two distinct layers. Unfortunately, no DNA data are available for *Occultammina*.

TENDALIA RETEFORMIS GOODAY & HOLZMANN GEN. ET SP. NOV.

(Figs 10, 11)

urn:lsid:zoobank.org:act:685E4D6D-294E-46FA-86B3-BE9BB2F57141

Xenophyophore sp. nov. A. Gooday *et al.*, 2017a, Supplementary Figure 1d therein

Diagnosis: As for genus.

Etymology: Latin: meaning reticulated or net-like.

Type specimens: All the material is highly fragmented. The largest fragment from a Megacorer deployment (deployment MC22) obtained at Station S08 during the AB02 cruise (12°11.417′N, 117°22.284′W, 4182 m) was selected as the holotype, registration number NHMUK PM PF74518 (Fig. 10A). Six additional fragments from this core, probably derived from the same specimen, are deposited under registration numbers NHMUK PM PF74519 (Fig. 10B) and NHMUK PM PF74520–74524 (Fig. 10C).

Other material: AB02 cruise (1) one fragment from Station U09 (MC14); (2) one fragment from Station U02 (MC02); (3) two fragments from Station U05 (MC04). AB01 cruise (1) 38 typical fragments from Station J (MC11), three of which (Fig. 10D) are deposited under registration numbers NHMUK PM PF74525–74527; (2) several fragments of the thicker variant from Station B (MC02).

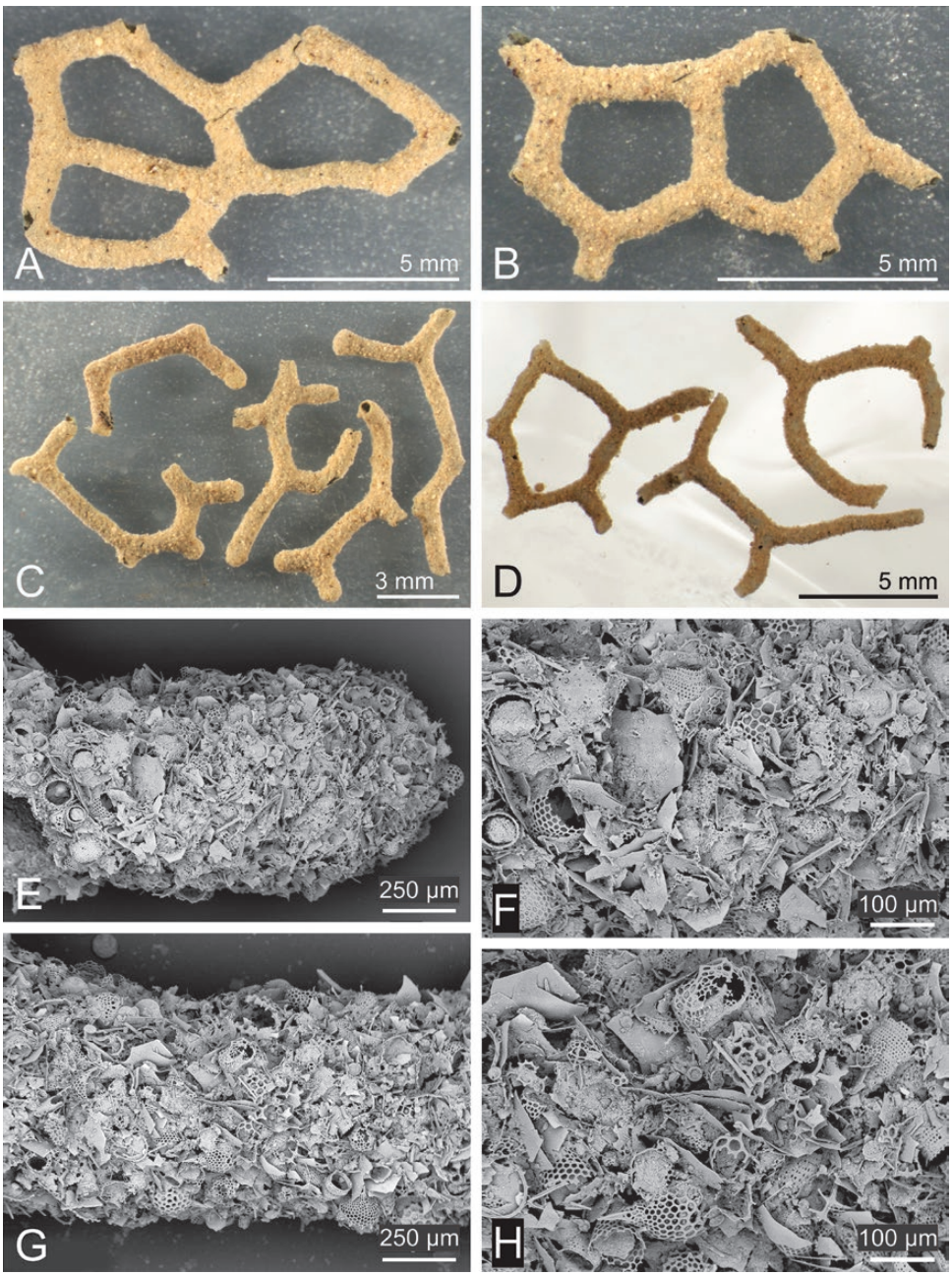

Figure 10. ***Tendalia reteformis*** **gen. et sp. nov.** A–C, shipboard photographs, AB02 cruise Station S08 (Megacorer deployment #22). A, holotype reg. no. NHMUK PM PF74518. B, paratype, reg. no. NHMUK PM PF74519. C, additional fragments, each including one or more branches with closed ends, reg. no. NHMUK PM PF74520–74524. D, shipboard photographs, AB01 cruise Station J (Megacorer deployment #11); test fragments, reg. no. NHMUK PM PF74525–74527. E–H, SEM images, AB02 cruise, Station S08, showing external surface of test with a jumble of radiolarian fragments and other particles at different magnifications.

Description

Test morphology: The test forms a network of pale brown/tan-coloured tubes that lie more or less in a single plane. The tubes are fragile and all available material is fragmented; our samples yielded one fragment (11.6 mm maximum dimension) in which the tubes form three complete circuits, one with two circuits, and seven with one circuit (Fig. 10A, B). The circuits are often approximately polygonal but sometimes have a more rounded shape. They measure 1.8 to 4.9 mm in maximum dimension but

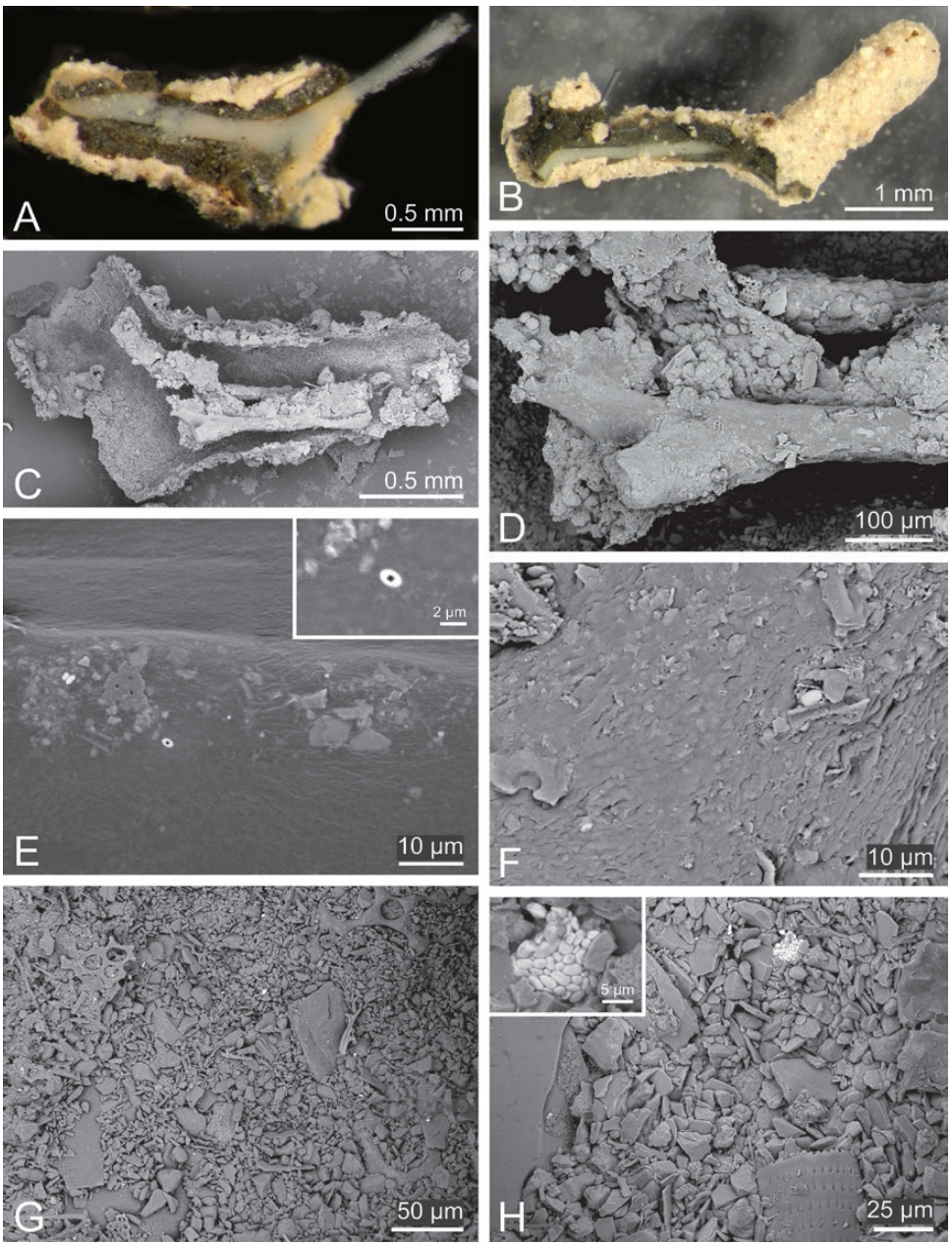

Figure 11. ***Tendalia reteformis*** **gen. et sp. nov.** from AB02 cruise Station S08 (Megacorer deployment #22). A, B, laboratory photographs showing tube fragments broken open to reveal stercomare and granellare. C–H, SEM images. C, interior of tube with stercomata and granellare. D, closer view. E, surface of granellare strand with a few barite crystals; the inset shows a crystals with a square, centrally placed hole. F, surface of granellare showing wrinkled surface, presumably the organic tube that surrounds the cytoplasm. G, inner surface of agglutinated tube. H, closer view; the inset shows a cluster of barite crystals that is incorporated into the wall.

are usually between 3.0 and 4.9 mm across. The tubular branches themselves have an approximately circular cross section and range from 0.56 to 0.92 mm (mean 0.73 ± 0.07 mm SD) in diameter. The ends of the tubes are usually broken but in 15 (22%) of 68 cases in the AB02 Stn S08 material, the branches end blindly in rounded ends (Fig. 10C, E). It seems likely that these unbroken ends are located around the edge of either one relatively large network or the edges of several smaller networks. There is no sign of obvious apertures, either in the form of open-ended tubes or smaller openings in rounded ends.

Wall structure: The test wall is 50–100 µm thick. The external surface displays a jumble of biogenic

particles, mainly complete and fragmentary radiolarians and plate-like diatom fragments, and is rough at a scale of 100s of microns (Fig. 10E–H). The inner surface is much smoother and consists largely of mineral particles, many of them angular and of varying sizes, generally between ~5 and 20 µm but with a few up to ~100 µm in size (Fig. 11G, H). Radiolarian and diatom fragments are occasionally present. In one place a cluster (~12 µm diameter) of tiny barite crystals was lodged between the larger detrital particles (Fig. 11H inset). In size and appearance, this cluster resembles the stercomata consisting entirely of such crystals ('granellae') mentioned by Tendal (1972: 73). There is no evidence for internal ridges or an organic test lining.

Test interior: There are no internal xenophyae. The interior is occupied mainly by the stercomare and to a lesser extent the granellare. The stercomare forms elongate strands (diameter 120–220 µm) that run along the branches of the tubular test, often with two strands running more or less parallel. Individual stercomata are usually oval and 16 to 25 µm maximum dimension. A single granellare strand runs alongside the stercomare and branches occasionally where the test itself branches. The strands are pale whitish to light grey and range in width from 110 to 200 µm, shrinking to ~50–100 µm when dried on an SEM stub. In the SEM the organic envelope that surrounds the cytoplasm appears as a very thin (<1 µm), wrinkled layer that is split in places. Granellae (barite crystals), 1.4–3.2 µm (usually 1.7–2.2 µm) in length, are occasionally visible on the surface of the granellare and stercomare but do not appear to be common within the cytoplasm. One distinctive crystal has an oval shape (length 2 µm) with a well-defined square hole (0.35 µm in size) in the middle (Fig. 11E inset).

Variant

The tubular branches of fragments from AB01 Station J (MC11) are distinctly wider (0.93–1.23 mm) than those from other samples. The open spaces enclosed by the two complete circuits of branches measure 2.5 and 3.7 mm in maximum, within the range of typical specimens.

Remarks

Tendal *et al.* (1982) speculated that 'infaunal xenophyophores with very regular polygonal networks of sediment tubes may exist.....and these could be makers of the well-known trace fossil *Paleodictyon*'. Swinbanks (1982) illustrated several small tubular fragments of a xenophyophore from the Japan Trench (6640 m) in which the tubes did indeed form polygons. According to Swinbanks (1982), most of his fragments 'have characteristics of the family Syringammindae'; he did not identify them further but speculated on their possible relationship to *Paleodictyon*. A recent analysis of modern *Paleodictyon* structures in the North Atlantic failed to uncover any evidence for a link between tubular xenophyophores and this enigmatic seafloor trace (Rona *et al.*, 2009).

Gooday (1991) illustrated several fragments similar to those of Swinbanks from the BIOTRANS area to the east of the Mid-Atlantic Ridge. Gooday (1996) subsequently described a large fragment (almost 19 mm across) of a xenophyophore from the Porcupine Abyssal Plain (NE Atlantic; 4844 m depth) that formed a network of tubes arranged on at least two levels. It was established as a new species, *Syringammina reticulata* Gooday, 1996, the assignment to the genus *Syringammina* being based on the three-dimensional reticulated arrangement of the tubular elements, their tendency towards a radial arrangement around the intact part of the test periphery and the presence of an organic layer lining of the tubes. Although its reticulated structure is similar to that of our new species, *S. reticulata* can be distinguished from it by the above-mentioned characters. The open spaces are also often larger (range 2–24 mm in maximum dimension) than in *T. reteformis* and more comparable to those in the fragments illustrated by Swinbanks (1982), which measured between ~2.2 and 10 mm. There are no molecular data for *S. reticulata* but, as mentioned above, sequences derived from *S. corbicula* suggest that it is not closely related to *T. reteformis*.

Distribution: Currently known from Strata A and B of the UK-1 license area and from the OMS stratum.

Bizarria Gooday & Holzmann **gen. nov.**

urn:lsid:zoobank.org:act:A8FF1EF9-CA52-4292-86FF-132A331D6851

Diagnosis: Test attached, relatively small and dome-like in overall form, comprising complex mass of inter-connecting branches rising up from substrate. Test wall transparent, composed largely of organic material. Interior filled with masses of dark stercomata at base and with pale tuft-like extremities filled with fine sediment particles. Granellare forms narrow branching strands in direct contact with the stercomata masses and visible in places through test wall. Xenophyae sparse, mainly radiolarian shells.

Etymology: The name refers to the unusual appearance of this genus.

Remarks: As discussed below, *Bizarria* is distinguished from *Cerelasma* Haeckel, 1889 by a number of morphological features. Unfortunately, the absence of molecular data for *Cerelasma* means

that the phylogenetic relationship between these two unusual xenophyophore genera is unknown.

BIZARRIA BRYIFORMIS GOODAY & HOLZMANN **GEN. ET SP. NOV.** (Figs 12, 13)

urn:lsid:zoobank.org:act:44FB3DD0-BC44-4988-8F1D-980508AD44FD

Xenophyophore sp. nov. B. Gooday *et al.*, 2017a, Supplementary Figure 1h therein

Material examined: The single specimen (the holotype) was collected in a box core (BC10) from Station S04 (12°00.567′N, 117°10.687′W, 4144 m) during the AB02 cruise. Registration number NHMUK PM PF74528.

Etymology: Greek: *bryon* meaning moss, referring to the moss-like appearance of the test.

Diagnosis: As for genus.

Description

Test morphology: The single specimen is attached to a nodule and forms a complex structure with an overall dome-like morphology, measuring 16.3 mm long, 11.4 mm wide and 9.6 mm high (Fig. 12A–C). Viewed from above, the test is light brown in colour and has

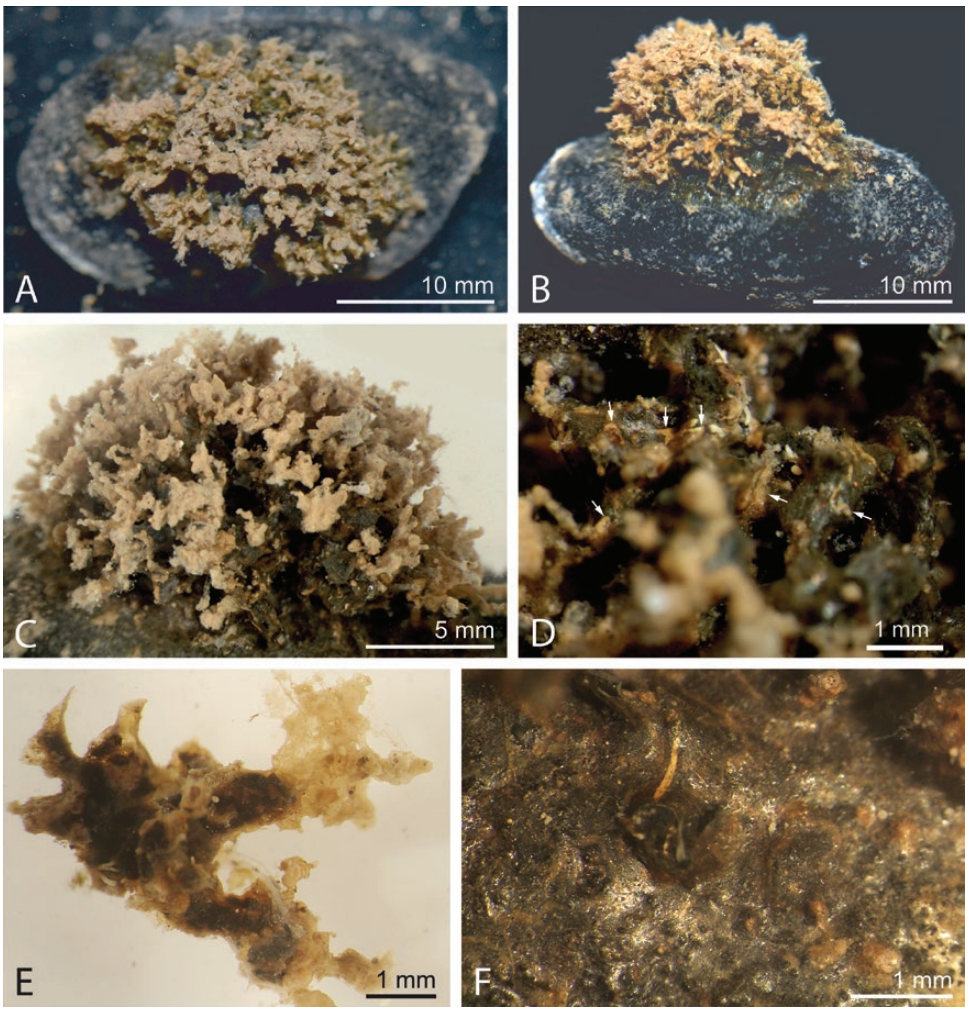

Figure 12. ***Bizarria bryiformis*** **gen. et sp. nov.** from AB02 cruise Station S04 (box corer deployment #10); unique holotype, reg. no. NHMUK PM PF74528, shipboard photographs. A, B, top and side views of complete test attached to a nodule. C, side view of test with a small part removed to show dark lower sections of the branches. D, detail of lower sections with granellare (cytoplasmic) strands (indicated by arrows) visible through transparent test. E, detached branch showing pale branched extremities. F, part of nodule surface adjacent to the test covered with an extension of the transparent test wall. Note the granellare strand visible through the transparent layer.

a soft, flexible consistency. It comprises a complicated system of interconnected branches and columns of very variable width; sections typically range from ~0.3 to ~1.0 mm, but may be wider. The branches are dark greyish in colour at the base with much lighter, pale brownish outer parts. At their extremities the branches break up into finger-like processes or more complex, often crooked, excrescencies of very variable width (generally between 0.2 and 0.8 mm) or irregular lobate masses (Fig. 12C, E). The whole structure is enclosed in a transparent organic test that extends out as a thin sheet covering the surrounding nodule surface (Fig. 12F). Some light-brown branches arise directly from this basal structure.

Wall structure: When observed in transmitted light under a compound microscope, fragments of the organic wall from the lower part of the test have a golden-yellow colour, which is also evident in the organic layer coating the adjacent nodule surface. The thickness of this organic layer when viewed by SEM is <1 µm (~0.35–0.45 µm) (Fig. 13A, B). The organic envelope surrounding the pale extremities, however, is colourless and even thinner than the yellowish organic wall in the lower part (Fig. 13C). Much of the test appears to be devoid of xenophyae. Agglutinated particles, mainly radiolarians, diatom frustules and small dark mineral grains as well as a few planktonic foraminiferal tests, are present but are sparse and mainly scattered across the test extremities.

Test interior: Masses of dark grey stercomare occupy the lower part of the test. The stercomata themselves range in diameter from 7.2 to 24.0 µm (mean 11.9 ± 3.2 µm, n = 34). The cytoplasm forms fine threads, typically 50–100 µm in diameter but with some wider sections up to 200–275 µm diameter, that are pale yellowish in colour and may branch. In places, they are visible through the transparent test wall (Fig. 12D) and appear to lie directly adjacent to the stercomata masses, with no evidence for being enclosed within an organic sheath. Some strands extend out from the main test underneath the extension of the organic test onto the adjacent substrate (Fig. 12F). SEM images show granellae scattered across the inner surface of the golden-yellow organic wall (Fig. 13B). Most of the crystals are between 1.6 and 3.8 µm (mean 2.4 ± 0.58 µm, n = 31) in size but a few are larger (4.8–6.1 µm). One crystal yielded a peak for Ti, but others are barite. The pale extremities of the test are filled with fine mineral particles and fragments of radiolarians and diatoms (Figs 12E, 13D, E). The mineral particles are more or less equidimensional but otherwise irregular in shape and appear dense in backscatter SEM images (Fig. 13F). They yield X-ray microanalysis spectra with strong Mn peaks.

Associated organisms

Several elongate transparent structures intergrown with the outer test branches are probably polyps of the ctenostome bryozoan *Nolella* (Gooday & Cook, 1984).

Remarks

Bizarria bryiformis exhibits some unusual characteristics, leading us to doubt that it was a xenophyophore until its placement in this group was confirmed by molecular data. It most closely resembles species of *Cerelasma*, notably *C. massa* Tendal, 1972. In particular, the overall consistency of the test is soft and elastic, the basal part comprises anastomosing branches, and the xenophyae are sparse and inconspicuous (Tendal, 1972; Kamenskaya *et al.*, 2016). One of the main distinguishing characteristics of *Bizarria* is that the stercomata masses and the granellare strands are both enclosed within a transparent envelope. Because the granellare clearly lies within this envelope, and the envelope spreads as an organic film over the adjacent substrate, we interpret this structure as a test rather than as the organic covering of the stercomare. On the other hand, the large amounts of 'organic cement' that characterizes the test in *Cerelasma*, and in particular *C. massa*, appear to have no equivalent in our new species.

In contrast to *B. bryiformis*, most *Cerelasma* species are described as being unattached and lacking a clear direction of growth (Tendal, 1972). An exception is *C. implicata* Kamenskaya, Gooday & Tendal 2016, an unusual species described by Kamenskaya *et al.* (2016) based on two specimens found attached to polymetallic nodules in the Russian exploration contract area of the CCZ. An agglutinated test is absent, as in *B. bryiformis*. However, the Russian species has a more elongate test morphology with a basal stalk and a more typical xenophyophore-like organization in which granellare strands and stercomare branches interweave. The pale, sediment-filled extremities of the test in *B. bryiformis* constitute another unusual feature that distinguish it from all *Cerelasma* species. Unfortunately, the availability of only one specimen precludes a more detailed description of the new species, particularly of the cytoplasm and its relationship to the stercomata masses.

There is some resemblance in general growth form between *B. bryiformis* and certain *Stannoma* species, particularly *S. coralloides* Haeckel 1889, in which the test forms a mass of branches with an overall domed morphology. However, *S. coralloides* has a single basal stalk and a completely different test structure that incorporates proteinaceous fibres (linellae) (Tendal, 1972).

Distribution: Currently known only from the OMS stratum.

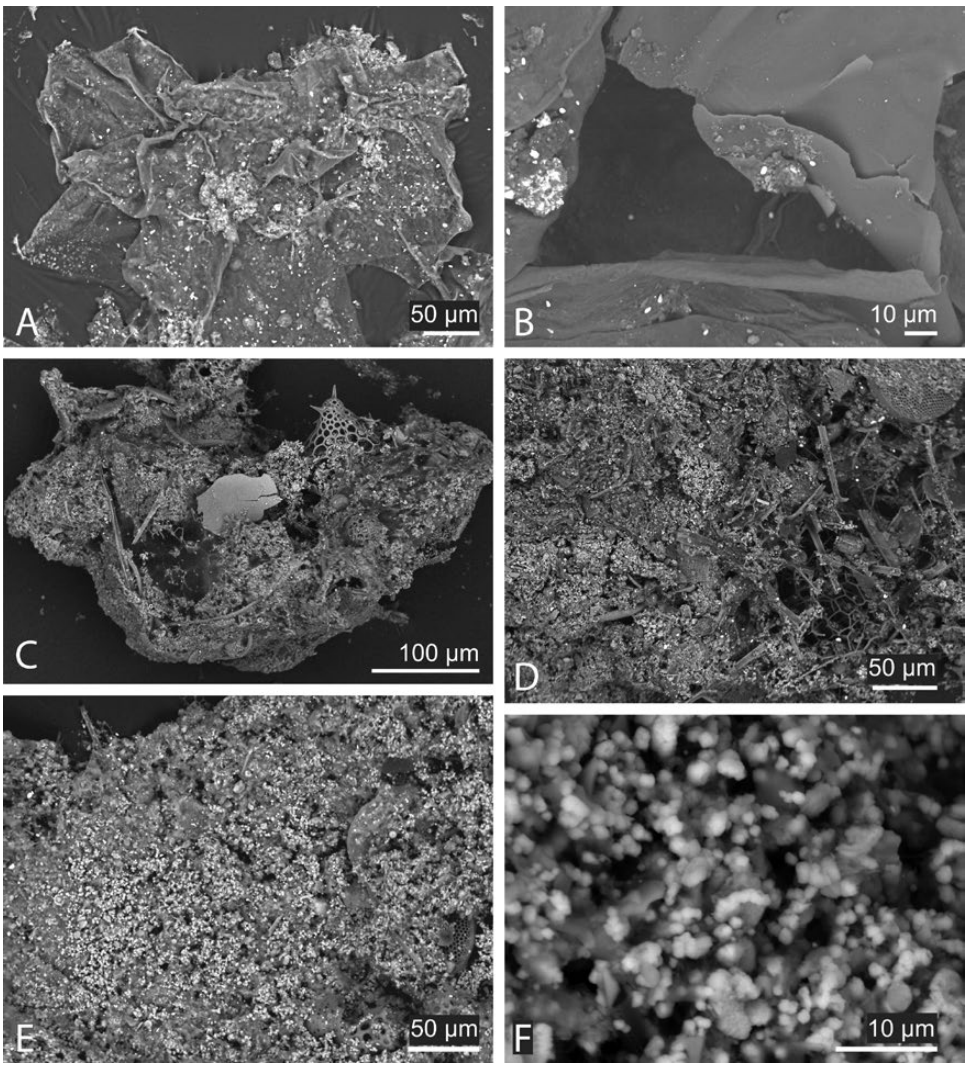

Figure 13. ***Bizarria bryiformis*** **gen. et sp. nov.** from AB02 cruise Station S04 (box corer deployment #10). Parts of the holotype viewed by scanning electron microscopy (backscatter images). A, fragment of the yellow test wall from the lower part of a detached branch with scattered particles including barite crystals. B, detail showing wall thickness and a few barite crystals. C, part of a pale test extremity with the remains of part of the organic wall covering some of the fragment like cling film. The wall is much thinner in the upper than in the lower part of the test. D, contents of another fragment from the upper part of the test, consisting of fine particles and diatom and radiolarian fragments. E, another detail showing numerous fine particles that appear bright in this backscatter image and yield strong Mn peaks. F, closer view of bright particles.

Molecular characterization

Reticulammina cerebriformis builds a strongly supported group (100% BV) with an undescribed xenophyophore (Hori *et al.*, 2013) and branches as sister to *S. contorta* and *S. lindsayi* (100% BV) (Fig. 3). The branching of *Reticulammina* and *Syringammina* is supported at 85% BV. A sister clade containing *B. bryiformis* and *S. mattaeformis* branches at the base of the former two clades but the branching is not supported. Two sister clades, one containing *T. reteformis* (100% BV) and the other consisting of *G. interstincta*, *Galatheammina* sp., *Psammina* sp. 3, *P. limbata* Kamenskaya, Gooday & Tendal, 2015 and *S. corbicula* branch at the base of all xenophyophores. The monophyly of xenophyophores and Clade C specimens is strongly supported (100% BV). Specimens belonging to Clades A and B are the closest relatives to Clade C and branch at its base.

DISCUSSION

These five new species, together with the recently established *Aschemonella monile* Gooday & Holzmann,

2017 and *Aschemonella aspera* Gooday & Holzmann, 2017 (Gooday *et al.*, 2017b), increase the number of formally described xenophyophore species in the global ocean from 68 to 75, and the number of genera from 13 to 15. All new taxa originate from a relatively small area in the eastern equatorial Pacific, emphasizing the high diversity of xenophyophores in this region (Tendal, 1972, 1996) and suggesting that numerous unknown xenophyophore species remain to be discovered in the World Ocean (Gooday *et al.*, 2017a). Many of the species described in Haeckel's (1889) *Challenger* Report were based on material collected in the tropical Pacific. Some are poorly known and the original material lost, leaving their taxonomic affinities (whether foraminifera or sponges) unresolved (Tendal, 1972: 63–65). Unfortunately, none of Haeckel's species appear to be represented in our collections and we can throw no light on their nature.

Challenges posed by xenophyophore taxonomy

The new species described here highlight some of the problems associated with morphology-based xenophyophore taxonomy, particularly within the genera *Galatheammina*, *Psammina*, *Reticulammina* and *Syringammina*. One of our new species, *S. contorta*, was placed in *Galatheammina* by Gooday *et al.* (2017a). This genus combines species with different morphologies (star-shaped with radiating branches, lump-like, plate-like) and either firmly or weakly agglutinated xenophyae. The main feature uniting them is that the surface layer of the test is distinct from the interior, which consists 'of a loose accumulation of xenophyae with granellare and stercomare' (Tendal, 1972: 28). However, despite the resemblance in test structure, there is no compelling reason to believe that these species are closely related. Indeed, our molecular data (Gooday *et al.*, 2017a) suggest that *Galatheammina* is polyphyletic. Prompted by the fact that the test is partly reticulated and its resemblance to the NE Atlantic species *R. cerebriformis*, we initially considered transfering our new species from *Galatheammina* to *Reticulammina*, the most appropriate genus based on test characteristics. However, although they appear in the same clade of the xenophyophore tree, sequence data provide no support for a close relationship between *S. contorta* and *R. cerebriformis*. On the contrary, they strongly support a close relationship between the new species and *S. lindsayi*. In the case of *G. interstincta*, we have followed Gooday *et al.* (2017a) in our generic assignment, although this species does display some features normally associated with *Psammina*, notably a row of apertures along the margin of the plate-like test. Unfortunately, *P. limbata*, the only species assigned to *Psammina* for which we have genetic data (Gooday *et al.*, 2017a), deviates from the original diagnosis of this genus in some important respects, so whether it really belongs in this genus is open to question. All that can be said at present is that *G. interstincta* and *P. limbata* are grouped fairly closely in the xenophyophore tree (Gooday *et al.*, 2017a).

The morphological distinction between *Syringammina* and our new genus *Tendalia* is somewhat blurred. Both genera include species with tubular, reticulated tests arranged on either one or more planes. There are currently no sequence data for the type species *Syringammina fragilissima*, but *T. reteformis* is genetically distant from *S. corbicula* (Gooday *et al.*, 2017a), which closely resembles the type species morphologically, so we feel confident that the two genera are distinct. However, it would be particularly useful to have sequence data for *S. reticulata*, a North Atlantic species that is on the borderline between these two genera in terms of test morphology.

Our new data suggest that test morphology is often a poor guide to phylogenetic relationships in xenophyophores and does not provide enough information on which to base a natural taxonomic system. This is well illustrated by our placement of two morphologically similar species, *S. contorta* and *R. cerebriformis*, in different genera based on DNA sequences. At present, members of the genus *Aschemonella* appear to be the only group in which there is some correspondence between morphology and genetics (Gooday *et al.*, 2017a). Genetic data are currently only available for 12 (including *Rhizammina algaeformis* Brady, 1879) of the 75 described xenophyophore species, in addition to 15 undescribed species. There is obviously a need for more sequences, including for the type species of commonly reported genera such as *Galatheammina*, *Psammina*, *Reticulammina* and *Syringammina*, as well as species of less well-known genera (e.g. *Cerelasma*, *Cerelpemma*, *Maudammina*, *Psametta* and *Stannoma*). Gooday *et al.* (2017a) obtained sequences from a single specimen of *S. zonarium*, the only stannomid xenophyophore in our material. These data did not support the distinction between the orders Stannomida and Psamminida. Additional stannomid sequences will be needed in order to confirm this result and to clarify supra-generic relationships within the xenophyophores.

New aspects of xenophyophore morphology

Two of the species described here display internal features that appear to be different from those of other xenophyophores. In *B. bryiformis*, distinct strands of cytoplasm and masses of stercomata are visible through the transparent organic wall of the test but the stercomata are not enclosed within a separate organic envelope and the granellare appears to lie

in direct contact with the stercomata. The division observed in this species between the lower part of the test, which is full of stercomata, and the upper part, which is full of pale, finely particulate material, is also unusual. Possibly, particles that have nutritional value are concentrated within the stercomata and those that have no nutritional value are used to bulk out the upper extremities of the test. The other unusual species, *S. mattaeformis*, displays typical stercomare masses but lacks an obvious granellare system, although extractions derived from several specimens yielded consistent DNA sequences. In *S. mattaeformis*, diffuse white material that is sometimes associated with the stercomare (Figs 8C, D, 9E) is probably cytoplasm. The collection and study of additional specimens of these two species (particularly *B. bryiformis*, of which we have only a single specimen) might help to elucidate the puzzling aspects of their organization. Our present observations suggest that much remains to be learnt about the basic cellular organization of xenophyophores, which appears to be more complex and diverse than previously believed.

Remarks on test particle selection

In general, the particles used in test construction by the xenophyophore species described here reflect the composition of the sediments present in our general study area. These are fairly uniform radiolarian oozes that include some micronodules and diatoms among the sand fraction (>63 µm). Calcareous particles (planktonic foraminiferal tests) are rare. The five species use different suites of particles ('xenophyae'), although all utilize radiolarians to varying degrees. In *Shinkaiya contorta* the test wall comprises mainly fine-grained material with scattered radiolarians and micronodules while the internal xenophyae are radiolarians with almost no fine-grained particles. In *G. interstincta* fine particles are largely absent and radiolarians and micronodules are the main test components with little differentiation between external and internal xenophyae. The outer part of the tubular test of *T. reteformis* is dominated by fragmented radiolarians and diatom frustules, while the inner surface consists mainly of small angular mineral grains. *Semipsammina mattaeformis* incorporates a variety of particles (radiolarians, diatoms, spicule fragments, micronodules) into its flimsy, fine-grained test wall. A similar array of particles, together with a few planktonic foraminiferan shells, are scattered across the basically organic test wall of *Bizarria.* Other xenophyophore species from the UK-1 and OMS areas display further variety in test wall composition (Gooday *et al.*, 2017a, b). In *P. limbata*, the agglutinated particles comprises a mixture of spicules, radiolarians and mineral grains, while in *A. monile* they include varying proportions of dark micronodules set in a matrix of fine mineral particles. The latter species, together with its relative *Aschmonella aspera*, are among the few xenophyophore species in our collections that do not agglutinate at least some radiolarians. The test of *Spiculammina delicata*, a common species in the central CCZ, is composed almost entirely of sponge spicules (Kamenskaya, 2005).

According to Tendal (1972: 76–77), xenophyophores normally construct their tests using 'siliceous sponge spicules, foraminiferan or radiolarian tests and mineral particles'. He further concluded that 'most species are strongly selective with respect to the type of xenophyae used'. Our observations are consistent with these generalizations. Some xenophyophore species agglutinate different kinds of particles in different parts of the test and are therefore clearly able to discriminate between them (Tendal, 1972; Tendal *et al.*, 1982). The differences between external and internal xenophyae in *S. contorta*, and between xenophyae forming the exterior and interior layers of the wall in *T. reteformis*, are examples among the new species described here. The ability of many agglutinated foraminifera to distinguish between particles having different sizes and compositions has been a source of wonderment among scientists for more than 100 years (e.g. Charles Darwin quoted in Sandon, 1957: 13; Heron-Allen, 1915; Bowser & Bernhard, 1993; Rothe, Gooday & Pearce, 2011). Nevertheless, despite the speculations of some authors (summarized by Rothe *et al.*, 2011), we are still far from understanding the cellular mechanisms involved.

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REFERENCES

Amon DJ, Ziegler AF, Dahlgren TG, Glover AG, Goineau A, Gooday AJ, Wiklund H, Smith CR. 2016. Insights into the abundance and diversity of abyssal megafauna in a

polymetallic-nodule region in the eastern Clarion-Clipperton Zone. *Scientific Reports* **6:** 30492.

Bett BJ. 2001. UK Atlantic Margin Environmental Survey: Introduction and overview of bathyal benthic ecology. *Continental Shelf Research* **21:** 917–956.

Bowser SS, Bernhard JM. 1993. Structure, bioadhesive distribution and elastic properties of the test of *Astrammina rara* (Protozoa; Foraminfera). *Journal of Eukaryotic Microbiology* **40:** 121–131.

Brady HB. 1883. *Syringammina*, a new type of arenaceous Rhizopoda. *Proceedings of the Royal Society* **35:** 55–161.

Gallo ND, Cameron J, Hardy K, Fryer P, Bartlett DH, Levin LA. 2013. Submersible- and lander-observed community patterns in the Mariana and New Britain trenches: influence of productivity and depth on epibenthic and scavenging communities. *Deep-Sea Research I* **99:** 119–133.

Goës A. 1892. On a peculiar type of arenaceous foraminifer from the American tropical Pacific. *Harvard College Museum of Comparative Zoology Bulletin* **23:** 195–198.

Gooday AJ. 1991. Xenophyophores (Protista, Rhizopoda) in box-core samples from the abysal northeast Atlantic (BIOTRANS area): their morphology, taxonomy and ecology. *Journal of Foraminiferal Research* **21:** 197–212.

Gooday AJ. 1996. Xenophyophores (Protista) including two new species, from two abyssal sites in the northeast Atlantic Ocean. *Journal of Foraminiferal Research* **26:** 193–208.

Gooday AJ, Aranda da Silva A, Pawlowski J. 2011. Xenophyophores (Rhizaria, Foraminifera) from the Nazaré Canyon (Portuguese margin, NE Atlantic). *Deep-Sea Research II* **58:** 2401–2419.

Gooday AJ, Cook PL. 1984. An association between komokiacean foraminiferans (Protozoa) and paludicelline ctenostomes (Bryozoa) from the abyssal northeast Atlantic. *Journal of Natural History* **18:** 765–784.

Gooday AJ, Holzmann M, Caulle C, Goineau A, Kamenskaya OE, Weber AAT, Pawlowski J. 2017a. Giant foraminifera (xenophyophores) are exceptionally diverse in parts of the abyssal eastern Pacific where seabed mining is likely to occur. *Biological Conservation* **207:** 106–116.

Gooday AJ, Holzmann M, Caulle C, Goineau A, Jones DOB, Kamenskaya OE, Simon-Lledo E, Weber AAT, Pawlowski J. 2017b. New species of the xenophyophore genus *Aschemonella* (Rhizaria, Foraminifera) from areas of the abyssal eastern Pacific licensed for polymetallic nodule exploration. *Zoological Journal of the Linnean Society*. doi:doi.org/10.1093/zoolinnean/zlx052

Gooday AJ, Kamenskaya OE. 2013. *Atlas of megafauna morphotypes of the Clarion-Clipperton Fracture Zone*. Available at: www.ccfzatlas.com

Gouy M, Guindon S, Gascuel O. 2010. SeaView version 4: a multiplatform graphical user interface for sequence alignment and phylogenetic tree building. *Molecular Biology and Evolution* **27:** 221–224.

Guindon S, Dufayard JF, Lefort V, Anisimova M, Hordijk W, Gascuel O. 2010. New algorithms and methods to estimate maximum-likelihood phylogenies: assessing the performance of PhyML 3.0. *Systematic Biology* **59:** 307–321.

Haeckel E. 1889. Report on the scientific results of the voyage of H.M.S. Challenger during the years 1873–1876:. *Zoology* **32:** 1–92, Plates 1–8.

Heron-Allen E. 1915. A short statement upon the theory, and the phenomena of purpose and intelligence exhibited by the protozoa, as illustrated by selection and behaviour in the foraminifera. *Journal of the Royal Microscopical Society* **6:** 547–557.

Hori S, Tsuchiya M, Nishi S, Arai W, Yoshida T, Takami H. 2013. Active bacterial flora surrounding foraminifera (Xenophyophorea) living on the deep-sea floor. *Bioscience, Biotechnology, and Biochemistry* **77:** 381–384.

Kamenskaya OE. 1987. Xenophyophoria and Komokiacea in trophic chains of the deep-sea benthos. In: *Feeding of marine invertebrates and its significance in formation of communities*. Academy of Sciences of the USSR. Moscow: P.P. Shirshov Institute of Oceanology, 15–22.

Kamenskaya OE. 2005. *Spiculammina delicata* gen. et sp. n., a new xenophyophore from the eastern Pacific (Psamminidae). *Invertebrate Zoology* **21:**23–27.

Kamenskaya OE, Gooday AJ, Tendal OS, Melnik VF. 2015. Xenophyophores (Protista, Foraminifera) from the Clarion-Clipperton Fracture Zone with description of three new species. *Marine Biodiversity* **45:** 581–593.

Kamenskaya OE, Gooday AJ, Tendal OS, Melnik VF. 2016. Xenophyophores (Rhizaria, Foraminifera) from the Russian license area of the Clarion-Clipperton Zone (eastern equatorial Pacific), with the description of three new species. *Marine Biodiversity*. doi:10.1007/s12526-016-0595-x.

Kamenskaya OE, Melnik VF, Gooday AJ. 2013. Giant protists (xenophyophores and komokiaceans) from the Clarion-Clipperton ferromanganese nodule field (Eastern Pacific). *Biological Bulletin Reviews* **3:** 388–398.

Lecroq B, Gooday AJ, Tsuchiya M, Pawlowski J. 2009. A new genus of xenophyophores (Foraminifera) from the Japan Trench: morphological description, molecular phylogeny and elemental analysis. *Zoological Journal of the Linnean Society* **156:** 455–464.

Levin LA. 1991. Interactions between metazoans and large, agglutinated protozoans: implications for the community structure of deep-sea benthos. *American Zoologist* **31:** 886–900.

Levin LA. 1994. Paleoecology and ecology of xenophyophores. *Palaios* **5:**32–41.

Levin LA, DeMaster DJ, McCann LD, Thomas CL. 1986. Effects of giant protozoans (class: Xenophyophorea) on deep-seamount benthos. *Marine Ecology Progress Series* **29:** 99–104.

Levin LA, Thomas CL. 1988. The ecology of the xenophyophores (Protista) on eastern Pacific seamounts. *Deep-Sea Research* **35:** 2003–2027.

Mullineaux LS. 1987. Organisms living on manganese nodules and crusts: distribution and abundance at three North Pacific sites. *Deep-Sea Research* **34:** 165–184.

Pawlowski J, Holzmann M, Fahrni J, Richardson SL. 2003. Small subunit ribosomal DNA suggests that the xenophyophorean *Syringammina corbicula* is a foraminiferan. *Journal of Eukaryotic Microbiology* **50:** 483–487.

Richardson SL. 2001. *Syringammina corbicula* sp. nov. (Xenophyophora) from the Cape Verde Plateau, E. Atlantic. *Journal of Foraminiferal Research* **31:** 201–209.

Rona PA, Seilacher A, de Vargas C, Gooday AJ, Bernhard JM, Bowser SS, Vetriani C, Wirsen CO, Mullineaux L, Sherrell R, Grassle JF, Low S, Lutz RA. 2009. *Paleodictyon nodosum*, a living fossil on the deep-sea floor. *Deep-Sea Research II* **56:** 1700–1712.

Rothe N, Gooday AJ, Pearce RB. 2011. Intracellular mineral grains in the xenophyophore *Nazareammina tenera* (Rhizaria, Foraminifera) from the Nazaré Canyon (Portuguese margin, NE Atlantic). *Deep-Sea Research* **58:** 1189–1195.

Sandon H. 1957. Neglected animals – the Foraminifera. *New Biology* **24:** 7–32.

Schulze FE. 1907a. Die Xenophyophoren, eine besondere Gruppe der Rhizopoden. *Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer "Valdivia" 1898–1899* **11:**1–55.

Schulze FE. 1907b. Die Xenophyophoren. *Bulletin of the Museum of Comparative Zoology at Harvard College* **51:**143–162.

Swinbanks DD. 1982. *Paleodictyon*: the traces of infaunal xenophyophores? *Science* **218:** 47–49.

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

Tendal OS. 1975. A new xenophyophore, living on solid substratum, and its significance. *Deep-Sea Research* **22:**45–48.

Tendal OS. 1980. *Stannophyllum setosum* sp.n., a remarkable xenophyophore (Rhizopodea, Protozoa) from the eastern Pacific. *Cahiers de Biologie Marine* **21:** 383–385.

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

Tendal OS, Lewis KB. 1978. New Zealand xenophyophores: upper bathyal distribution, photographs of life position, and a new species. *New Zealand Journal of Marine and Freshwater Research* **12:** 197–203.

Tendal OS, Swinbanks DD, Shirayama Y. 1982. A new infaunal xenophyophore (Xenophyophorea, Protoza) with notes on its ecology and possible trace fossil analogues. *Oceanologica Acta* **5:** 325–329.