New species of the xenophyophore genus *Aschemonella* (Rhizaria: Foraminifera) from areas of the abyssal eastern Pacific licensed for polymetallic nodule exploration

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We describe **Aschemonella monile** Gooday and Holzmann **sp. nov.** from the Clarion–Clipperton Zone (CCZ, abyssal eastern equatorial Pacific), a region characterized by commercially significant concentrations of polymetallic nodules. The new species is the most abundant xenophyophore (giant agglutinated foraminifera) in our main sampling area (12–14°N; 116°30′–117°26′W). Additional specimens originate from the central CCZ, and from a third area, ~900 km NW of the main area, where *A. monile* numerically dominates the megabenthos in photographic surveys of the seafloor (average densities 1.54 individuals/m²; peak densities > 3 individuals/m²). *Aschemonella monile* is much larger (≥ 7 cm in length) than previously described species of the genus, with a test comprising an irregular sequence of self-contained, partly overlapping 'segments', creating a multichambered structure. A similar, much rarer species from the main study area, described here as **Aschemonella aspera** Gooday and Holzmann **sp. nov.,** has an unsegmented test with a very rough, coarsely agglutinated wall. Genetic data suggest that *A. monile* is distinct from *A. aspera* and most closely related to a group comprising *Rhizammina algaeformis* and *Aschemonella ramuliformis*. Both new species have delicate tests that are often attached to nodule surfaces, making them particularly vulnerable to seafloor disturbances.

ADDITIONAL KEYWORDS: abyssal megafauna – biodiversity – Clarion–Clipperton Zone – deep-sea benthos – deep-sea mining – protist.

INTRODUCTION

Xenophyophores are a group of large agglutinated protists confined to deep-sea habitats ([Tendal, 1972]). Although regarded by some early authors as sponges,

and more recently as members of a distinct protistan taxon, molecular data have now placed them firmly within the monothalamous foraminifera ([Pawlowski *et al.*, 2003]; [Kaminski, 2014]; [Gooday *et al.*, 2017]). Xenophyophores are characterized by a set of distinctive internal features, namely the accumulation of waste pellets (stercomata) in large masses (stercomare), the organization of the cell body as a branching strand enclosed within an organic sheath (together constituting the granellare system) and the accumulation of

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barite crystals ('granellae') within the cytoplasm. It has long been known that xenophyophores are abundant and diverse at abyssal depths and on seamounts in the Clarion–Clipperton Zone (CCZ) of the eastern equatorial Pacific (Schulze, 1907a, b; Levin & Thomas, 1988; Tendal, 1996). A recent study based on extensive new collections from this region has revealed the existence of ~50 morphospecies, 45 of them new to science (Gooday *et al.*, 2017). At the same time, photographic surveys have shown that they dominate the megafauna over large areas of abyssal seafloor in the eastern Pacific (Kamenskaya, Melnik & Gooday, 2013; Amon *et al.*, 2016). In recent years, a number of species have been described from the CCZ based on morphological data, the majority of them from a relatively small area in the central part of this zone (Tendal, 1980; Kamenskaya, 2005; Kamenskaya *et al.*, 2015, 2017).

Aschemonella is perhaps the most widely distributed xenophyophore genus, having been reported from the Pacific, North and South Atlantic and Arctic Oceans (Brady, 1884; Tendal, 1996; Kamenskaya, 2014). Around eight species have been described (Tendal, 1996), but only *Aschemonella scabra* Brady 1879 (the type species) and *Aschemonella ramuliformis* Brady 1884, together with the recently described *Aschemonella tubulosa* Kamenskaya, Gooday & Tendal 2016, are well known. Species of *Aschemonella* were traditionally classified within the Hormosinidae, a family of multichambered agglutinated foraminifera (e.g. Loeblich & Tappan, 1964). However, Gooday & Nott (1982) demonstrated that *A. ramuliformis* exhibits a suite of internal features that are typical of xenophyophores, an attribution that was later confirmed by molecular analyses (Gooday, Aranda da Silva & Pawlowski, 2011; Gooday *et al.*, 2017) and is accepted in recent morphology-based classifications of agglutinated foraminifera (e.g. Kaminski, 2014). Here, we describe two new species of *Aschemonella* based on a combination of morphological and molecular data. One of these species is by far the most abundant xenophyophore in the eastern CCZ. Many of the specimens were attached to polymetallic nodules, which are abundant on the seafloor in this region. Most of the material was obtained during two research cruises (AB01, AB02) at sites within a 76 000 km² area ('UK-1') that has been licensed for seabed exploration to the UK company Seabed Resources Development Ltd (SRDL) by the International Seabed Authority (ISA), and within an adjacent area ('OMS') licensed to Ocean Mineral Singapore. The work was undertaken as part of ABYSSLINE, a biological baseline study funded by SRDL that encompasses both of these exploration areas. A few additional specimens and extensive quantitative seafloor imagery were collected on the northern margin of the CCZ in an Area of Particular Environmental Interest (APEI-6) during RRS *James Cook* cruise 120 (JC120) (Jones, 2015) and in the Russian exploration license area in the central CCZ.

MATERIAL AND METHODS

SAMPLE COLLECTION AND ENVIRONMENTAL DATA

Specimens of the new species were collected at 23 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 km² centred around 13°49′N, 116°36′W (4036–4182-m depth) in the northern part of the UK-1 exploration claim area. The AB02 cruise sampled in UK-1 Stratum B, centred around 12°28.9′N, 116°36.3′W (4136–4258 m) in the SW part of the UK-1 area, and in a stratum, centred around 12°8.2′N, 117°17.7′W (4015–4291 m depth), in the southern part of the OMS claim area. Specimens were recovered using either an USNEL box core or an OSIL Bowers & Connelly Megacorer equipped with 10-cm-diameter core tubes. Additional material was obtained during the JC120 cruise in the southwest corner of APEI-6 (17°N, 123°W; around 4100-m water depth) in April/May 2015 (Jones, 2015) and during R/V *Yuzhmorgeologiya* cruise 4–11 at a deeper site (~4850 m) in the Russian exploration claim area.

During the AB01 and AB02 cruises, 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 photographed using either a Canon 60D SRL digital camera attached to an Olympus SZX7 microscope or a handheld Nikon D3100 SLR digital camera fitted with a Nikon 62-mm macro lens. Parts of specimens, dissected fragments of cytoplasm, or in a few cases entire specimens, were preserved in RNAlater® for later molecular analysis. Others were fixed in 4% borax buffered formalin for morphological analysis. A few *Aschemonella monile* tests were rinsed in fresh water and left to dry in the laboratory at room temperature. Additional photographs were taken in the Southampton laboratory using the same system that was used on the ship.

Some environmental data are available from the APEI-6 and UK-1 areas. During the AB01 cruise, the bottom-water temperatures in the UK-1 Stratum A were ~2 °C, bottom-water oxygen concentrations were ~3.2 mL/L and bottom current velocities did not exceed sediment erosion thresholds (Amon *et al.*, 2016). Bottom-water temperatures in the APEI-6 were ~1.5 °C, oxygen concentrations ~2.9 mL/L and salinity 34.7. The sediments in both areas were radiolarian oozes with a total organic carbon (TOC) content of 0.43% (SD 0.044%, n = 37) in the APEI-6 area, based on samples collected during the JC120 cruise (D.O.B. Jones and E. Simon-Lledo, unpubl. data). A single sample collected from the UK-1 area during the same cruise had a TOC value of 0.71%. The average size of surficial sediments

Table 1. Station data for samples yielding analysed xenophyophores

Cruise	Deployment	Site	Latitude N	Longitude W	Depth (m)
UK-1 Stratum A					
AB01	BC08	F	13°48.700′	116°42.600′	4076
AB01	BC11	H	13°53.299′	116°41.399′	4150
AB01	BC12	K	13°51.801′	116°32.800′	4050
AB01	BC13	J	13°54.100′	116°35.400′	4163
AB01	BC14	L	13°43.597′	116°40.201′	4160
UK-1 Stratum B					
AB02	MC01	U01	12°24.977′	116°42.889′	4125
AB02	MC02	U02	12°22.024′	116°31.020′	4150
AB02	MC05	U04	12°37.741′	116°43.424′	4236
AB02	MC25	U15	12°34.953′	116°39.058′	4224
AB02	BC01	U01	12°24.977′	116°42.891′	4127
AB02	BC02	U02	12°22.020′	116°31.017′	4158
AB02	BC04	U05	12°22.259′	116°36.819′	4160
AB02	BC13	U07	12°27.066′	117°35.661′	4130
AB02	BC17	U10	12°34.190′	116°32.333′	4228
AB02	BC20	U13	12°35.813′	116°29.614′	4255
OMS area					
AB02	MC07	S01	12°07.074′	117°20.604′	4185
Ab02	MC19	S09	12°05.992′	117°11.798′	4050
AB02	MC20	S07	12°08.163′	117°12.898′	4054
AB02	BC11	S05	12°13.042′	117°19.523′	4090
AB02	BC12	S06	12°08.695′	117°19.526′	4044
AB02	BC21	S07	12°08.156′	117°12.900′	4054
AB02	BC24	S08	12°11.406′	117°22.282′	4182
AB02	EBS05		12°06.12′–12°06.93′	117°10.85′–117°09.87′	4072–4100
APEI-6					
JC120	BC07	050	17°18.851′	122°54.053′	4045
Russian exploration license area					
R/V *Yuzhmorgeologiya* cruise 4–11		8751	12.69°	133.30°	4852

BC, Box corer; MC, Megacorer; EB, Epibenthic sledge.

(0–5 cm), calculated using a geometric method, was 7.75 μm (SD = 3.96, n = 16) in the APEI-6 area and 18.06 μm (n = 1) in the UK-1 area.

SEAFLOOR IMAGERY

Data on *A. monile* were derived from seabed photographs obtained in the southwest corner of APEI-6 during JC120. Downward-facing photographs were taken using a Point Grey Research Grasshopper2 GS2-GE-50S5C camera mounted on the autonomous underwater vehicle Autosub 6000. A total of 7860 non-overlapping pictures, obtained at heights of 2–4 m above the seabed, were examined. They were collected along nine replicate imaging transects encompassing ~15 000 m² of seabed. Individual specimens of *A. monile* were identified in the images, counted and their maximum lengths measured using photogrammetry as described by Morris *et al.* (2014).

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 provided 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.

Table 2. Sequencing details for specimens ('DNA isolates') of *Aschemonella* collected during the AB01 and AB02 cruises in the UK-1 and OMS exploration license areas (in bold) and previously sequenced foraminiferal specimens from other studies outside the CCZ

DNA isolate	Species	Morphological type	Sampling site	Accession numbers
18080	**Aschemonella monile sp. nov.**	Rough wall	AB01–Site H	LT796779, LT796780, LT796781, LT796809, LT796810
18082	**Aschemonella monile sp. nov.**	Rough wall	AB01–Site H	LT796793, LT796804, LT796805
18083	**Aschemonella monile sp. nov.**	Rough wall	AB01–Site H	LT796785
18085	**Aschemonella monile sp. nov.**	Rough wall	AB01–Site H	LT796806, LT796807, LT796808
18236	**Aschemonella monile sp. nov.**	Smooth wall	AB02–Site U05	LT796789, LT796790, LT796811
18237	**Aschemonella monile sp. nov.**	Smooth wall	AB02–Site U05	LT796791, LT796792, LT796812
18238	**Aschemonella monile sp. nov.**	Smooth wall	AB02–Site U05	LT796782, LT796813
18244	**Aschemonella monile sp. nov.**	Smooth wall	AB02–EB05	LT796773, LT796774, LT796775
18245	**Aschemonella monile sp. nov.**	Smooth wall	AB02–EB05	LT796776, LT796777, LT796778
18246	**Aschemonella monile sp. nov.**	Smooth wall	AB02–Site S05	LT796769
18247	**Aschemonella monile sp. nov.**	Smooth wall	AB02–Site S05	LT796770, LT796771, LT796772
18254	**Aschemonella monile sp. nov.**	Rough wall	AB02–Site S04	LT796786, LT796787, LT796788
18271	**Aschemonella monile sp. nov.**	Delicate form	AB02–Site U13	LT796794, LT796795, LT796796
18272	**Aschemonella monile sp. nov.**	Delicate form	AB02–Site U13	LT576135, LT796797
18273	**Aschemonella monile sp. nov.**	Delicate form	AB02–Site U13	LT796798, LT796799
18274	**Aschemonella monile sp. nov.**	Delicate form	AB02–Site U13	LT796800, LT796801
18275	**Aschemonella monile sp. nov.**	Delicate form	AB02–Site U10	LT796802, LT796803
18277	**Aschemonella monile sp. nov.**	Delicate form	AB02–Site U10	LT796783, LT796784
18232	**Aschemonella aspera sp. nov.**		AB02–Site U07	LT796816, LT796820, LT796821
18263	**Aschemonella aspera sp. nov.**		AB02–Site U07	LT576132, LT796814, LT796815
18264	**Aschemonella aspera sp. nov.**		AB02–Site U07	LT796817, LT796818, LT796819
9340	*Aschemonella ramuliformis*		NE Atlantic	LT576134
9373	*Aschemonella ramuliformis*		NE Atlantic	LT796828
9341	*Aschemonella ramuliformis*		NE Atlantic	LT796827
3411	*Rhizammina algaeformis*		Weddell Sea	AJ514853
3412	*Rhizammina algaeformis*		Weddell Sea	AJ514854
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*		King George Is	FR875094
3929	*Psammophaera* sp.		New Harbor	LT796822
1916	Allogromia NH		New Harbor	AJ307745
1212	Allogromia NH		New Harbor	AJ307744

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 sequences of xenophyophores were deposited in the EMBL/GenBank database (accession numbers LT96769–LT968021; Table 2).

PHYLOGENETIC ANALYSIS

The obtained sequences were added to an existing database using the Muscle automatic alignment option as implemented in SeaView vs. 4.3.3. (Gouy, Guindon & Gascuel, 2010). Sequence length varied from 828 to 1024 base pairs (*Psammosphaera* sp. and *A. monile* isolate number 18275, respectively), and 25 sequences were used for analysis. The alignment contains 1340 sites of which 607 were used for the analyses. The GC content ranges from 35.9 to 43.1%.

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.

SYSTEMATIC DESCRIPTION

We use a few special terms that have been used traditionally in the descriptions of xenophyophores. The definitions below are adapted from those given by Tendal (1972).

Granellare. The cell body and the organic tube system that encloses it.

Granellae. Crystals of barite (barium sulphate) that occur in large numbers, mainly within the cytoplasm.

Stercomata. Waste pellets, composed largely of clay minerals, that are retained within the tests of xenophyophore and some other foraminifera.

Stercomare. Accumulations within the test of stercomata in the form of strings and more complex masses.

Xenophyae. The particles that constitute the agglutinated test.

The type material is deposited in the Natural History Museum, London, under registration numbers NHMUK PM PF74529–74535. For simplicity, and because the classification of monothalamids is in a state of flux, we follow the suprageneric classification of Pawlowski *et al*. (2013).

PROTISTA

SUPERGROUP RHIZARIA CAVALIER-SMITH, 2002

PHYLUM FORAMINIFERA D'ORBIGNY, 1826

'MONOTHALAMIDS' *SENSU* PAWLOWSKI, HOLZMANN & TYSZKA, 2013

GENUS *ASCHEMONELLA* BRADY, 1879

Diagnosis. Test free or attached, comprising either a number of segments arranged in single or branching series or a roughly segmented branching tube. Segments tubular or inflated, unequal in size and irregularly shaped. Apertures either at the ends of short stolons or forming a cluster of tiny openings. Agglutinated wall fairly thin and firmly cemented (modified from Brady, 1884: 271).

ASCHEMONELLA MONILE GOODAY AND HOLZMANN **SP. NOV.**

(FIGS 1–8)

urn:lsid:zoobank.org:act:994DC65F-58D3-4680-9A42-128C3D1FCA8D

Aschemonella sp. nov. 1. Gooday *et al*., 2017: figure 2d, supplementary figure 1e.

Derivation of name

From the Latin *monile* meaning 'necklace'.

Diagnosis

Large species of *Aschemonella*, often partly attached to hard substrates (polymetallic nodules), with test comprising sequence of more or less globular, chamber-like 'segments', creating a multichambered structure. Test sometimes branched and extending for up to ~7 cm with tendency to break between segments. Clusters of tiny raised apertures sometimes present, and one to two straight, tubular structures arise from surfaces of some specimens. Agglutinated wall rigid to slightly flexible, dark brown to dark grey; xenophyae comprising variable mixture of micronodules and fine mineral grains. Outer surface varies from fairly smooth to fairly rough with projecting xenophyae. Test interior devoid of xenophyae. Granellare strands pale, typically 180- to 240-μm diameter and occasionally branching. Stercomare forms globular or more elongate masses linked together in strings.

Type specimens

*Holotype (*Fig. 1*):* AB02 cruise, Box core 21, Site S07: 12°08.156′N; 117°12.900′W; 4054 m. Registration number NHMUK PM PF74529.

Paratypes: AB02 cruise, Box core 04, Site U05 (Fig. 2A, B). Registration number NHMUK PM PF74530. AB02 cruise, Box core 11, Site S05 (Fig. 2H, I). Registration number NHMUK PM PF74531 (specimen partly encrusting nodule). AB02 cruise, Box core 12, Site S06 (Fig. 8C). Registration number NHMUK PM PF74532 (delicate form). AB02 cruise, Box core 20, Site U13 (Fig. 8A, B). Registration number NHMUK PM PF74533 (delicate form). AB01 cruise, Box core 11, Site H (Figs 2E, F; 3G). Registration number NHMUK PM PF74534.

Other material

Thirty-four typical specimens and five delicate specimens or specimen clusters from the following samples. AB01 cruise, UK-1 Stratum A, Box cores 8, 11, 12, 13, 14 (sites F, H, K, J, L, respectively). AB02 cruise, UK-1 Stratum B, Megacorer deployments 1, 2, 5, 25 (sites U01, U02, U04, U15, respectively); Box cores 01, 02, 04, 13, 17, 20 (sites U01, U02, U05, U07, U10, U13, respectively). OMS Stratum, Megacorer deployments 07, 19, 20 (sites S01, S09, S07, respectively); Box cores 11, 12, 21, 24 (sites S05, S06, S07, S08, respectively).

Description

Test morphology: The test is irregular and morphologically variable, consisting of segments arranged in a

linear series following a course that is always slightly crooked, sometimes curved or angled and sometimes branched or with short side branches or single lateral segments (Figs 1; 2A–C, E). It is delicate and tends to break between the segments, resulting in the fragmentation of many individuals. Specimens are typically a few centimetres long but a few reach a length of up to ~7 cm (measured along the test). The segments are generally 3–5 mm long and tend to be approximately globular (Table 3). However, the shape is variable and some segments are wider than they are long, while others are elongate, almost tubular or somewhat irregular in shape. Damaged specimens demonstrate that the segments are self-contained structures that resemble chambers, rather than being constrictions of a tube. The segments abut and may overlap to some extent, with one segment enclosing part of the preceding segment (Fig. 4B). Tiny apertures (described below) are sometimes visible on the distal (enclosed) part of the segment (Fig. 4C), suggesting the possibility of communication between the segments. This is seen most clearly in specimens with a relatively smooth test wall.

Specimens are often attached to nodules. In most cases, only part of the test is in contact with the substrate (Fig. 1) but occasionally the association is more intimate, the test forming a chain of attached, dome-shaped segments before rising up and growing free from the surface (Figs 2H, I; 5A). The domes are usually strongly flattened. In specimens from the AB01 cruise, in which the test contains a large proportion of dark micronodules (see below), it may be difficult to distinguish the segments from the nodule substrate.
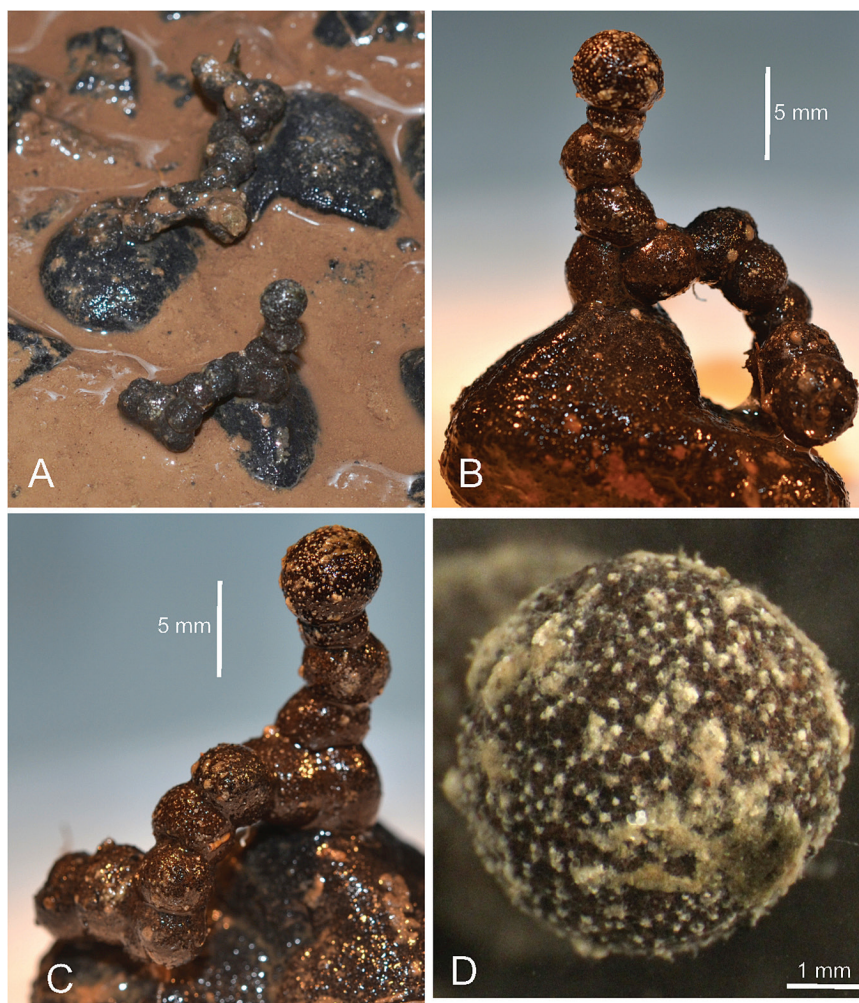

Figure 1. *Aschemonella monile* **sp. nov.**, Holotype, reg. no. NHMUK PM PF74529; Box core 21 (AB02 cruise, Station S07). Shipboard photographs. A, Holotype (foreground) and another specimen as originally seen on the surface of the box core. Note the attachment of both specimens to polymetallic nodules. B and C, Opposite sides of test. D, Rounded upper extremity of test densely encrusted with a *Telammina* network.
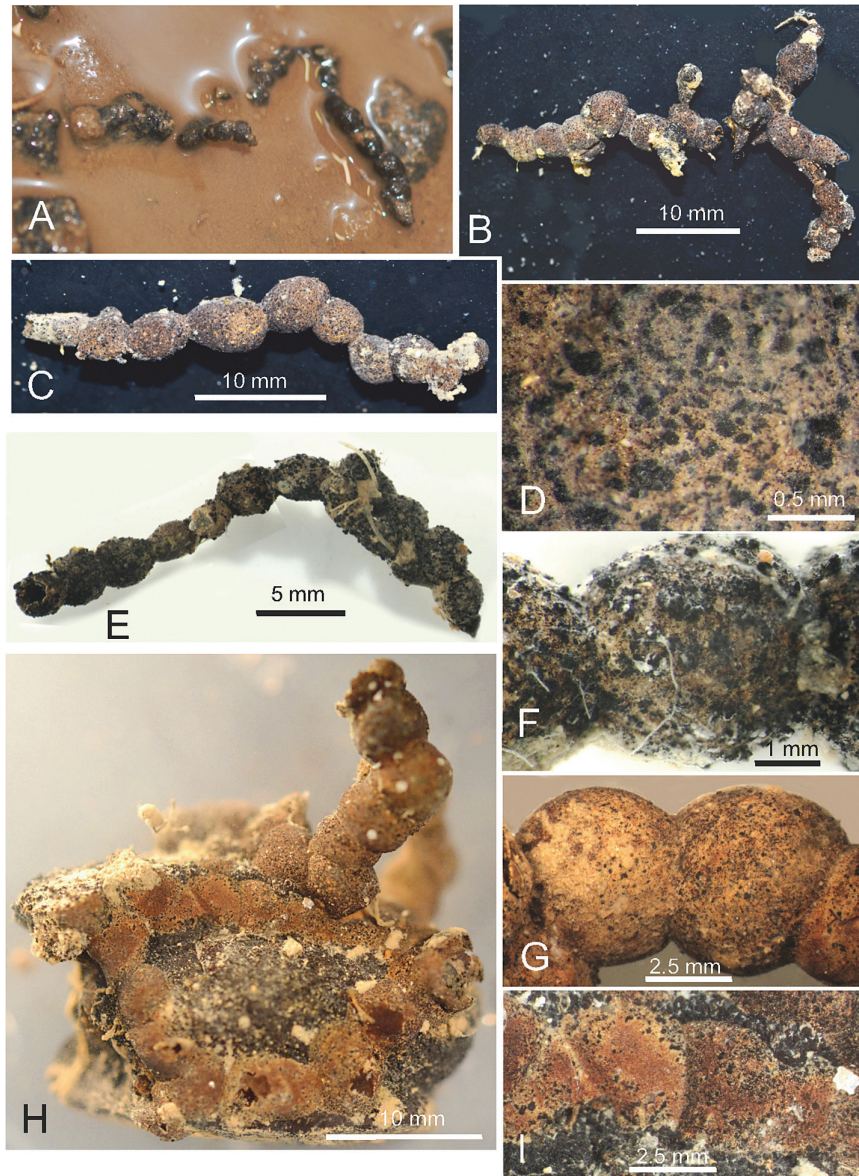
Figure 2. *Aschemonella monile* **sp. nov.**, Shipboard photographs except where indicated otherwise. A and B, Complete paratype as originally seen on the surface of a box core and following removal from the sample; reg. no. NHMUK PM PF74530; Box core 04 (AB02 cruise, Station U05). C, Complete specimen; Box core 04. D, Same specimen; detail of test surface showing black micronodules in fine-grained matrix. E, Complete paratype, laboratory photograph; NHMUK PM PF74534; Box core 11 (AB01 cruise, Station H). F, Same specimen, laboratory photograph; detail of test surface showing dominance of black micronodules. G, Detail of two chambers showing orange test wall with relatively few small black particles (fragments of micronodules); Megacorer deployment 19 (AB02 cruise, Station S07); H, More or less complete paratype encrusting nodule before growing away from surface; reg. no. NHMUK PM PF74531; Box core 11 (AB02 cruise, Station S05). I, Same specimen, detail of encrusting segments forming low domes; note that black micronodules are a relatively sparse component of the wall.

Apertural structures: Several specimens from the UK-1 area display clusters of 30 or more tiny round apertures raised on very short tubes or pustules, 150–220 μm wide (Fig. 3C, D), at the ends of the terminal segment. These features are particularly well developed in a large complete test from APEI-6, which bears numerous raised apertures at the ends of three terminal segments, as well internally as the ends of earlier chambers exposed by breakage. The apertures are somewhat smaller (100–140 μm wide) than those
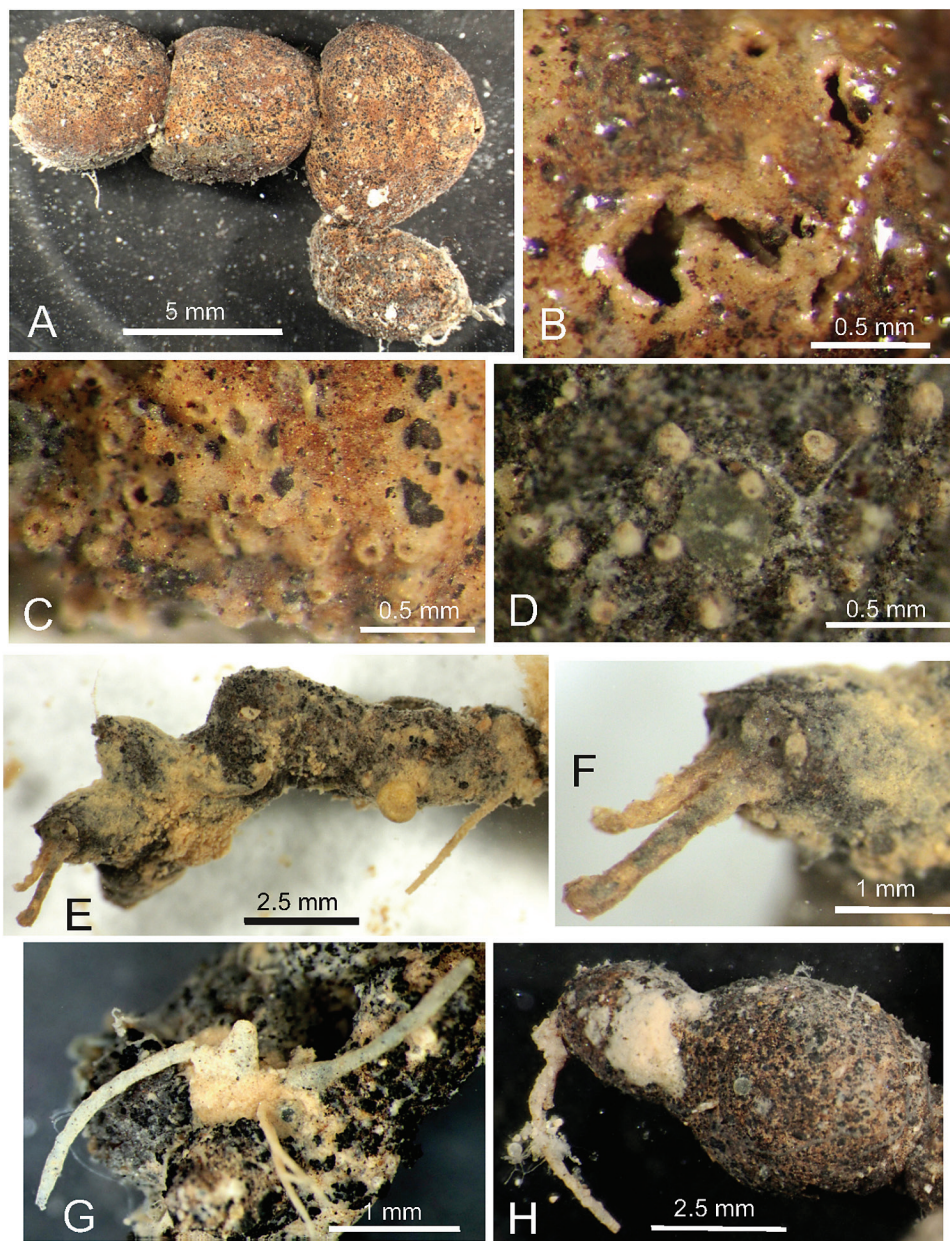
Figure 3. *Aschemonella monile* **sp. nov.**, apertural features. Shipboard photographs except where indicated otherwise. A–C, Megacorer deployment 02 (AB02 cruise, Station U02). A, Complete specimen. B, Detail of irregular apertural openings at the end of the largest chamber of the same specimen. C, Detail of another specimen showing scattering of small apertures with raised rims. D–G, Box core 11 (AB01 cruise, Station H). D, Detail of specimen showing small apertures. E, Part of another specimen showing three apertural tubes. F, Detail of the end of the same specimen showing two tubular structures with single small openings above each. G, Detail of another specimen showing two tubular structures arising from a common base (the complete test is shown in Fig. 2E), laboratory photograph; NHMUK PM PF74534. H, Detail of complete specimen shown in Figure 2B with a single tube arising from the end of the test; Box core 04 (AB02 cruise, Station U05).

seen in the UK-1 specimens but are more numerous, with ~50–75 being grouped together in each cluster (Fig. 4D, E). An individual collected during the AB02 cruise had a series of larger, irregularly shaped, basically slit-like openings (100–670 µm long) in addition to a small circular aperture (Fig. 3B). These slit-like features probably developed by elongation of rounded apertures. Another feature present in some
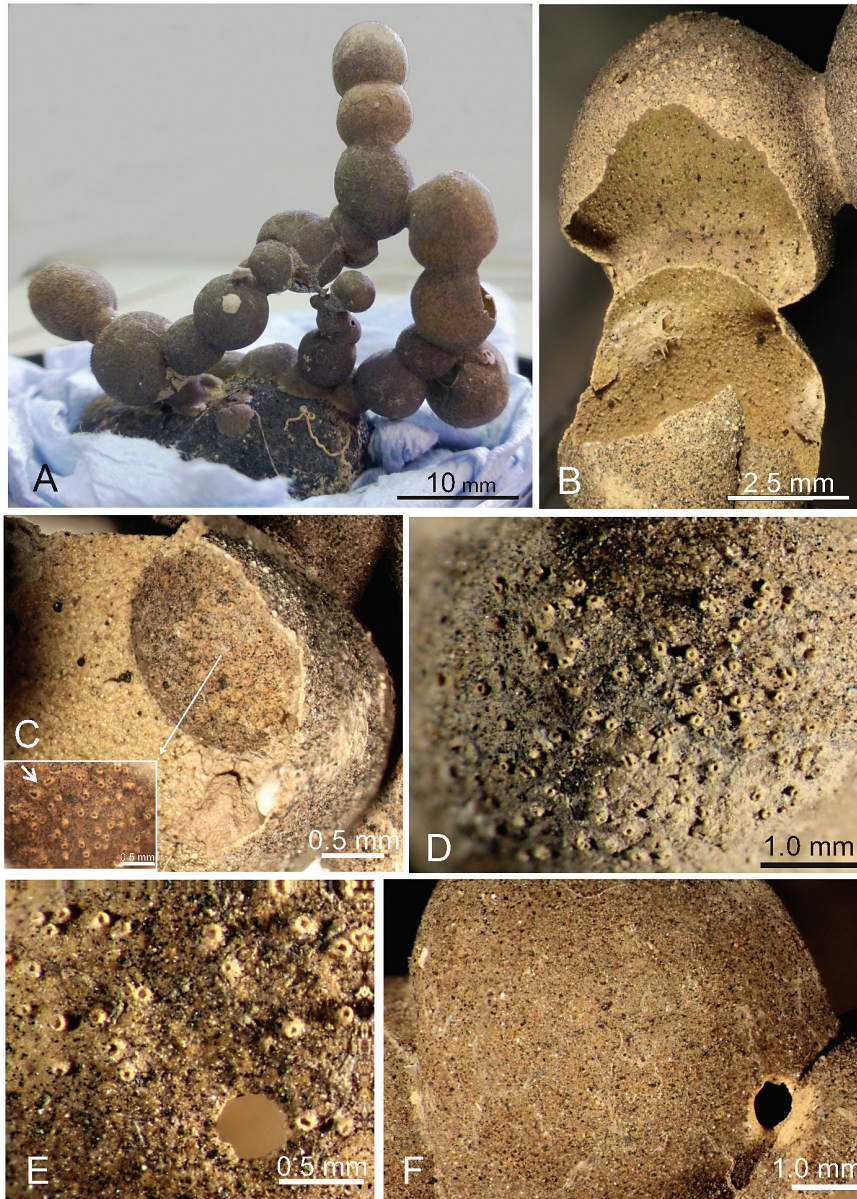
Figure 4. *Aschemonella monile* **sp. nov.**; specimen from APEI-06, Station JC120-050, laboratory photographs except where indicated otherwise. A, General view of the test, shipboard photograph. B, Detail of a damaged section of the test showing a later chamber (at the top) overlapping an earlier chamber; a cluster of apertures is visible on the exterior of the later chamber (at top of photograph). C, View of the base of the lower chamber in (B) showing the dome-shaped end of the preceding chamber protruding into it. The inset shows part of a cluster of apertures at the end of this preceding chamber; the smaller arrow indicates two somewhat larger and elongate apertures. D, Clusters of apertures at the end of one of the terminal segments. E, Round hole, presumably the work of a predator, with part of a cluster of apertures. F, A similar hole near the junction of two chambers.

individuals comprises a straight or slightly curved, open-ended pale cream tube (length 1.2–4.2 mm, width 0.17–0.3 mm) that is more finely agglutinated than other parts of the test (Fig. 3E–H). A single test may give rise to two or more of these structures, sometimes with a pair of tubes arising from a common bulbous base (Fig. 3G). In one specimen from the AB01 cruise, the terminal segment bears two tubes with small, round openings above each (Fig. 3E, F).

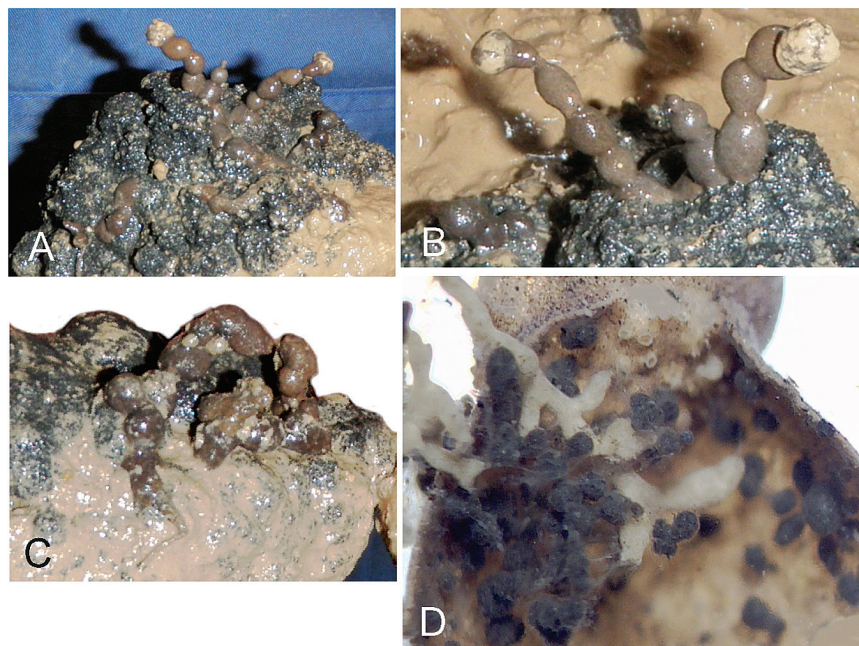*Test wall:* The wall ranges from reddish brown to light or dark grey, depending on the proportion

Figure 5. *Aschemonella monile* **sp. nov.** from the Russian exploration claim area; R/V *Yuzhmorgeologiya* cruise 4–11, Station 8751. Shipboard photographs courtesy of V. K. Melnik. A, Complete individual attached to nodule. B, Detail of upstanding part of the same specimen. C, Second specimen from the same box core. D, Interior of a different specimen showing globular stercomare masses and pale branched cytoplasmic strands. Note the tiny apertures on short tubes on the end of the previous segment at the top of the photograph (compare with Fig. 4C).

of micronodules that it incorporates. The lighter coloured specimens mainly originate from UK-1 Stratum B but are also represented in APEI-6 (Fig. 4) and the Russian exploration claim area (Fig. 5A–C). The wall generally has a smooth or slightly rough outer surface with a variable proportion of small dark particles, and sometimes a few larger micronodules, set in a lighter-coloured, orange to reddish-brown, fine-grained matrix (Fig. 2B–D, G–I). Those with dark grey walls, mainly from the AB01 cruise, incorporate a larger, sometimes dominant, proportion of micronodules (Fig. 2E, F), although the proportion and hence the colour can vary even within a specimen. The micronodules in these dark grey specimens often project above, and to a lesser extent below, the general thickness of the wall, resulting in distinctly rough outer and inner surfaces. They sometimes incorporate a few other large particles, usually the tests of agglutinated foraminifera. The wall is rather delicate but somewhat flexible and easily fractured or torn, particularly in the finer-grained brownish tests, although it does not include an obvious organic layer. The thickness varies from 70 to 130 µm, the brown walls being towards the lower end of this range and the dark grey walls (not including the projecting micronodules) towards the upper end.

Stercomare and granellare (light and scanning electron microscopic observations): There are no internal xenophyae. The test interior is occupied to a greater or lesser extent by stercomare and granellare, which are closely associated (Fig. 6). The stercomare sometimes has a greenish tinge and often appears as more or less globular masses (length 210–410 µm, width 190–320 µm), sometimes isolated but usually linked together in strings, together with more elongate masses of undulating width (Figs 5D; 6A–D; 7A). The individual stercomata are 14- to 22-µm maximum dimension. The pale granellare strands are usually straw-coloured (light grey in the Russian specimen), branch occasionally, and may vary in width (100–190 µm) along their length. Like the stercomare, some parts of the granellare appear to be isolated from other parts (Fig. 6E). In unfixed specimens examined during the cruise, pale, diffuse cobweb-like material in the form of single and multiple strands and sheets pervaded much of the test interior, stretching between, and often merging with, the denser granellare strands and the stercomare (Fig. 6C, E). This is presumably part of the cellular system. The cytoplasm contains numerous granellae (Fig. 7C–F), measuring 1.7–4.9 µm long (mean 2.6 ± 0.66 µm, $n = 33$) and ranging from angular to rounded in shape; a few are interrupted by an elongate hole.
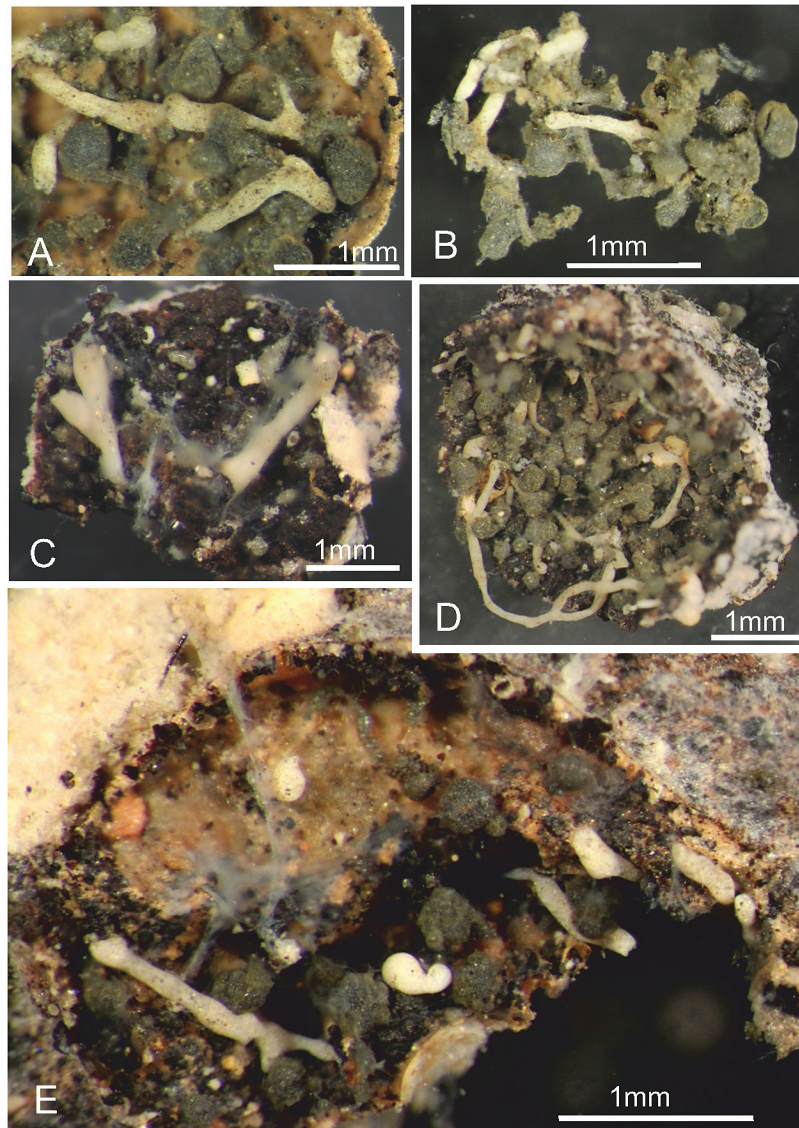
Figure 6. *Aschemonella monile* **sp. nov.**, test interiors showing granellare and stercomare; AB02 cruise, shipboard photographs except where indicated otherwise. A and B, Megacorer deployment 20 (Station S07), laboratory photographs. A, General view of pale granellare strands and greenish stercomare. B, Fragment of stercomare and associated granellare removed from the same specimen. C, Granellare strands and diffuse cytoplasm; Box core 17 (Station U10). D, Megacorer deployment 07 (Station S01). E, Broken section of test showing apparently isolated granellare strands and lumps, isolated globular stercomare masses and diffuse cytoplasm; Box core 04 (Station U05).

Delicate variant: The material of *Aschemonella* from UK-1 Stratum B and the OMS Stratum includes specimens that are smaller and more delicately constructed than others from the southern sites. Groups of several such specimens are sometimes present on a single nodule and have dark, uneven test walls (Fig. 8). The individual segments of these delicate forms tend to be more elongate than those of typical specimens (mean L:W ratio 1.44 compared with 1.06), as well as being considerably smaller (Table 3). In addition, the size and shape of segments often vary within individual tests. In some cases, a series of globular segments gives rise to smaller, more elongate segments, or occasionally to tubular or conical extensions. Despite these differences, genetic data suggest that the delicate variant represents the same species as typical specimens (Table 2; Fig. 9).

Remarks

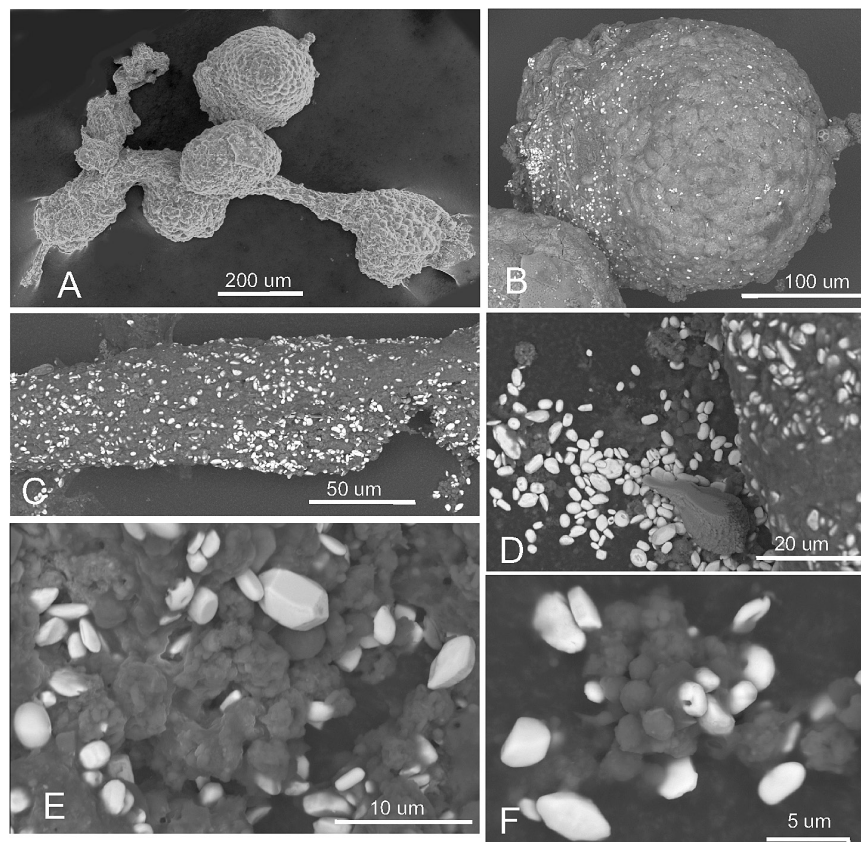*Aschemonella* includes a number of species with irregular, segmented test morphologies. Brady (1884:

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Figure 7. *Aschemonella monile* **sp. nov.**, scanning electron microscopic images; Megacorer deployment 20 (Station S07). A, Fragment of stercomare showing bulbous swellings linked by narrow necks. B, Detail of one swelling showing individual stercomata beneath organic covering. C, Fragment of granellare strand (cytoplasm and its organic envelope) with numerous granellae (high backscatter barite crystals). D, Part of granellare strand with organic envelope (on right side) with scatter of granellae that have spilt out of it. E, Detail of granellare with granellae; note the angular shape of the largest crystal. F, Isolated cluster of granellae and low-backscatter particles that are rich in calcium (EDX, data not shown).

271) notes that the 'characteristic features of the genus *Aschemonella* are the great variety of shape exhibited by the segments, their irregularity and want of symmetry, and the extreme tenuity of the walls of the test in comparison with the bulk of the sarcode cavities, especially in the larger specimens'. *Aschemonella monile* exhibits all of these characteristics. In particular, the segments range from globular to more elongate and occasionally tubular and the overall growth form is highly irregular. We continue to use the terminology of Brady in referring to the test as segmented, despite the fact that where the test interior is visible through breakage, the segments appear as self-contained units (Fig. 4B) resembling the chambers of multilocular foraminifera. Micro-computed tomography scans of several specimens, including the holotype, also reveal the chamber-like nature of the segments (D. Sykes, A. Gooday, A. Glover, unpubl. data). This point is discussed further below.

In terms of test morphology, the new species is closest to *A. scabra* Brady, 1879, the type species of the genus, which has been reported from the abyssal Pacific by Brady (1879) and Schröder *et al.* (1988). It was originally described as follows: 'Test free, consisting of one or more chambers of irregular size and shape. Chambers inflated, often with one or more tubulated apertures, any of which may produce a fresh segment' (Brady, 1879: 25). The main morphological difference is that, rather than adjoining directly as in *A. monile*, the segments are separated by tubular stolons, which originate as extensions of the chambers. Similar characteristics distinguish *Aschemonella catenata* (Norman, 1876) from our new species.

The most widely reported species of the genus, *A. ramuliformis* Brady, 1884, is also known from the North Pacific (Brady, 1884; Schröder *et al.*, 1988). Its basically tubular test morphology ('an irregular, more or less branched, sometimes segmented tube, with numerous apertures, lateral and terminal'; Brady, 1884: 273) is clearly different from that of *A. monile*. Recent photographs and collections obtained using a remote
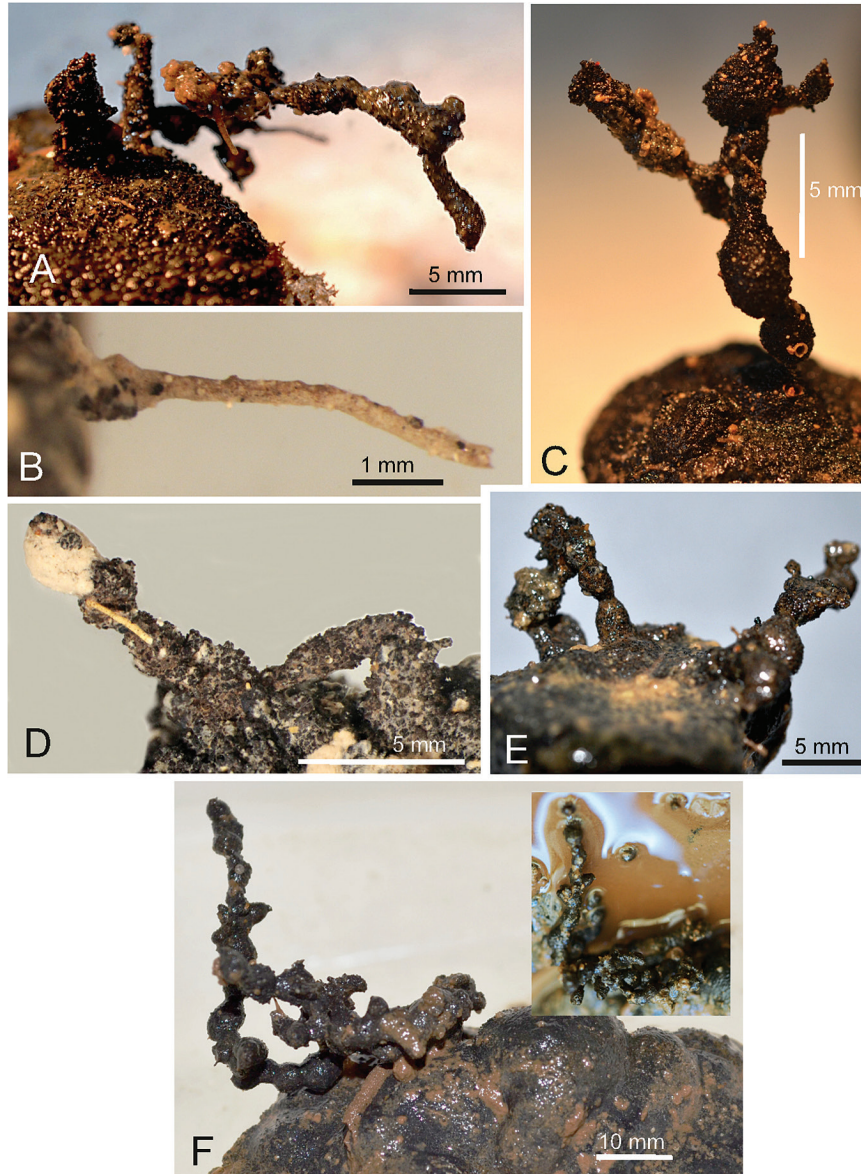
Figure 8. *Aschemonella monile* **sp. nov.**, delicate form; shipboard photographs from AB02 cruise, except where indicated. A, Entire specimen; NHMUK PM PF74533; Box core 20 (Station U13). B, Same specimen, detail of tubular structure. C, NHMUK PM PF74532; Box core 12 (Station S06). D, Specimen partly encrusting nodule surface; Box core 17 (Station U10). E, Cluster of three upstanding branches arising from a nodule surface, probably representing the same individual; Megacorer deployment 01 (Station U01). F, Specimen attached to a nodule; the inset shows a core-top photograph of the same specimen; Box core 08 (AB01 cruise, Station F).

operated vehicle in the Nazaré canyon (Portuguese margin) revealed that *A. ramuliformis* formed clusters of vertically orientated tubular elements exposed on the sediment surface (Gooday *et al.*, 2011). DNA sequences obtained from this material indicate a close relationship with *A. monile* (Fig. 9), although the two species are clearly distinct morphologically. Gooday (1996) described a single large and apparently complete *Aschemonella* specimen from the Porcupine Abyssal Plain (NE Atlantic) that he identified as *A. ramuliformis*. An interesting feature was the presence of several fragile, pale-coloured tubes, up to 16 mm long, arising from different parts of the test. These structures closely resemble the tubular extensions developed in some specimens of the new Pacific species. In both cases, they are relatively much longer and slenderer than the 'tubulated apertures' of *A. scabra*, as well as being more finely agglutinated than other parts of the test.

Table 3. *Aschemonella monile* **sp. nov.**, dimensions of segments of specimens collected during the AB01 (UK-1 Stratum A) and AB02 (UK-1 Stratum B, OMS Stratum) cruises

Cruise and morphology	N	Segment length (mm)		Segment width (mm)		Segment L:W ratio	
		Range	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD
AB01	28	2.71–4.9	3.60 ± 0.68	2.04–4.41	3.43 ± 0.76	0.76–1.53	1.07 ± 0.20
AB02: typical	50	2.9–6.0	4.49 ± 0.96	2.5–7.5	4.46 ± 1.09	0.69–2.4	1.06 ± 0.33
AB02: delicate	13	0.97– 3.75	2.47 ± 1.37	0.97–3.75	2.05 ± 1.08	1.0–2.75	1.44 ± 0.48

For those from AB02, separate measurements are given for 'typical' and 'delicate' specimens. The typical specimens are those with more or less regular 'segments' (as shown in Figs 1, 2, 3A). Delicate specimens are smaller and have less regular segments (Fig. 8).

Not all the specimens of *A. monile* that we collected contained fresh stercomare and granellare. Some that were broken, either naturally or deliberately, were empty or contained decayed stercomare. The proportion is impossible to estimate without damaging additional material, but our impression is that at least 50% of specimens were dead when collected. Whatever the precise figure, it is clear that the test can remain intact for some period of time after the death of the organism. However, it seems unlikely that specimens of *A. monile* survive long enough to become part of the permanent fossil record, particularly given the low sedimentation rate in the abyssal eastern Pacific (Khripounoff *et al.*, 2006).

Density and distribution of A. monile *in seafloor images*

Aschemonella monile was the most abundant organism visible in imagery covering an area of 14 206 m² of seafloor in the southwestern corner of APEI-6 (Fig. 10). A total of 21 992 individuals of this xenophyophore were identified, making it the most abundant megafaunal organism, either protistan or metazoan, seen in the surveyed area. The average density among all replicate transects was 1.54 individuals/m² (SD = 1.29), with peak densities > 3 individuals/m² being found in regions of elevated topography (low ridges). A random selection of 1000 individual tests (excluding those that were obviously broken or partly obscured by sediment) ranged from 1.3 to 8.6 cm in length (average 3.57 cm; SD = 1.10) and their size was consistent between replicate transects. Less than a third (30.2%) of all individuals were situated on top of, and apparently attached to, polymetallic nodules. The remaining 69.8% appeared to lie directly on the sediment surface, although it cannot be excluded that a proportion of these were associated in some way with nodules that were obscured by the surficial sediment.

Interactions with other organisms

The tests of *A. monile* often serve as a substrate for a rich assortment of encrusting organisms, almost all of them foraminifera including many forms that also encrust the surfaces of nodules. Agglutinated tests, including mat-like and chain-like formations, domes, flat-lying and erect tubes (branched and unbranched), predominate, but calcareous species, among them the rotaliid *Cibicides* and a large miliolid with a cribrate aperture, probably *Involvohauerina globularis* Loeblich & Tappan, 1955, are also sometimes present. Several specimens, including the holotype, host dense networks of *Telammina*, typically best developed on upper segments that were elevated furthest into the water column (Fig. 1D). Specimens from Station S07 (BC21) and S08 (BC24) provided substrates for a small plate-like xenophyophore and a gromiid, respectively.

Mobile megafauna, including ophiuroids and isopods, are sometimes associated with *A. monile* individuals in seafloor images obtained from APEI-6 during the JC120 cruise. Four small, neat, round holes (diameters 329–660 μm) penetrate the wall of different segments of the large specimen collected in a box core at Station JC120-050 (Fig. 4E, F). These probably resulted from the activities of predators, possibly a mollusc.

ASCHEMONELLA ASPERA GOODAY AND HOLZMANN **SP. NOV.**
(FIG. 11A–F)

urn:lsid:zoobank.org:act:6A3EE211-D050-48C2-B700-61A07315C7B4

Aschemonella sp. 2. Gooday *et al.*, 2017: supplementary figure 8a, b.

Derivation of name

From the Latin *aspera* meaning 'rough'.

Diagnosis

Species of *Aschemonella* with highly irregular test attached to nodule surface. The test comprises one or more approximately tubular structures (≥ 5 mm in length) growing upwards from substrate and their flat-lying extensions on the nodule surface. Structures may branch or give rise to short lateral
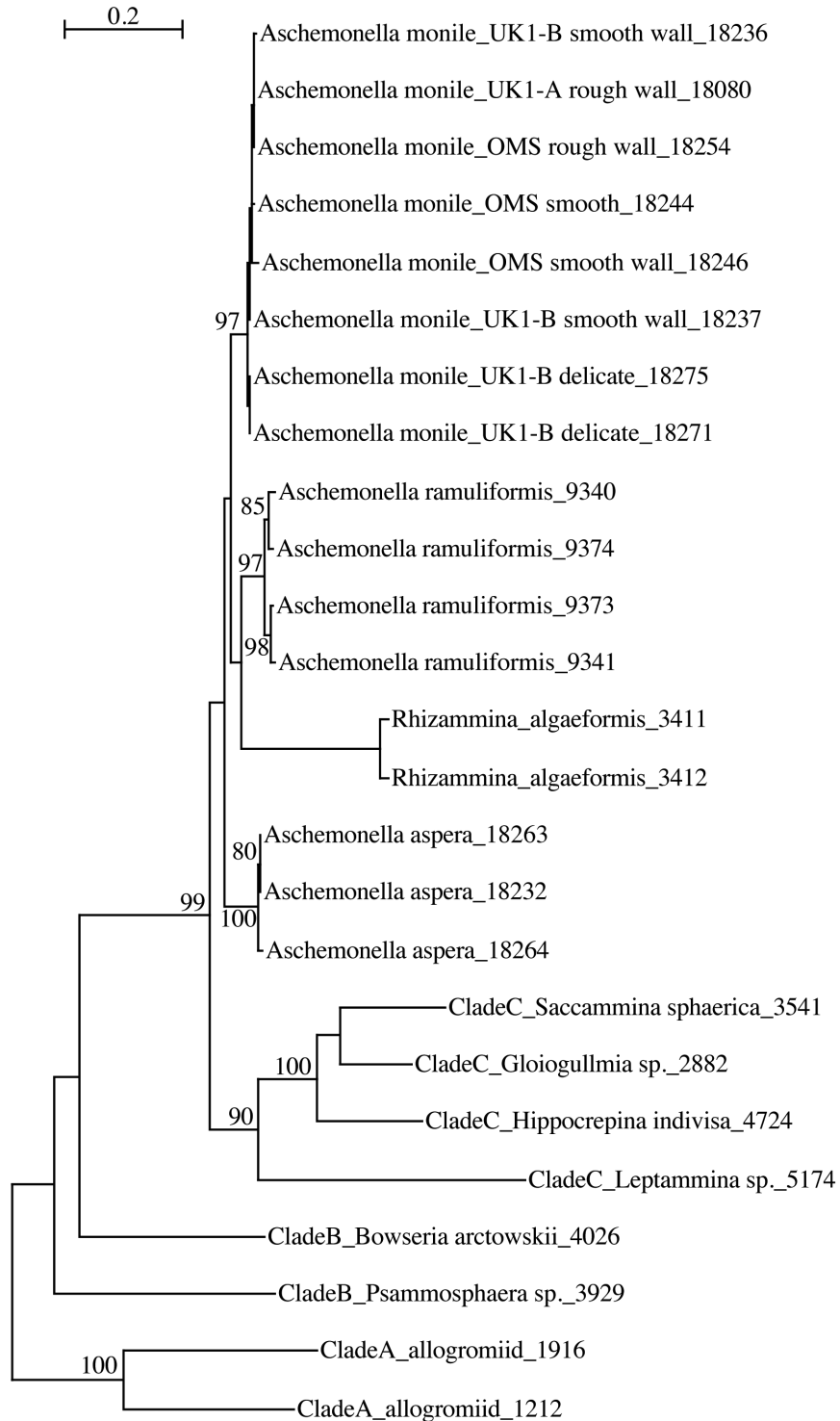
Figure 9. PhyML phylogenetic tree showing evolutionary relationships of ***Aschemonella monile* sp. nov.**, *A. ramuliformis* and *A. aspera*, together with eight specimens of monothalamid clades A, B and C. The tree is rooted in clade A. Numbers at nodes indicate bootstrap values (BVs).
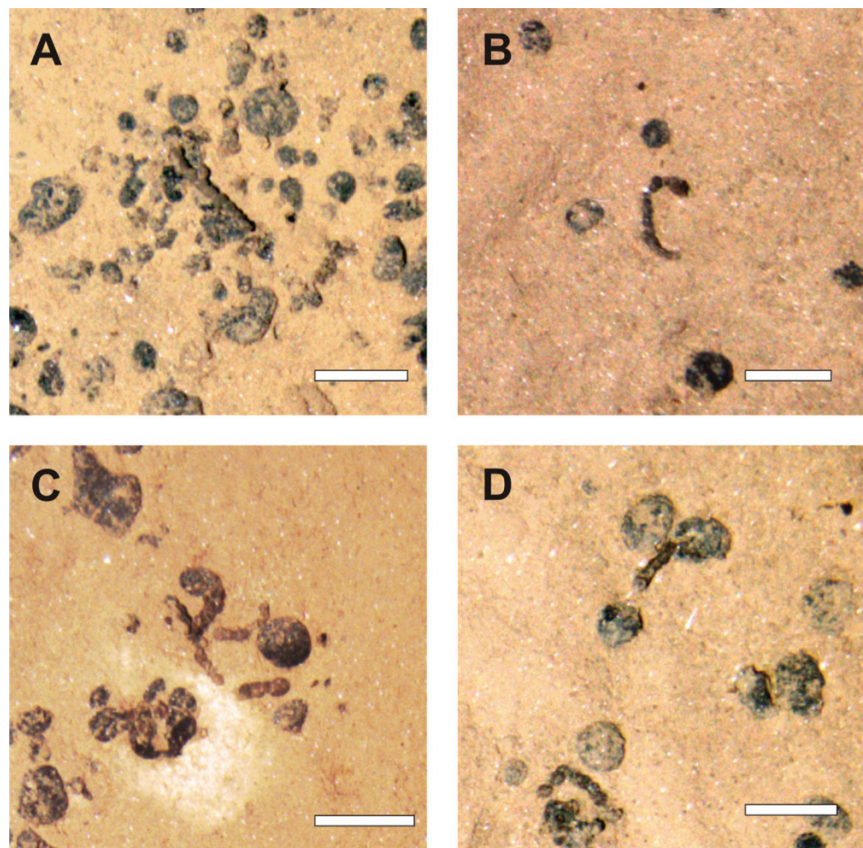
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Figure 10. Seafloor photographs showing individuals of ***Aschemonella monile* sp. nov.** from the SW corner of APEI-6. Scale bars = 5 cm.

processes but are not obviously segmented. Wall with rough, uneven surface, very coarsely agglutinated mainly using micronodules with variable proportion of coloured mineral grains. Obvious apertures absent. Test interior with pale granellare strands, 85- to 130-µm diameter, and relatively large stercomare masses.

Type specimen

The holotype (registration number NHMUK PM PF74535) comprises fragments of an originally upstanding structure (Fig. 11C, D) and the nodule to which it was attached with the bases of the two 'legs' of the structure (Fig. 11E, F) and their extensions onto the adjacent surface. The nodule was collected during the AB02 cruise, Box core 13, Site U07 in Stratum B of the UK-1 license area: 12°27.066′N, 117°35.661′W; 4130-m depth.

Description

The test is highly irregular in shape. The most visually obvious components are one or more basically tubular structures that extend more or less vertically from the surface of a nodule. The holotype comprises two such structures (now detached and damaged), one about 10 cm long and the other about half that length, connected by a transverse element (Fig. 11C, D). A second specimen (or cluster of specimens) comprised a cluster of four tubular structures extending to heights of between 4 and 5 mm (Fig. 11A, B). In both cases, these upstanding structures are highly irregular in width with a tendency to branch or develop short lateral processes. At their bases, they continue onto the nodule surface as flattened tunnels that extend across the substrate. Their generally low relief and construction largely from micronodules make the encrusting structures difficult to distinguish from the substrate, particularly in the holotype.

The agglutinated wall is one grain thick and has a very rough, dark grey outer surface with numerous projecting grains. It is composed mainly of micronodules with a variable but subordinate proportion of mineral grains, most of them orange or brownish and of varying sizes. The test interior is occupied by stercomare and granellare and lacks internal xenophyae (Fig. 11E, F). The granellare forms pale whitish strands, 85- to 130-µm diameter, as well as more diffuse and indistinct threads. The stercomare masses are relatively large and enclosed in a distinct organic membrane. Where the test encrusts the nodule surface, the interior is in direct contact with the substrate with no intervening wall.

Remarks

This rare species can be confused with delicate individuals of *A. monile* of the type illustrated in Figure 8. The main distinguishing morphological features are the very coarse agglutination of the test and the lack of distinct swellings or segments. The stercomare masses do not form the globular formations seen in *A. monile*. The two species are also genetically distinct. Because the available material is limited, we could not determine whether the test interior is partitioned.

MOLECULAR PHYLOGENY

Aschemonella monile builds a strongly supported monophyletic clade (97% BV) that branches next to a sister clade containing *A. ramuliformis* (97% BV) and *Rhizammina algaeformis*. *Aschemonella aspera* (100% BV) branches at the base of these clades, but the branching is not supported. The monophyly of xenophyophores and clade C specimens is strongly supported (99% BV). Specimens belonging to monothalamid clades B and A are the closest relatives to clade C and branch at its base (Fig. 9). The analysed specimens of *A. monile* include those with smooth brownish tests and well-formed bulbous segments (Fig. 2H, I), rough dark-coloured tests (Fig. 2E, F) as well as the delicate variant (Fig. 8A). Despite this considerable variation in the morphology and construction of the test, the new species displays relatively modest intra-specific sequence divergence (0.0–0.008), suggesting that these morphotypes represent a single, genetically coherent species. The sequence divergence for *A. aspera* is similar (0.001–0.005) to that for *A. monile*, while the sequence divergence between the two species ranges from 0.029 to 0.039, confirming that they are distinct.

DISCUSSION

ASCHEMONELLA MONILE – A MULTICHAMBERED MONOTHALAMID

As mentioned in Introduction, *Aschemonella* was originally placed within the family Hormosinidae, subfamily Aschemonellinae (Loeblich & Tappan, 1964), a group of multichambered agglutinated foraminifera (textulariids) raised to subordinal rank by Kaminski (2014). Of all known modern species of the genus, *A. monile* most closely resembles the hormosinids in terms of test morphology. It is particularly similar to members of the genus *Hormosina*, in which the test is 'uniserial and rectilinear to slightly arcuate', comprising 'large globular chambers increasing rapidly in size' and with a terminal aperture 'at the end of a distinct tubular neck, later chambers overlapping the previous ones to enclose the neck' (Loeblich & Tappan, 1987: 61). In *A. monile*, the segments form self-contained units that may overlap to some extent and can communicate via tiny apertures (Fig. 4B, C). In this sense, they resemble the 'true' chambers found in members of the Globothalamea (a group that includes the multichambered textulariids and rotaliids; Pawlowski *et al.*, 2013) rather than the 'pseudochambers' that are formed by the constriction or subdivision of a basically tubular test in some monothalamids (Mikhalevich, 2005, 2013, 2014). However, the sequence data clearly indicate that *A. monile*, like other xenophyophores, groups as one of the terminal branches of monothalamid clade C. Although clade C is related to clades A and B, which branch as sisters to the Globothalamea, there is no evidence that xenophyophores or other members of this clade are related to the hormosinids or any other globothalameans. The multichambered test of *A. monile* is another example of a process (termed 'polymerization' in the publications of Mikhalevich) by which parts of an organism, in this case the chambers, are multiplied. This phenomenon has arisen independently in different foraminiferal lineages (Pawlowski *et al.*, 2013; Mikhalevich, 2014) in the same way that aggregative multicellularity has arisen independently in various protistan groups (Brown *et al.*, 2012).

Without molecular data or any information about the cellular organization (granellare and stercomare), the chamber-like segments of *A. monile* would be difficult to distinguish from those of a hormosinid such as *Hormosina normani* (Brady, 1884: pl. 39, figs 19–23). This problem would apply particularly to any possible fossil material. The test generally tends to be more irregular in *A. monile* and related species than in hormosinids, and it sometimes branches (Fig. 2B). The absence of an obvious aperture, or the presence of multiple tiny apertures (discussed below) rather than a single simple aperture at the end of a short neck, is another character that might distinguish *A. monile* from hormosinids. The Cretaceous hormosinid genus *Cribratina* has multiple apertures, but these are much larger than those seen in *A. monile* (Loeblich & Tappan, 1987: 64). In addition to these test features, concentrations of barium associated with the test could provide evidence that a fossil species was a xenophyophore.

NOVEL APERTURAL FEATURES

Discrete apertures are rarely clearly developed in xenophyophores. Tendal (1972: 67) notes the presence of well-defined 'pores' in *Galatheammina calcarea*, *Psammina nummulina*, *Psammina globigerinum* and *Stannophyllum zonarium*. In *S. zonarium*, these features are described as being 'numerous', present over all parts of the test, and up to ~5 mm in diameter although considerably smaller. *Psammina globigerinum* has a series of openings around the outer edge of its discoidal

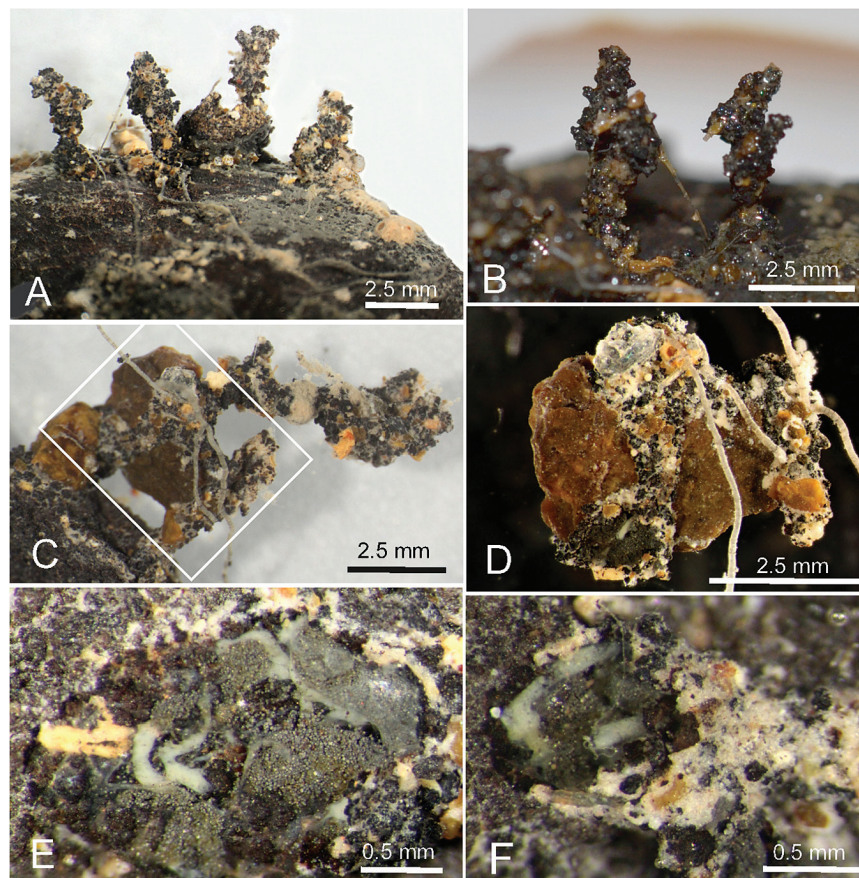**Figure 11.** *Aschemonella aspera* **sp. nov.**; Box core 13 (cruise AB02, Station U07). A–C, Shipboard images. D–F, Laboratory images. A, Cluster of tubular agglutinated structures, apparently part of the same individual test, extending upwards from the surface of a nodule. B, Detail of two of the structures. C–F, Holotype, reg. no. NHMUK PM PF74535. C, Main part of the test extending from nodule surface and comprising two tubular structures, one longer than the other, linked by a transverse element. The test incorporates a large flat brown mineral particle to which parts of the structure are attached. The white rectangle encloses the part shown in (D), which includes the large brown particle. D, Broken fragment of holotype with tubular structures (including the transverse element) attached to the surface of the large brown particle. The base of the structure (close to where it was attached to the nodule surface) is at the bottom of the image. Narrow grey tubes of the foraminiferan *Rhizammina* are loosely attached to the fragment. E and F, Nodule surface with broken bases of the upright parts of the test; (E) corresponds to the left-hand structure and (F) to the right-hand structure in (D). Pale cytoplasmic strands and stercomare masses are visible inside the broken test. Note that the broken base in (F) extends into a tunnel on the nodule surface.

test (Haeckel, 1889: pl. VII, fig. 2B) and similar features are present in *Psammina sabulosa* (Gooday & Tendal, 1988). *Aschemonella ramuliformis* and *A. scabra* have fairly obvious openings, presumably apertures, located at the ends of short side branches or swellings. Although apertures of this type are absent in both of our new species, a few specimens of *A. monile* exhibit clusters of tiny raised openings in the test wall located at the ends of segments. These are most evident in specimens with smooth test walls and particularly the large individual from APEI-6 in which several chambers bear clusters of up to 70 or more rounded apertures that project

slightly above the general level of the smooth test surface (Fig. 4C, E). These clusters of tiny apertures have not been described before in xenophyophores. They are somewhat similar to the cribrate apertures seen in some multichambered foraminifera, including agglutinated species such as *Cyclammina cancellata* (e.g. Mikhalevich, 2014), but are much smaller. They are closer in size and appearance to the tiny raised openings in the 'balloon chamber' of certain calcareous foraminifera (e.g. *Tretomphalus*) through which gametes are released during the planktonic stage of the lifecycle (Banner, Pereira & Desai, 1985). The fact that the openings are retained

on inner segments of *A. monile*, however, suggests that they are apertures for pseudopodia rather than ephemeral openings for the release of gametes.

Some specimens of *A. monile* give rise to one or more approximately straight, rigid tubes (Figs 3E–H, 8B), similar to those illustrated by Gooday (1996: pl. 9, figs 4, 5) in a single large specimen assigned to *A. ramuliformis* from the Porcupine Abyssal Plain. The function of these structures, which are absent in *A. aspera*, is not clear. They could be conduits for pseudopodia of the kind observed in some calcareous foraminifera (e.g. Alexander & DeLaca, 1987). Tubular extensions of the test, sometimes interpreted as 'pseudopodial tubes', are described in *S. zonarium*, but they seem to be more flaccid than the tubes in *Aschemonella* and are associated with 'tufts' of the proteinaceous fibres (linellae) that are characteristic of this genus (Tendal, 1972).

Novel internal features

Aschemonella monile also displays some interesting cellular features. In xenophyophores, the cell body is typically enclosed within an organic tube system, these two components together constituting the granellare system (Tendal, 1972). The presence of an organic tube is not evident in *A. monile* when the cytoplasm is viewed with a light microscope, but there are indications of a very thin organic layer enclosing the cytoplasm in scanning electron microscopic images (Fig. 7C, D). The accumulations of stercomata are clearly enclosed within a transparent organic layer to form the stercomare, which typically form globular masses in *A. monile*, although apparently not in *A. aspera*. Examination of some unfixed specimens of *A. monile* at sea soon after collection revealed diffuse threads and sheets of material resembling cytoplasm linking discrete masses of much denser cytoplasm (Fig. 6C, E). This diffuse cytoplasm was sometimes closely associated with the stercomare, which often forms more or less discrete rounded masses in this species. The impression is gained from these observations that an intimate connection exists between the cytoplasm and stercomare in *A. monile* and probably other xenophyophore species. This is consistent with transmission electron microscopic observations of another species, *Shinkaiya lindsayi*, in which cytoplasm was seen to be associated with the stercomare (Lecroq *et al.*, 2009).

Distribution of the new species and vulnerability to disturbance

Aschemonella monile is a very common foraminifera in the eastern equatorial Pacific with a test of megafaunal size. Unlike the majority of xenophyophores in the ABYSSLINE samples (Gooday *et al.*, 2017), it appears to be widely distributed in the central, eastern and northern parts of the CCZ, having been identified, based on morphological data, in the Russian exploration claim area as well as the APEI-6, where it is abundant in seafloor photographs. It is therefore remarkable that this distinctive species has not been recorded before. The Russian specimens (Fig. 5) have smooth, light greyish tests and are similar to the largest of the APEI-6 specimens (Fig. 4A). We include them in *A. monile* based on their similarity to individuals in ABYSSLINE samples from the eastern CCZ. However, confirmation that the APEI-6 and Russian specimens are conspecific with those from the UK-1 and OMS areas will require molecular data, which are currently available only from the two latter areas. There is no evidence for the occurrence of *A. monile* in other parts of the Pacific or in other oceans; for example, it is not present in the NE Atlantic including the Porcupine Abyssal Plain site where the xenophyophore assemblage is well studied (Gooday, 1991, 1996). At present, therefore, this appears to be a Pacific species. Nothing can be said at present about the distribution of *A. aspera*.

Gooday *et al.* (2017) argue that seabed mining in the CCZ is likely to have an important impact on xenophyophores. There is evidence that xenophyophores can grow quickly (Gooday, Bett & Pratt, 1993) and can colonize new soft substrates (Hess *et al.*, 2001), suggesting that they could recover fairly quickly following the cessation of mining in a particular area. However, like many other xenophyophores in our samples, specimens of *A. monile* collected in the UK-1 and OMS areas were often attached, more or less securely, to polymetallic nodules. Some 30% of those seen in seafloor images from APEI-6 displayed an obvious association with nodules. In the case of *A. aspera*, the tests of the two available specimens partly encrust the surfaces of their host nodules. Both new species may therefore be at risk from mining activities.

Acknowledgements

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