New xenophyophores (Foraminifera, Monothalamea) from the eastern Clarion-Clipperton Zone (equatorial Pacific)

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Abstract

Xenophyophores are large, agglutinated foraminifera that dominate the benthic megafauna in some parts of the deep sea. Here, we describe an assemblage of largely fragmentary specimens from the Clarion-Clipperton Zone (CCZ), an area of the eastern abyssal Pacific hosting large, commercially significant deposits of polymetallic nodules. We recognised 18 morphospecies of which eight yielded DNA sequences. These include two new genera and three new species, *Claraclippia seminuda* gen. & sp. nov., *Stereodiktyoma mollis* gen. & sp. nov., and *Aschemonella tani* sp. nov., three that are assigned to known species, *Abyssalia foliformis, Aschemonella monilis* and *Shinkaiya contorta*, and two assigned to open nomenclature forms *Abyssalia* aff. *foliformis* and *Stannophyllum* aff. *granularium*. An additional ten forms are represented only by morphology. The following seven are placed in known genera, species and open-nomenclature forms: *Aschemonella?* sp., *Homogammina* sp., *Psammina multiloculata, P.* aff. *multiloculata, P.* aff. *limbata* form 1 sensu Gooday et al., 2018, *P.* aff. *limbata* form 2 sensu Gooday et al., 2018, and *Stannophyllum* spp. The other three could not be identified to genus level. This new collection brings the total of described and undescribed species and morphotypes from the CCZ to 27 and 70, respectively, reinforcing the already high diversity of xenophyophores known from this part of the Pacific.

Keywords: Monothalamids, Protists, DNA barcoding, molecular phylogeny, biodiversity, seabed mining, polymetallic nodules

Introduction

Since the publication of Tendal's (1972) monograph, and particularly with the more recent advent of large-scale photographic surveys of the ocean floor (Durden et al., 2016), it has become increasingly apparent that xenophyophores constitute a major part of the megafauna in many deep-sea settings. These giant agglutinated foraminifera are particularly common on seamounts and continental slopes, in submarine canyons, and on abyssal plains (Tendal & Gooday 1981; Levin and Thomas 1988; Bett 2001; Gooday *et al.* 2011). In the equatorial

Pacific, they are a dominant group among the megafauna seen in seabed images across large areas of the Clarion-Clipperton Zone (CCZ), where they often outnumber all the metazoan megafauna combined (Kamenskaya et al., 2013; Amon et al., 2016; Simon-Lledó et al., 2019a, 2019b; Durden et al. 2021; Uhlenkott et al., 2023). Although xenophyophores are typically the most common organisms visible on the deep ocean floor, they are difficult to incorporate into ecological studies. Particular problems in the case of data derived from photographic surveys include the estimation of biomass and the need to distinguish living from dead specimens (De Jonge et al., 2020; De Smet et al., 2021). Nevertheless, they remain an important taxon, not least for their contribution to habitat structure and megafaunal biodiversity (Gooday et al., 2020d; 2021).

The CCZ has attracted a lot of attention because it hosts extensive seafloor deposits of polymetallic nodules that are rich in valuable metals and hence of great commercial importance. Since this vast area lies beyond national jurisdictions, licences for exploration and prospecting are issued to state-sponsored companies and other entities that are interested in exploiting these resources by the International Seabed Authority (ISA), a United Nations body. This in turn has generated a considerable body of research aimed at better understanding the functioning and biodiversity of seabed biological communities before any commercial mining begins. The research effort has focused particularly on the eastern CCZ and has included work on the xenophyophores. These giant foraminifera have proved to be particularly diverse, with 24 new species having been described, two known species identified, and a further 39 undescribed species recognised (Gooday et al., 2017a, 2020d, 2021). Another five hitherto unrecognised morphotypes were recently found in epibenthic sledge material from five areas in the eastern CCZ (Gooday and Wawrzyniak-Wydrowska, 2023). Here, we extend these studies with a survey of xenophyophore diversity in samples collected with a box core in the Ocean Mining Singapore (OMS) and Seabed Resources Limited (UK-1) license area during February and March 2020.

Materials and Methods

Shipboard methods

Xenophyophores were collected at 19 sites in the UK-1 and OMS license areas during the Resource Cruise 01 (hereafter RC01), which took place aboard the M/V *Pacific Constructor* between February 14 to March 23, 2020 (Table 1). All specimens were picked from the surfaces of cores collected with an USNEL-type box corer. As soon as possible after collection, specimens were placed in a bowl of chilled seawater on ice and transferred to the ship’s laboratory where they were photographed using a hand-held Canon PowerShot S100 camera, a Nikon 0800 SLR camera with a Nikon 50 mm f/2.8 macro lens mounted on a stand, or an Olympus DP27 camera mounted on an Olympus SZX16 stereomicroscope. Parts of specimens, or in some cases entire specimens, were preserved in RNAlater solution (Qiagen) for later molecular analyses. Others were preserved in either 4% borax-buffered formalin, 96% or 99% ethanol, or in a few cases dried. The dried specimens were transported directly to Geneva, but all other material was shipped to Singapore. After some months, specimens in RNAlater were shipped from Singapore to Geneva for genetic analysis and those in formalin were sent to Southampton. Once the genetic work had been completed in Geneva, specimens were transferred from RNAlater to formalin and taken to Southampton.

Land-based Photography

In Geneva, specimens and test fragments, as well as isolated granellare strands and stercomare masses, were photographed using a Leica M205 C motorized stereomicroscope equipped with a Leica DFC 450 C camera prior to being prepared for genetic analysis. In all cases, specimens and fragments were placed in LifeGuard solution (Qiagen) for photography in order to avoid the formation of crystals that occurs rapidly in RNAlater. Additional photographs were taken in Southampton using an Olympus SZX7 stereomicroscope and an Olympus BH2 compound microscope, both equipped with a Canon 60D SRL digital camera.

DNA extraction, PCR amplification, and sequencing

For the present study, fourteen DNA extractions were obtained from eight xenophyophore species (Table 2, Figure 1) using the DNeasy Plant Mini Kit (Qiagen). Semi-nested PCR amplification was carried out for the 18S rRNA barcoding fragment of foraminifera (Pawlowski and Holzmann, 2014) using forward primers s14F3 (5'acgcamgtgtgaaacttg3') -s20r (5'gacgggcggtgtgtacaa3') for the first and primers s14F1 (5'aagggcaccacaagaacgc3')-s20r for the second amplification. Thirty-five and 25 cycles were performed for the first and the second PCR, with an annealing temperature of 50°C and 52°C, respectively. The amplified PCR products were purified using the High Pure PCR Cleanup Micro Kit (Roche Diagnostics). Sequencing reactions were performed using the BigDye Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems) and analyzed on a 3130XL Genetic Analyzer (Applied Biosystems). The resulting sequences were deposited in the NCBI/GenBank database. Isolate and Accession numbers are specified in Table 2.

Phylogenetic analysis

The obtained sequences were added to 65 monothalamid sequences (Table 2) that are part of the publicly available 18S database of monothalamous foraminifera (NCBI/Nucleotide; www.ncbi.nlm.nih.gov/nucleotide/). All sequences were aligned using the default parameters of the Muscle automatic alignment option as implemented in SeaView vs. 4.3.3. (Gouy, et al. 2010). The alignment contains 79 untrimmed sequences with 1544 sites used for analysis and was deposited at Figshare (DOI 10.6084/m9.figshare.24983280). The phylogenetic tree was constructed using maximum likelihood phylogeny (PhyML 3.0) as implemented in ATGC: PhyML (Guindon et al. 2010). An automatic model selection by SMS (Lefort et al. 2017) based on Akaike Information Criterion (AIC) was used, resulting in a GTR+G+I substitution model being selected for the analysis. The initial tree is based on BioNJ. Bootstrap values (BV) are based on 100 replicates.

Systematic Descriptions

Rhizaria Cavalier-Smith, 2002
Retaria Cavalier-Smith, 1999
Foraminifera D'Orbigny, 1826
'Monothalamanids' *sensu* Pawlowski, Holzmann and Tyszka, in Kaminski, 2014
Astrorhizida Lankester, 1885
Xenophyophoroidea Tendal, 1972

The type material is deposited in the Lee Kong Chian Natural History Museum, Singapore, under registration numbers ZCR.FOR.0001-0004

Genus *Aschemonella* Brady, 1879

Aschemonella monilis Gooday & Holzmann, 2017

Fig. 2; Supplementary Figs S1

Aschemonella monila Gooday and Holzmann in Gooday et al., 2017b, Figs 2A–E, 3A–F; Supplementary Fig. S1, Figs 1–8.
Aschemonella monilis Gooday and Holzmann. Gooday et al., 2020a, p. 4-6, figs 2-3.

Material examined
BC001 RC0056: morphology and genetics (isolates 21438, 21439)
BC010 RC049B: morphology and genetics (isolate 21431)
BC025 RC1042: morphology only
BC026 RC1056: morphology and genetics (isolate 21108)
BC031 RC1345: morphology only
BC040 RC1689: morphology and genetics (isolate 21435)
BC040 RC1731: morphology only
BC045 RC1900.1: morphology and genetics (isolate 21444)

Sequenced isolates: 21108, 21431, 21435, 21444 (Table 2)

Description and remarks
Aschemonella monilis is by far the most abundant xenophyophore species in our collection. It is represented by around 34 complete and fragmentary specimens (Table 2), although not all of these were examined in detail. They conform closely to the original description (Gooday et al., 2017b). Nineteen specimens were found attached to nodules, of which three encrusted the host nodule for their entire length and the others extended upwards from the surface to a greater or lesser extent. The remaining 15 were unattached, at least when found. The majority of specimens are dark grey with either a smooth, relatively fine-grained wall or a rougher, more coarsely grained wall. Some of the latter type resemble the 'delicate' form distinguished by Gooday et al. (2017b) (Supplementary Fig. S1A, B). Other specimens aree paler, dull orange to yellowish in overall colour but speckled with a variable density of dark grains (Fig. 2C, D, F; Supplementary Fig. S1D). These lighter coloured tests have generally smoother surfaces than the darker ones. Most sequenced specimens were of the paler, smooth-walled type, but they grouped together with one having a darker, rougher wall (Fig. 2A). This is consistent with the earlier genetic data (Gooday et al., 2017), and strongly indicates that they represent the same species.

Apertural structures were observed in two specimens from BC045 (RC1900.1 & 2). One has a smooth, blister-like dome, measuring 1.42 × 1.00 mm, located near the junction between several chambers (Fig. 2D, E). It gives rise to two tubular extensions, one 0.83 mm long and of fairly even width (~0.17 mm), the other 1.06 mm long and of variable width (0.26 to 0.45 mm). The other structure is located on the final chamber and comprises a swelling ~1.20 mm long that is associated with two tubes (Fig. 2F, G). The longer tube is 3.5 mm in length and again of fairly even width (0.21 to 0.26 mm), the shorter is ~0.85 mm in length and 0.36 to 0.53 mm wide. The longer tube is relatively smooth, but the shorter tube has a lumpy, very uneven surface and the associated swelling has a similarly irregular shape. Several short, pustule-like tubes ~0.18 mm long and of similar width, are present elsewhere on the final chamber of this specimen. Similar apertural features (swellings, long tubes and clusters of short, pustule-like tubes) were described by Gooday et al. (2017b, Figs 3,4 therein).

Aschemonella monilis is widely distributed across an area spanning some 3,800 km, being common in samples from the UK-1 license area (adjacent to the OMS area), as well as present in the Russian area in the central CCZ and APEI 4, a protected area in the western CCZ (Gooday et al., 2017a,b, 2020a). In the latter case, the three recorded specimens were morphologically atypical but genetically identical to those from the eastern CCZ. *Aschemonella monilis* is also the dominant faunal component in seafloor photographs from the southwestern part of APEI 6 (now APEI 3), located in the northeastern CCZ (Gooday et al., 2017b; Simon-Lledó et al., 2019).

Aschemonella tani Gooday & Holzmann **sp. nov.**
Figs 3, 4

Diagnosis. Species of *Aschemonella* with attached test forming tubular branching structures that grow free from solid substrate. Branches are relatively wide compared to their length and in places display vague segmentation. Upstanding parts extend into basal system of flat, branching tubes that encrust parts of the substrate surface. Stercomare forms irregularly shaped, sometimes discontinuous masses, but more elongated, continuous masses run along branches. Granellare forms pale yellowish, branching strands, typically 21–36 μm wide.

Zoobank registration. LSID urn:lsid:zoobank.org:pub:88353CBA-6C4D-40E3-8475-B1FCA2C48637

Etymology. The new species is named for Dr Koh Siang Tan, Head of the Marine Biology and Ecology Laboratory at the Tropical Marine Science Institute, Singapore, who has led research by Singapore scientists in the Clarion-Clipperton Zone.

Type specimen and locality
The holotype (Lee Kong Chian Natural History Museum, Singapore, reg. no. ZRC.FOR.0002, preserved in 10% formalin) was collected in box core BC036 (specimen RC1555); OMS license area, 12° 26' 45.5''N, 117° 49' 41.1''W; 4196 m water depth. A fragment was used for genetics (sequenced isolate: 21430). There were no other specimens.

Description

Shipboard photographs. The main part of the test (labelled ‘1’ in Fig. 3A) stands erect at the summit of a roughly conical nodule. Its overall height is around 3.9 mm. There is a short stalk, ~1.45 mm long and 0.9–1.1 mm wide, that gives rise to three branches, also short and relatively wide (length 1.5–1.7 mm; width 0.60–1.0 mm). At its top, the test bifurcates into two further branches, the longer one 1.7 mm in length and 0.63–0.77 mm wide. The structure is rusty brown in overall colour. The base of the stalk continues as an encrusting structure that spreads across part of the nodule summit. The base also gives rise to two short branches that project from the nodule surface near the summit; one is ~1.20 mm long and the other at least of similar length. The summit region of the nodule hosts at least two other projecting structures (labelled ‘2’ and ‘3’ in Fig. 3A) with a weakly segmented appearance.

Preserved fragments. Parts 1, 2 and 3 in Fig. 3A are all recognisable among the preserved fragments. They are identical in general appearance and wall structure, suggesting that they are parts of the same organism. The wall is pale, brownish yellow, and about 40 μm thick. It is composed largely of small mineral grains (less than about 25 μm in size), mainly resembling quartz but with a scattering of blackish and reddish grains, and with sponge spicule fragments making a subordinate but important contribution. A few tests of agglutinated foraminifera are also incorporated into the wall.

The stercomare can be seen dimly through the test wall when illuminated with transmitted light. In the central parts of the fragments (Fig. 4A), it forms irregularly shaped, apparently disconnected masses of various sizes, up to ~800 µm in maximum dimension but usually less. More elongated, continuous masses are visible running along the branches of the part 1 fragment (Fig. 3B). Part 3 appears to have more strongly developed stercomare since the interior is filled with dark material when viewed through the test wall. The granellare forms pale yellowish, branching strands, typically 21–36 µm wide but swelling in places to 50–65 µm (Fig. 4D).

The test, including the lower encrusting part, is to some extent obscured by another agglutinated structure. This is basically tubular, branches and is to some extent reticulated. The width is variable (0.40–0.80 mm) and there are several inflated segments. It is most likely another monothalamid species. In preserved fragments as well as in shipboard photographs (Fig. 3A¬D), the branches have a lighter greyish colour compared to the *Aschemonella* that they partly overgrow.

Molecular characterisation

Aschemonella tani branches at the base of *Aschemonella* sp. 3 with *A. aspera* forming a sister group to these two species (Fig. 1). The grouping is not supported by the BV. The sequenced fragment of 18S gene of *A. tani* contains 1028 nucleotides and the GC content is 34 %.

Remarks

The branching, basically tubular test, and the fairly large, irregularly shaped stercomare masses of *Aschemonella tani* distinguish it from *A. monilis*, in which the test is clearly segmented and the stercomare masses resemble pellets. It is much more similar to *Aschemonella aspera*, another species from the CCZ that also has an approximately tubular test growing upwards from the substrate to which it is attached. However, the test is more strongly branched in the new species and has a brownish yellow wall composed small mineral with a smooth outer surface, unlike that of *A. aspera*, in which the wall is dark grey and much more coarsely agglutinated with a rough surface composed of micronodules and mineral grains. The most similar described species is *A. ramuliformis.* This also forms branching tubes, but they are more elongate and regular than those of the new species (Brady, 1884; Gooday et al., 2011). There are no records of *A. ramuliformis* being attached to a hard substrate.

These three species (*A. aspera, A. monilis, A. ramuliformis*) are genetically distinct from *A. tani* (Fig. 1). Based on molecular data, the new species is most closely related to *Aschemonella* sp. 3 of Gooday et al. (2017a), also from the CCZ. The test of this undescribed species forms an irregular system of reticulated tubes that are sometimes vaguely segmented and either attached to a nodule surface or grow free. The lower encrusting part of our *A. tani* specimen, which comprised tubular structures spreading across the nodule surface, is rather similar to the attached parts of *Aschemonella* sp. 3. However, the upper, free-standing part of the test does not form the same kind of reticulated structure.

***Aschemonella*? sp.**

Supplementary Fig. S2

Material examined

BC040 RC1698 (morphology)

Description

The two illustrated fragments are around 7 and 19 mm in maximum dimension. The larger (Supplementary Fig. S2B) forms an irregular mass that is perforated by several open spaces, up to 2.20 mm across, so that parts of it appear broadly reticulated. The smaller (Supplementary

Fig. S2A) has a single round open space, 1.24 mm in diameter, that is surrounded by broad bars, between 1.40 and 2.00 mm wide.

Both fragments are pale yellowish brown, with a smooth, generally finely agglutinated outer surface. However, the wall also incorporates relatively large, black grains, probably fragments of micronodules, that are concentrated in certain areas. This is most clear in the smaller fragment, where the dark grains occur mainly in bands across the bars, in one case being largely restricted to a distinct zone where the largest grain is 230 μm in size. The test wall is very delicate and no more than about 30-40 μm thick. There are no internal xenophyae and the test interior is filled with dark grey decayed stercomare. There is no sign of granellare.

Remarks.
The thin, delicate wall composed of mineral grains and the absence of internal xenophyae suggest a placement for these distinctive fragments in *Aschemonella.*

Abyssalia foliformis Gooday and Holzmann 2020
Fig. 5

Abyssalia foliformis Gooday and Holzmann 2020, pp. 15-18, Figs 9,10

Material examined.
BC015 RC0612 (morphology and genetics).
Sequenced isolate: 21442

Description
Shipboard photographs show a test fragment attached to a nodule (Fig. 5A). The fragment was detached when seen later in the laboratory (Fig. 5B). It is plate-like, about 21 mm long and 2.0¬2.6 mm thick with a slight twist and widening from about 7.0 mm near the base to about 13 mm at its upper end. The agglutinated particles consist almost entirely of sponge spicules, apart from one or two agglutinated foraminifera. A felted mesh of these spicules forms a poorly defined surface layer from which some of them project. This layer merges into a more open framework of spicules occupying the test interior.

The stercomare, which comprises small, rounded pellet-like masses (Fig. 5F), originally occupied much of the test interior. However, the are quite loose, and many had fallen out from the central part of the fragment following preservation. In peripheral areas, however, the stercomare is denser and has largely retained its coherence (Fig. 5B), Here, it appears to consist of tightly packed pellets that are presumably bound together in some way.

Branched granellare strands are well-developed and pervade much of the test interior (Fig. 5C, D). They are pale cream and of variable width (34–140 μm), often with more or less bulbous sections. The organic tubes that enclose the cytoplasmic branches are relatively thick and clearly visible under a stereomicroscope, given suitable lighting. The tubes are closely associated with the internal spicules, to which they are attached at multiple points (Fig. 5E).

Remarks.
The holotype and unique specimen of *Abyssalia foliformis* from the western CCZ (Gooday et al., 2020) was attached to a nodule by a stalk that merged gradually with the wider upper part of the test. Our new specimen includes only the stalk, but the shape is consistent with the morphology of the holotype. Other features, notably the use of spicules in test construction, the

pellet-like stercomare and the granellare strands with their well-developed organic tubes attachment to spicules, are very similar to those described for *A. foliformis.* We are therefore confident that this fragment represents the same species as that described by Gooday et al. (2020). The only apparent difference is that the holotype has a homogenous test that lacks a surface layer, whereas there is some differentiation between the outer and inner parts of our fragment. This is possibly because the original description was based mainly on the upper part of the test whereas we have only the basal stalk.

Gooday and Wawrzyniak-Wydrowska (2023; Fig. 6F, G therein) recently illustrated a xenophyophore fragment from the IOM license area that may have been derived from an *Abyssalia* species. Unfortunately, granellare from which DNA could potentially be amplified was not present, and not enough of the morphology was preserved to determine whether it could be assigned to *A. foliformis*.

Abyssalia* aff. *foliformis
Figs 6, 7

Material examined
BC011 RC0520 (morphology and genetics)
Sequenced isolate: 21429

Description

Shipboard photographs. Most of our morphological information about the single specimen comes from photographs taken soon after its collection (Fig. 6). These show a complex branching, plate-like test attached to a nodule by a short, relatively wide basal stalk, about 4.3 mm wide and 4.0 mm high. The entire test is estimated to be roughly 22 mm high with a maximum horizontal span of about 58 mm. The stalk widens rapidly into a central plate-like part that gives rise to a series of elongate lobes of different sizes, radiating in different directions and in some cases appearing slightly twisted. The most prominent of these is roughly 13 mm long and widens from about 5.8 mm near the base to about 11 mm at the end. Others are shorter and do not widen to the same extent. One lobe, which can be measured accurately because there is a corresponding scale, is 11 mm long, 5.3 mm wide near the base and 8.1 mm wide near the end (Fig. 6D).

The overall colour of the test in these photographs is greyish brown, with a paler rim that is most obvious around the ends of the lobes. The yellow agglutinated tube of a foraminifera, probably *Saccorhiza ramosa*, winds around the stem and extends along the underside of one of the lobes.

Preserved fragment. One small lobe was available for more detailed study (Fig. 7). It measures ~6.5 cm long, a maximum of ~4 cm wide, and about 1.60 to 1.75 mm thick. There is a clearly defined test wall, about 220 to 245 µm thick, composed mainly of short, sponge spicule fragments and tiny transparent mineral grains (~10–50 µm in size), as well as occasional radiolarian shells. A few agglutinated foraminiferal shells are also incorporated. The spicules form a three-dimensional mesh that creates a very distinctive, somewhat labyrinthic appearance. There are few if any internal xenophyae and the test interior is largely occupied by dense stercomare. Narrow, pale cream granellare strands are exposed on the broken end of the fragment (Fig. 7D). They are generally 20–40 µm wide but sometimes wider at branching points. A few larger masses (up to ~60 µm) are also visible.

Molecular characterisation

Abyssalia aff. *foliformis* branches at the base of *A. foliformis* (90%BV) and both taxa build a well sustained (89%BV) group with *A. sphaerica*. The sequenced fragment of the 18S gene of *Abyssalia* aff. *foliformis* contains 1018 nucleotides and the GC content is 37%.

Remarks

This species is closely related genetically to *Abyssalia foliformis,* but morphologically distinct. The test is a branching structure that is considerably more complex than the leaf-like test of the type specimen of *A. foliformis* (Gooday et al., 2020). The test wall of both species is composed almost entirely of sponge spicules, but the spicule framework of *A.* aff. *foliformis* is much more intricate that the relatively simple felted wall of *A. foliformis.*

Abyssalia aff. *foliformis* is very likely the same as *Galatheammina* sp. 7 of Gooday et al. (2017a, Supplementary Fig. S3A), a small, semi-circular plate, less than 1 cm in width and height, that was attached to a nodule in the UK-1 area. It was much smaller and simpler than our specimen, presumably a young individual, and lacked a basal stalk. Both share the same very distinctive wall structure comprising an intricate framework of spicule fragments and mineral gains, but since sequences were not obtained from *Galatheammina* sp. 7, we cannot confirm that it represent the same species.

Claraclippia Gooday & Holzmann gen. nov.

Diagnosis. Body attached, delicate, somewhat flexible. Distinct test absent although dusting of fine, loosely attached surficial particles present when freshly collected. Instead, body is composed largely of closely packed, branching stercomare branches (typically 100–150 µm diameter) that tend to fuse into more continuous sheets. Overall morphology complex but basically plate-like. A large irregular, three-dimensional structure with no obvious centre of organisation is formed by plate-like elements perforated by occasional small open spaces; in places, plates merge into bar-like elements that define larger open spaces.

*Zoobank registration.*LSID urn:lsid:zoobank.org:pub:88353CBA-6C4D-40E3-8475-B1FCA2C48637

Etymology. The name reflects the occurrence of the new genus in the Clarion-Clipperton Zone.

Remarks. The more or less naked body of *Claraclippia* is reminiscent of the genus *Cerelasma,* in which an agglutinated test is weakly developed or virtually absent (Tendal, 1972). The main difference between the new genus and the three species included by Tendal (1972, 1996) in *Cerelasma* (the genotype *C. gyrosphaera, C. lamellosa,* and *C. massa*) is that the test is larger with a basically plate-like structure compared to its relatively simple, 'lumpy', rounded shape in *Cerelasma.* The stercomare branches are also considerably narrower and much more numerous and densely packed in the new genus. A fourth species, *Cerelasma implicata,* recently described from the Russian license area in the central CCZ (Kamenskaya et al., 2017), is constructed from narrow, densely packed stercomare branches and granellare strands and therefore shows a greater morphological resemblance to *Claraclippia.* However, sequences have not been obtained from this or any other *Ceralasma* species and so their relationships, if any, to *Claraclippia* are unclear.

Claraclippia seminuda Gooday & Holzmann **gen. & sp. nov.**

Figs 8, 9

Diagnosis. As for genus.

Zoobank registration. LSID urn:lsid:zoobank.org:pub:88353CBA-6C4D-40E3-8475-B1FCA2C48637

Etymology. The name reflects the appearance of the type specimen, which, when freshly collected, was covered with a thin layer of fine sediment that was not retained when the specimen was preserved.

Type specimen and locality

The holotype (Lee Kong Chian Natural History Museum, Singapore, reg. no. ZRC.FOR.0001, preserved in 10% formalin) was collected in box core BC005 (specimen RC0202); OMS license area, 14° 06' 38.2"N, 117° 13' 54.2"W; 4200 m water depth. A fragment was used for genetics (sequenced isolates: 21436, 21437). There were no other specimens.

Description

Shipboard photographs. Photographs of the specimen as first seen on the box core surface shows it spread across several nodules with part of the base attached to at least one nodule (Fig. 8A, B). The photograph gives the impression that the body was somewhat flexible and had collapsed from a more upright position when the overlying water was drained from the box core. The test formed a complex but basically, plate-like structure, brownish grey in colour, that included several lobes, the main part being strongly curved.

When photographed in the shipboard laboratory after removal from the box core, the specimen appeared somewhat damaged with several obvious breaks, an indication of its fragility (Fig. 8C–F). It measured about 8 cm in overall maximum dimension. The largest part, which had broken into two main pieces, formed a folded, undulating plate, 6.4 cm in maximum dimension. The outer margin, which seemed largely intact, was curved with a broad concave section and two short tapering outgrowths, the larger being about 5 mm long and 3 mm wide at the base. Very vague, concentric zonation patterns were visible under low-angle lighting (Fig. 8C). These had different orientations, suggesting that there were several directions of growth. The plate was also perforated by a number of small open spaces, 0.5–1.2 mm in maximum dimension, some of them arranged in a rough arc (Fig. 8C¬F). The other main body part visible in these photographs was more complicated. Although basically plate-like, it curved around to form what appears to be a funnel-like structure and was perforated by several relatively large open spaces, 1.4 –4.9 mm maximum dimension (Fig. 8F).

The photographs (Fig. 8) show that the test surface was originally covered with a veneer of fine-grained material. In some patches this appeared to be absent, exposing the tightly packed strands of the stercomare system. Under low-angled lighting, the strands created a hair-like surface pattern, even where the fine-grained veneer was present. The margin of the structure was often fairly even, but in places, possibly where damage has occurred, it has a frayed appearance with a fringe of exposed stercomare branches.

Preserved fragments. There are two main fragments that probably correspond to the two parts recognisable in shipboard photographs. Both are dark grey and somewhat flexible but very delicate. The larger fragment (Fig. 9C–E) measures between 4.7 to 5.5 cm maximum dimension and 2.6 to 4.1 cm minimum dimension, depending on the viewing angle. The structure has no obvious regularity or centre of organisation. It forms a complex and irregular three-dimensional system comprising plates, in places interrupted by open spaces or merging into bars that define open spaces (Fig. 9C, E). These spaces are highly variable in size, ranging from ~0.5 mm or less to 6.6 mm in the case of the largest one that is easily visible. The second fragment (Fig. 9F) is a much simpler undulating plate, 4.8 cm long, a maximum of 2.8 cm wide, and around 1.0 to 1.2 mm thick. The plate is interrupted by a few small open spaces (up to 1.1 mm maximum dimension), most of which are concentrated in one area.

The preserved fragments are composed largely of naked stercomare, mainly in the form of closely packed strands that are most distinct around the edges where they project slightly to form a dense fringe (Fig. 9A, B). Here, they are 75 to 150 µm, typically 90–120 µm, wide and branch but rarely anastomose. At least some of these sections probably represent the original margin of the test, although others appear damaged. Away from the edge, the strands lose their identity to varying extents. In places, they are still quite distinct. Elsewhere they become more tightly meshed and reticulated, with only chinks of space between them, and up to 200 µm wide. Sometimes they merge to form a more continuous sheet perforated by small open spaces.

When examined in Geneva after transport from Singapore the fragments retained some patches of the pale, fine-grained surface veneer that was seen in the shipboard photographs (Fig. 9A, B). Usually, this was found filling spaces between the stercomare branches. By the time they reached Southampton, no obvious trace of the fine-grained material remained (Fig. 9C–F). However, careful examination revealed a scattering of tiny mineral particles across the surface of the stercomare. Some of these grains stand out because they are white or because they glint in the light.

The granellare strands are clearly visible only around parts of the margin, where they are closely associated with the stercomare branches (Fig. 9B). They are distinctly reddish and stand out in contrast to the dark grey stercomare. The organic tube that contains the cytoplasm is very thin. The strands are of irregular width, generally between ~100 and 200 µm but occasionally somewhat wider. Some peripheral strands have slightly expanded ends. Away from the margin, the reddish strands can sometimes be glimpsed in gaps within the grey stercomare system.

Molecular characterisation

Claraclippia seminuda (100% BV) branches as sister to *S. mattaeformis* (100% BV), but the grouping of the two species is not supported by the BV. The two 18S sequences of *C. seminuda* are identical, they contain 908 nucleotides and the GC content is 44%.

Remarks.

A distinctive feature of *Claraclippia seminuda* is the lack of any real test. Shipboard photographs of the freshly collected specimen show a layer of fine sediment particles covering much of the surface, although this veneer was very thin and did not totally obscure the underlying stercomare. Some parts of the veneer survived transport in RNAlater to Geneva, but it had disappeared when the fragments, now preserved in formalin, were examined in Southampton a year later.

There are intriguing morphological similarities between *Claraclippia seminuda* and *Semipsammina mattaeformis* Gooday & Holzmann, 2017, a species also described from the CCZ that lives attached as a flat structure on nodule surfaces. In particular, the stercomare of *S. mattaeformis* 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……. Elsewhere, the masses are less closely packed and form a more open system of anastomosing branches (again generally 100–200 µm width)*' (Gooday and Holzmann, 2017c). When the test is removed, these stercomare formations look remarkably similar to those of *C. seminuda,* although individual strands are somewhat wider and there are no obvious granellare branches. A test is present in *S. mattaeformis* but it is thin, flimsy and easily detached, which tends to enhance the similarity with *C. seminuda*. The two species also branch as sister in the phylogenetic tree, although without bootstrap support (Fig. 1).

The construction of the body of *Claraclippia seminuda* largely from stercomare is a characteristic shared with *Ceralasma massa.* In other respects, however, the two species are quite different. The body is a rounded lump comprising wide (2–4 mm) stercomare branches in *C. massa* (Tendal, 1972), compared to mainly plate-like elements made up of much narrower (100–150 µm) stercomare branches in *C. seminuda.* The new species is also much larger (~8 cm), almost three times the size of the largest specimen of *C. massa* (2.8 cm; Tendal, 1972). It is more similar to *Cerelasma implicata* Kamenskaya, Gooday & Tendal, 2017, which has a test composed of relatively narrow, closely packed stercomare branches interwoven with granellare branches. The main difference is that *C. implicata* is much smaller (14 mm or less) and morphologically simpler, with a basal trunk attached to a nodule and an expanded, flattened, fan-shaped upper part (Kamenskaya et al., 2017). The stercomare branches are also narrower (50–60 µm) than those of *C. seminuda* (75–150 µm). It is possible that the small specimens described by Kamenskaya et al. (2017) are juveniles of *C. seminuda*, but confirmation of this hypothesis would require genetic data. *Stannophyllum mollum* Tendal, 1972 is another species that is largely devoid of xenophyae. However, like other members of the genus, the test is held together by fine organic fibres (linellae), forming a distinct surface layer that clearly distinguishes *S. mollum* from *C. seminuda* (Tendal, 1972).

Stereodiktyoma Gooday & Holzmann **gen. nov.**

Diagnosis. Test attached, delicate, forming a complex three-dimensional network of tubular elements, not arranged according to any particular pattern. Wall soft, finely agglutinated.

Zoobank registration.
urn:lsid:zoobank.org:pub:88353CBA-6C4D-40E3-8475-B1FCA2C48637

Etymology. From the Ancient Greek *στερεός* (*stereós)*, literally meaning "solid" but in this context three-dimensional, and the Greek *diktyoma* meaning a 'network'. Gender neuter

Remarks.
Stereodiktyoma has morphological characteristics that resemble those of several existing genera. *Tendalia* has a reticulated arrangement of tubes, but these lie more or less in one plane and the walls are thinner, coarser-grained and more rigid and brittle than those of the new genus. In some species of *Syringammina*, notably the type species *S. fragilissima,* the test comprises a three-dimensional system of tubes. However, like those of *Tendalia,* the tubes are relatively thin-walled, rigid and brittle, as well as being arranged, at least peripherally, in a distinct pattern, with 'radial branches' and 'anastomosing lateral branches (that) form consecutive layers' (p. 36 in Tendal, 1972). The new genus is most similar morphologically to *Shinkaiya lindsayi,* also the type species of its genus. This has a test comprising a meshwork of anastomosing tubes, the walls of which are relatively thick, fine-grained, soft delicate, and therefore quite similar to those of the new genus.

There is no genetic support for a close relationship between *Stereodiktyoma* and either *Shinkaiya* or *Syringammina* (Fig. 1). It does branch in the same clade as *Tendalia*, although with no bootstrap (BV) support. The closest species to *Stereodiktyoma* genetically is *Galatheammina* sp. 2 of Gooday et al. (2017a). This relationship is supported by 100% BV, but as explained below, there is very little morphological similarity between the two species.

Stereodiktyoma mollis Gooday & Holzmann gen. & sp. nov.
Fig. 10, Supplementary Fig. S3

Diagnosis. As for genus.

Zoobank registration.
urn:lsid:zoobank.org:pub:88353CBA-6C4D-40E3-8475-B1FCA2C48637

Etymology. Latin *mollis,* meaning soft, a reference to the poorly cemented test wall.

Type material and locality
The holotype (Lee Kong Chian Natural History Museum, Singapore, reg. no. ZRC.FOR.0003, preserved in 10% formalin) was collected in box core BC039 (specimen RC1623); OMS license area, 12° 22' 05.1"N, 117° 33' 01.0"W; 4157 m water depth. The specimen is in the form of numerous small fragments.
The paratype (Lee Kong Chian Natural History Museum, Singapore, reg. no. ZRC.FOR.0002, preserved in 10% formalin) was collected in box core BC040 (specimen RC1697); OMS license area, 12° 20' 37.4"N, 117° 28' 50.6"W; 4174 m water depth. The specimen is in the form of numerous small fragments, some of which were used for genetics (sequenced isolate 21433).

Description

Shipboard photographs. The holotype was intact when photographed (Fig. 10A, B). It was pale, brownish tan in colour and attached to a nodule. The base of the test extended for about 5 mm in one direction across the nodule surface, less in other directions. The width at the base, including these encrusting parts, was about 23 mm. The maximum height was almost 11 mm, of which about 6.2 mm was elevated above the surface of the nodule. This upper part was narrower (width ~14 cm) than the base. The attached part of the test comprised bars that had mainly coalesced to form plates interrupted by open spaces, although retaining some identity in places. It had an uneven margin with short, projecting finger-like or lobate processes. The upper elevated section formed a three-dimensional framework that consisted mainly of bars, 0.7–1.0 mm wide, around open spaces.

The paratype was also originally attached to a nodule but broke into two fairly large fragments when removed (Fig. 10C, D). One fragment measured 11.2 by 10.9 cm and had a subrectangular outline. The other measured 11.8 by 9.2 cm and had a semicircular outline; the flattened part may have been the base of the specimen. Both fragments comprised a three-dimensional framework of branches, each ~ 0.54¬0.92 mm in diameter. A photograph of a nodule from the same box core (BC040) showed the remains of an encrusting xenophyophore that probably represents the same species (Supplementary Fig. S3A). It formed a mat-like structure covering an area measuring at least 17.5 by 15 mm. In places the surface was fairly smooth, but elsewhere it was uneven and appeared to be formed from coalescing tubes, a few of which stood up for a short distance from the general surface. It was possibly the basal part of an upstanding test.

Preserved material. Both specimens were very fragile. The holotype, preserved in formalin, arrived in Southampton as small fragments, the largest a few milliimetres in size (Supplementary Fig. S3C¬F). Fragments of the paratype, preserved in RNAlater, were initially sent to Geneva and included two larger pieces (Fig. 10E, F), around 6.0 and 8.7 mm maximum dimension. Further disintegration occurred during onward transport to Southampton. Most of the surviving fragments are basically cylindrical, although sometimes coalescing to form more plate-like structures (Supplementary Fig. S3D). This tendency for the tubes to coalesce is also evident in the shipboard photographs of the intact holotype (Fig. 10A, B).

The test wall has a very thin (no more than ~5 µm) basal layer composed of small but discernible transparent grains, and pale yellowish in colour. This is overlain by a much thicker (typically 130 to 260 µm) layer of soft, very fine-grained and easily disaggregated, sediment-like material (Supplementary Fig. S3C¬D). The branches are tubular and there are no internal xenophyae, much of the internal space being occupied by a stercomare branch, typically 100 to 200 µm diameter (Supplementary Fig. S3F). Several branches often emerge from plate-like fragments or are visible along their broken edges. A narrow granellare strand is sometimes seen running parallel to the stercomare (Supplementary Fig. S3B). The granellare is pale yellowish, usually 30 to 50 µm diameter, and branches together with the stercomare where the tubular test elements bifurcate.

Molecular characterisation

Stereodictyoma mollis branches as sister to *Galatheammina* sp. 2 (100%BV). The length of sequenced fragment of 18S gene of *S. mollis* is 1068 nucleotides and the GC content is 30%.

Remarks

There are some morphological differences between the two specimens of *Stereodiktyoma mollis*. In particular, the holotype from box core included a fairly high proportion of plate-like fragments whereas fragments of the paratype were predominantly tubular. This difference is in the small preserved fragments is consistent with the appearance of the more intact specimens in shipboard photographs. However, in other respects, notably the wall structure, they are very similar and hence we consider them to represent the same species.

DNA sequences obtained from the paratype reveal a strongly supported relationship (100% BV) between *Stereodiktyoma mollis* and *Galatheammina* sp. 2 of Gooday et al. (2017c), albeit with fairly long branches in both cases. The *Galatheammina s*pecies is known from a single specimen, possibly a fragment, from the UK-1 area. This forms a flat plate composed of radiolarians in a fine-grained matrix and with radiolarians also occupying the test interior, together with stercomare and granellare. The two species therefore have little in common morphologically.

Shinkaiya contorta Gooday & Holzmann, 2017

Figs 11, 12

Shinkaiya contorta Gooday & Holzmann, 2017, in Gooday et al. 2017c, p. 727–730, Fig. 2A–F.

Material examined

BC004 RC0160 (morphology and genetics)

Sequenced isolates: 21448, 21449

Description

The shipboard photographs show a single plate-like fragment with an intact semicircular margin and concentric 'growth lines' clearly developed over parts of the surface (Fig. 11A). It was originally attached to a nodule and the lower margin was broken when it was removed from the substrate. The plate was strongly undulating so that it did not lie in one plane. It was still largely intact when seen in Geneva, where it measured 44 mm in maximum dimension.

By the time it reached Southampton, however, the fragment had broken into several smaller pieces, some almost flat but others curved, and the largest with a maximum dimension of about 15 mm (Fig. 11B). They are greyish, with a smooth surface, in places overlain by patches of lighter material resembling fine-grained sediment. 'Growth lines' are sometimes visible. The wall is 60–95 µm thick, in a few places up to 115 µm (Fig. 11D, E; 12E), quite soft, delicate, and very fine-grained with a scattering of darker flecks.

The test interior is occupied mainly by masses of stercomare (Fig. 12C¬F), some of which are attached to the underside of the wall. On detached wall fragments the stercomare forms distinctive strands, typically 50–105 µm in width, that branch and usually anastomose to varying degrees, sometimes forming dense networks (Fig. 12C–E). Granellare strands are whitish, typically 45–75 µm in width and weave between the stercomare. A granellare tube is not clearly visible under stereomicroscope.

Remarks

The wavy, plate-like morphology of the preserved fragment is consistent with that of the unique holotype of *Shinkaiya contorta* from the UK-1 area of the CCZ (Gooday et al., 2017c). This was an intact specimen, with a maximum dimension (46 mm), similar to that of the new specimen, but with a more complex structure that comprised a number of curved, plate-like elements, often with well-developed growth lines. The soft, finely agglutinated test wall, and the reticulated stercomare branches, are similar but some other test features are different. Particularly notable is that the plate itself, and particularly the wall of the plate, are much thinner (about 0.5–1.0 mm and 60–95 µm, respectively) than those of the type specimen (1.3–2.0 mm and 270–500 µm, respectively). Nevertheless, sequences obtained from the new fragment confirm its identification.

***Psammina multiloculata* Kamenskaya, Gooday, Tendal, 2015**

Fig. 13

Psammina multiloculata Kamenskaya, Gooday, Tendal, 2015: p. 584–585, Figs 2,3.
Psammina multiloculata Kamenskaya, Gooday, Tendal, 2015. Kamenskaya et al., 2017, 300–301, Fig. 1a–d.

Material examined

Box core 10. Specimen RC0490 (morphology)

Description

Shipboard photographs. The single specimen stood vertically on the surface of the nodule to which it was attached (Fig. 13A, B). It comprised a basal stalk and an upper part with a number of plate-like elements radiating out from a central axis. The apparent height of the test, viewed from different angles, ranged from about 7.0 to 7.5 mm (mean 7.2 mm), but this was strongly influenced by foreshortening. The width varied from 4.43 to 5.89 mm (mean 5.37), depending on which plates were in view. Three main plates were visible when the test was viewed from above (Fig. 13C); they were more or less straight or slightly curved, measured 3.26, 2.47 and 1.98 mm in length and of fairly even width (0.33–0.48 mm). The plate of intermediate length divided at the end into two short side plates, about 0.90 and 1.10 mm long. The height of the stem, measured as the distance between the base and the highest side plate but again foreshortened to varying degrees, ranged from 2.16 to 3.14 mm depending on the orientation, and the width from 1.15 to 1.90 mm. It tapered downwards but widened slightly at the base.

Most of the test surface was dark, but with a paler zone around the plate rims, particularly along their upper edges (Fig. 13A, B). A vague, approximately concentric zonation is visible on some of the plates, and a faint pattern comprising small, slightly raised patches and shallow depressions, corresponding to the compartmentalization described below, can sometimes be discerned.

Preserved specimen. The test, detached from the nodule, measures 10.7 mm long and 6.2 mm wide, as orientated in Fig. 13D. Most of the stem and the three upper plates are intact (Fig. 13D–E), although there is some damage around the edges of the plates. The test wall is very thin (~20 µm) and delicate (Fig. 13F–H). It is composed of fine transparent mineral grains, probably quartz, mixed with sponge spicules fragments, scattered dark particles and occasional reddish grains. Most of the non-biogenic grains are ~35 µm or less in size, although some are larger. At least one agglutinated foraminiferan test is incorporated into the wall. Where the edge of the test is intact, the wall continues around it with no obvious apertures. The overall colour is dark grey, influenced by the stercomare that largely fill the test and are dimly visible through the thin wall.

The test interior is partitioned into cell-like compartments. These are visible on the surface as slightly raised patches filled with dark stercomare, except for the pale peripheral zone, which is empty (Fig. 13F). These patches are often somewhat rectangular and tend to be arranged concentrically, particularly towards the margin. It is difficult to give precise sizes, but they are on the order of ~600–700 µm long and ~420 µm wide. The cytoplasm is visible on broken edges as pale whitish strands enclosed within a delicate, transparent granellare tube, as well as larger, more irregular masses, notably in the stem.

Remarks

This is the first record of *Psammina multiloculata* from outside the Russian license area in the more central part of the CCZ. Our specimen agrees fairly well with the original description (Kamenskaya et al., 2015), particularly as regards the basically plate-like test morphology and its characteristic internal subdivision into small, cell-like compartments. There are some differences. The four Russian specimens either lacked a stalk (as in the holotype) or had a very short stalk. One of the two additional specimens described by Kamenskaya et al. (2017) had a short, tapered stalk, 5 mm long and up to 15 mm wide, while the other comprised the stalk, 5 mm long and 8 mm wide, and just the base of the upper plate-like part. The much larger size of the Russian specimens (usually > 20 mm maximum dimension) suggests the greater proportion of the test occupied by the stalk in our specimen may be a juvenile feature.

Our specimen of *P. multiloculata* shares many features with *Psammina* sp. 3 from Stratum B of the UK-1 area, illustrated and briefly described in the supplementary material for Gooday (2017a; Supplementary Figure 4d, e therein). This earlier specimen is similar in size, 8.5 mm high and a maximum of 5.5 mm wide. The test wall contains a high proportion of sponge spicules, and the interior is partitioned into compartments that are occupied by stercomare masses of irregular width (typically 200–300 µm) and granellare strands (65–80 µm wide). The main difference is that the test is curled around to form an almost tubular structure. Possibly, they are conspecific, but this cannot be confirmed in the absence of genetic data.

Psammina* aff. *multiloculata Kamenskaya, Gooday, Tendal, 2015

Supplementary Figs S4, S5

Material examined (morphology only)

BC044, RC1830

Shipboard observations. The specimen was found lying flat on the surface of the box core and was probably incomplete. In shipboard photographs it formed a flat plate, fairly elongated, more than 57 mm long and ~29 mm in maximum width, making it the largest specimen in our collection (Supplementary Fig. S4A). One of the longer sides was convex and probably included parts of the intact margin. The opposite side of the test was concave and appeared broken, as did the two irregularly shaped ends.

Preserved specimen. On arrival in Geneva, the plate had broken into several fragments, the largest about 13.5 mm long and 1.1–1.5 mm thick (Supplementary Fig. S5A). The following description is based mainly on observations made at this stage, since the fragments themselves had almost totally disintegrated by the time they reached Southampton.

The surface showed concentric lineations following a rather irregular, wavy course, in places comprising a series of short, curved sections to create a scalloped effect. The lineations are sometimes joined by faint transverse lines, reflecting the cell-like compartments that occupy the test interior. The outer wall is very thin (30–68 µm), delicate and easily damaged (Supplementary Fig. S5B–D). It is composed of very small mineral grains, which include a scattering of tiny orange and white grains, together with sponge spicule fragments and occasional radiolarians. The internal compartments are clearly visible in broken sections (Supplementary Fig. S5E, F) and are defined by partitions with the same thickness and composition as the external walls, with which they merge. Some of the partitions span the two outer walls more or less transversely, but overall, the compartments are not particularly regular and the partitions between them are orientated in various directions with respect to the outer walls.

Remarks.

This specimen resembles *Psammina multiloculata* in terms of its wall structure and composition, as well as the compartmentalised test interior. However, although damaged, it is still much larger than the specimen described above (57 mm compared to only 7.5 mm!), and has a flat, plate-like morphology with no sign of a stalk or multiple radiating plates. Nevertheless, the holotype of *P. multiloculata* was originally described as being flat and plate-like (Kamenskaya et al., 2015). It was much smaller (24 mm) than the present specimen, although an intact example of the species described in a later study (Kamenskaya et al., 2017), which was also flat and plate-like, was closer in size (45 mm compared to 57 mm). It is therefore possible that this large plate should be assigned to *P. multiloculata.* However, this and the specimen described above are so different morphologically that in the absence of genetic data we prefer to keep them separate.

***Psammina* aff. *limbata* form 1** sensu Gooday et al. 2018

Supplementary Fig. S6

Psammina aff. *limbata* form 1. Gooday et al., 2018, 930–934, Figs 3–5, Supplementary Fig. S1C–F.

Material examined

Box core 040. Specimen RC1699 (morphology)

Box core 036. Specimen RC1588 (morphology). Dried

Remarks

RC1677 (Fig. 6A, B). The specimen includes only the upper fan-shaped part of the test, which has broken off near the top of the stalk. The fan is ~11 mm and whole fragment is 8.4 mm high. There is a very obvious pale rim, devoid of the stercomare that occupy the remainder of the test. The specimen is undoubtedly the same as the form described by Gooday et al. (2018), particularly in terms of the agglutinated particles, which includes numerous agglutinated foraminifera, many of them orange in colour. This form is probably the same as *Psammina limbata* from the Russian license area, although this cannot be confirmed in the absence of genetic data for any of the Russian specimens.

RC1558 (Fig. 6C¬F). The specimen was dried soon after collection and is greyish-brown in overall colour. The upper part is fan shaped, gently curved, and somewhat asymmetrical, merging into the stalk on one side and joining it more abruptly and at a higher point on the other side. The maximum width is 25.7 mm and the overall height 22.4 mm, of which ~5.9 mm is occupied by the stalk and ~16.6 mm by the fan. The fan-like part is 1.80–2.06 mm thick. The stalk is strongly tapered, from about 5.88 mm to 1.56 mm. The bases of several rod-like 'roots' arise from the lower part of the fan and the top of the stalk, 5 on one side, 2 on the other.

The test surface is fairly smooth, apart from clearly-developed, concentrically zoned undulations. The wall comprises a matrix of small mineral grains and tiny spicule fragments in which are embedded radiolarians, a few longer spicules and occasional agglutinated foraminiferan tests and larger mineral grains. The margin of the fan is abraided, exposing the interior, which comprises an open meshwork of spicules to which are attached radiolarians. The test wall is very thin, around 40–60 µm.

***Psammina* aff. *limbata* form 2** sensu Gooday et al., 2018
Supplementary Fig. S7

Psammina aff. *limbata* form 2. Gooday et al., 2018, 934–935, Fig. 6, Supplementary Fig. S2.

Material examined
Box core 034. Specimen RC1492 (morphology only)
Box core 040. Specimen RC1337 (morphology only)
Box core 042. Specimen RC1743 (morphology only). Dried.

Description

RC1337 (Supplementary Fig. S7A¬C). The test comprises a semicircular, fan-shaped upper part, almost 33 mm wide, merging into a tapered stalk attached to a nodule. The test (stalk plus fan) is around 26 mm high and almost intact apart from some damage to the margin and several holes within the fan. The upper part is distinctly asymmetrical, being better developed on one side than the other. As a result, the stalk is also asymmetrical and longer on the side where the fan is less well developed. The base of the stalk extends into at least three branched root-like structures that spread across the nodule surface. . The fan displays clearly developed 'growth lines' that delimit concentric zones. The upper part appears to be empty, the lower part is filled with dark material, probably decayed stercomare.

RC1492 (Supplementary Fig. S7D). The upper part of the test is damaged with little or none of the original margin surviving. What remains is 18 mm wide and displays a well-developed concentric zonation. The overall height is also 18 mm. However, the lower part is intact and tapers to a very short (1.2 mm) but relatively wide (3.0 mm) stalk. In addition to the main stalk there is a wide secondary support developed from the base of the fan, and two long, straight, bar-like processes (6.5 and 7.7 mm long and 0.5–0.6 mm wide), arise from the intact margin on the side of the test and are directed obliquely downwards.

*RC1743 (*dried). The specimen is badly cracked, but basically forms a semicircular fan with a fairly straight lower margin and the base of a stem. It measures 29.3 mm (width) by 25.8 mm (height). The wall has a rough surface with concentric growth zones. It comprises a mesh of sponge spicules, radiolarians and subordinate numbers of agglutinated foraminiferal tests and fragments, mainly yellow or orange in colour. Parts of the test interior are visible through gaps in the cracked wall, revealing parts of several very thin partitions corresponding to the external furrows that define the zones. Otherwise, the interior is empty.

Remarks.
These three specimens are very similar to *Psammina* aff. *limbata* form 2 from the UK-1 license area, as illustrated in Figs 6E, G of Gooday et al. (2018). The concentric zonation with corresponding internal partitions is a typical feature and distinguishes this form from other stalked *Psammina* species described by Gooday et al. (2018). The straight, bar-like processes (Supplementary Fig. S7D) are also present in the UK-1 specimen.

***Homogammina* sp.**
Supplementary Fig. S8

Homogammina sp. Gooday et al. 2017, Supplementary Fig. 7c.
'Mud xenophyophore' Gooday and Wawrzyniak-Wydrowska 2023, Fig. 6C, Supplementary Fig. S16C, D.

Material examined
Box core 034. Specimen RC1494 (morphology only)
Box core 034. Specimen RC1495 (stercomare only)
Box core 040. Specimen RC1700 (stercomare only)

This species is represented by at least 7 fragments, the largest of which is roughly rectangular and may be largely intact (Supplementary Fig. S8A). It measures 22.8 mm long, 15.4 mm wide and 2.9 to 4.9 mm thick. The test is light brownish and consists of fine-grained sediment ('mud'). Much of the surface, which appears to be undamaged, is slightly undulating but otherwise featureless otherwise featureless. However, the sides are abraided and expose the test interior. This is homogeneousis homogeneous except for being ramified by black stercomare branches, generally 67–110 µm wide, which stand out clearly against much lighter-coloured test material. The only other feature of note is a domed komokiacean, measuring 3.70 mm wide and 3.20 mm high, attached to one side of the test. It is densely covered with grey dots, presumably stercomata-filled chambers.

The stercomare is more resilient to damage than the test and sometimes found as strands, to which cling small amount fine coherent 'mud', the remains of test material. Two examples are illustrated in Supplementary Fig. S8D, E, one of them from the same box core (BC034) as the main test fragment. The stercomare branches are somewhat crooked and of distinctly uneven width, with wider sections sometimes separated by narrow necks (particularly in RC1495). They branch frequently with occasional anastomoses and with some branches ending blindly. A scale is only available for photographs of specimen RC1700 in which the branches range from 38 to 75 µm wide, occasionally up to ~100 µm.

Remarks.

This species is probably the same as *Homogammina* sp. of Gooday et al. (2017a) from the UK-1 license area and 'Mud xenophyophore' of Gooday and Wawrzyniak-Wydrowska (2023) from InterOcean Metal (IOM) license area. These specimens were also ramified by dark grey stercomare branches.

Curved muddy plate

Supplementary Figs S9, S10

Material examined

BC032 RC1366 (morphology only).

Description

Shipboard photographs. These show two plate-like specimens. The first was intact and had a strongly curved test attached to a nodule without any intervening stalk (Supplementary Fig. S9A, B). The height cannot be determined because of the oblique angles of the photographs, but the width across the base of the test was ~11 mm. The fine-grained, muddy wall includes a relatively large (0.56 mm diameter) transparent brown, organic-walled sphere containing stercomata. This was probably incorporated into the test rather than being part of the xenophyophore. The wall also included a scattering of smaller whitish and black particles.

The second specimen, which was somewhat damaged, was roughly semi-circular in shape and again attached directly to a nodule surface (Supplementary Fig. S9C¬F). It was more gently curved than specimen 1. The plate was about 11.6 to 13.5 mm high (based on different photographs), ~14 mm wide, with a thickness of ~0.75 to 0.85 mm. The fine-grained test included a few larger whitish particles. Vague, concentric 'growth' lines are visible in some photographs (Supplementary Fig. S9E). Broken edges show a sandwich-like cross section with fairly thick (200–300 µm) walls and a dark, stercomata-filled interior (Supplementary Fig. S9F).

Preserved material. Only two small, preserved fragments of the test were available for further study (Supplementary Fig. S10A, B). Both are basically plate-like, one measuring 6.55 × 3.89 mm and the other 5.12 × 4.53 mm. The larger piece undulates along its length and is more evenly curved across its width. The other has an uneven appearance and a smaller side plate arising at right angles from the edge of the main part. The thickness of the larger fragment is 600–700 µm (Supplementary Fig. S10C, E) and of the smaller fragment 300–400 µm. The overall colour is pale creamy brown. The wall is soft, consisting of fine-grained material in which are embedded scattered radiolarians of various sizes. Along parts of the broken edges a very thin (no more than 10–12 µm), delicate but more coherent basal layer, composed of fine transparent grains (~4–6 µm) is visible beneath the softer, thicker, overlying layer.

The stercomare is extensively developed and fills most of the test interior (Supplementary Fig. S10E, F), but does not conform to any clear pattern. Irregularly shaped masses, usually several hundred microns in size, often merge into and are connected by irregular branches, ranging from around 30 to 70 µm in often of uneven width. Strands of the granellare system can be found between these masses. They are whitish and 20 to 65 µm in width, although sometimes forming larger masses >100 µm in size. There are no obvious internal xenophyae.

Remarks
Sequences were obtained from the preserved specimen, but they were identical to those from specimen RC0372, described below. Since the two species have very different morphologies and are unlikely to be conspecific, the sequences were not considered reliable.

In terms of its generic placement, this species is most similar to *Psammina*, which it resembles in having a basically plate-like morphology and lacking internal xenophyae. However, in the absence of convincing genetic data, we prefer to leave it under open nomenclature in order not to further complicate this already unwieldy genus.

Dark complex plate with micronodules
(Supplementary Figs. S11, S12

Material examined
BC008 RC0372 ((specimen 1, preserved in RNAlater)
BC008 RC0373 (specimen 2, preserved in formalin)

Specimen 1
Shipboard photographs. These show a relatively simple plate that was gently curved around a vertical axis when viewed from above (Supplementary Fig. S11A, B). The upper two-thirds was roughly semicircular and tapered into a broad, approximately parallel-sided stalk attached to the nodule at its base. Several vague ‘growth lines’ ran parallel to parts of the semicircular margin. The test wall was dark grey and dotted with agglutinated foraminiferal shells and shell fragments.

Preserved material. The surviving fragment was originally preserved in RNAlater. It is curved, 12.9 mm long measured across the curve, and 10.5 mm wide. The overall colour is greyish. There is some indication of concentric zonation, clearly defined in a couple of places by abrupt changes in the thickness of the test. The thickness is typically 0.50 to 0.75 mm but increases to almost 1 mm across one of these zones.

The test wall is 90–140 µm thick and has a very distinctive appearance. It incorporates sponge spicules and numerous tests of agglutinated foraminifera, including a large whitish tube. These are most evident on the convex side of the test and are set a matrix comprising shell fragments and fine-grained material. The wall is also peppered by numerous holes of different sizes and shapes that appear to result from the loss of some agglutinated particles.   A long, agglutinated tube that can be seen in the shipboard photograph is visible, confirming that they are the same specimen. However, the numerous dark particles that were originally present are not obvious in the preserved fragment.

Specimen 2
Shipboard photographs. These show a test very similar in general appearance to specimen 1, but with a more complex morphology, albeit still plate-like. Viewed from above, it follows an irregular course with abrupt changes of direction and a short flange projecting on one side (Supplementary Fig. S11C). The sharp bend in the test and the projecting rectangular flange are clearly apparent when the test is viewed from the side (Supplementary Fig. S11E). From other angles the outline is roughly circular, but with many irregularities, including short lobate projections and indentations of the margin (Supplementary Fig. S11D, F). There is a fairly large open space near the centre of the plate. The wall is very similar to that of specimen 1, dark grey and incorporating numerous agglutinated foraminiferal tests and test fragments.

The test is attached to a nodule at its base. There is no distinct stalk, but the attachment area appears to be fairly restricted. Root-like extensions arise from the base of the test in several of the photographs. In one image, a main trunk, much paler than the main part of the test, extends down the side of the nodule before dividing into several branches (Supplementary Fig. S11F). Two additional projections near the base of the test appear to be incipient root-like structures, but they do not reach the nodule surface. Another image shows several fairly long, straight projections, also pale and finely agglutinated, arising from the base of the test, in addition to the main trunk (Supplementary Fig. S11E). They have open ends (possibly broken) and are therefore clearly tubular.

Preserved material. The specimen was preserved in formalin and had broken into nine main fragments, 7.3¬21.0 mm in maximum dimension, by the time it reached Southampton. They are all basically plate-like, although strongly and irregularly undulating, and typically 0.50 to 1.00 mm thick. Two are perforated by small open spaces, in one case measuring 1510 by 320 µm, in the other case 795 by 950 µm. A weakly-developed zonation is visible on the surface of some fragments under oblique lighting.

The test wall is ~50 to 100 µm thick. The main constituents are dark, almost black particles of different sizes, but typically smaller than about 300 µm, and in many cases <100 µm. These are probably fragments of micronodules and are set in a pale grey, fine-grained matrix. Scattered amongst the dark grains are the complete and fragmentary tests of agglutinated foraminifera, many of them orange in colour.

Remarks

Shipboard photographs show both specimens with dark tests dominated by micronodules. Their different appearance when examined later in the laboratory must reflect the fact that specimen 1 was preserved in RNAlater, in which nodules (in this case micronodules) dissolve, whereas specimen 2 was preserved in formalin. Sequences were obtained from specimen 1, but for reasons already explained, they were considered unreliable. Like the ‘Curved Muddy Plate’, this species is closest morphologically to the genus *Psammina*..

Dark plate dotted with radiolarians

Supplementary Fig. S13

Material examined

BC025 RC1019 (morphology from photographs)

Description

The specimen was originally attached to a nodule and appears to be more or less intact. Shipboard photographs show a flat plate, 17.6 mm long and 12.5 mm wide, with a small side lobe. The wall is dark, almost black, but studded with whitish rounded particles that stand out clearly against the dark background. Most are probably radiolarians but there are some agglutinated foraminifera as well. More detailed photographs show that the dark particles are micronodules.

In Geneva, the vial corresponding to this specimen was found to contain only some conglomerations of radiolarians and spicules, together with a few remnants of cytoplasm. Presumably, the micronodules had dissolved in the RNAlater used to preserve the specimen.

Remarks

The specimen is morphologically similar to *Galatheammina* sp. 6 of Gooday et al. (2017), based on a single specimen from the OMS area. Both are plate-like and composed of micronodules speckled with radiolarian tests. *Galatheammina* sp. 6 was transferred to *Moanammina semicircularis* by Gooday et al. (2020) based on molecular data showing the two species to be genetically identical. The fragments of cytoplasm from the sample vial yielded DNA but no genetic data were obtained.

Stannophyllum* aff. *granularium Tendal, 1972
Figs 14, 15

Material examined
Box core 10, specimen RC0489 (morphology and genetics)
Box core 15, specimen RC0608 (morphology)
Sequenced isolates: 21445, 21446

Descriptions

RC0489 (sequenced)
The test is flexible, attached to a nodule in shipboard photographs (Fig. 14A, C). It measures 15.6 mm long and 11.5 mm wide. The overall shape is roughly and asymmetrically ovate, with one side more or less straight, the other side broadly curved, and the end gently rounded (Fig. 15B). There is no distinct stalk, but the attached margin is relatively short, about 4.6 mm in width.

The preserved specimen is 730–870 µm thick. The surface is rather uneven and fairly dark greyish brown when viewed in natural light. There is a lighter peripheral fringe that is only obvious in laboratory photographs of the fixed specimen, where it is best developed around the distal end of the test (Fig. 14D, E). In some areas, notably near the upper margin, the wall is composed of radiolarian shells with sponge spicule fragments also visible, leaving substantial gaps between these particles (Fig. 14E). Elsewhere, the gaps are largely filled in by much finer material. A few larger agglutinated foraminifera are also incorporated into the structure. The wall is pervaded and held together by a meshwork of fine proteinaceous fibres (linellae). Gaps in the surface are criss-crossed by linellae, through which dark grey stercomare masses are visible. The linellae are particularly well-developed and obvious in the peripheral zone.

The test interior was not examined, but the darker appearance of the test away from the lighter peripheral zone clearly results from the presence of stercomare masses. A row of eight more or less straight, slightly radiating granellare strands were visible at the distal end of the test, immediately inside the peripheral zone, before most were removed for genetic analysis (Fig. 14D, E). One of the strands branched once, but the others were unbranched. They were 88¬117 µm wide, in some cases expanding to ~145–175 µm at their outer end. The granellare strands that had been removed for sequencing measured 76¬190 µm wide (Fig. 14F).

RC0608 (not sequenced)
Shipboard photographs show the test bent over from what, presumably, was an upright orientation on the seafloor (Fig. 15A, B). It is considerably larger than RC0489, measuring 30.6 mm long with a maximum width of 21.4 mm. The shape is asymmetrically oval (Fig. 15A, C), similar to that of the sequenced specimen, although with a short wide proximal stem 7.8 mm wide and ~4 mm long that merges with the upper part of the test (Fig. 15D).

The preserved specimen is 520–650 µm thick. The test surface has a vague pattern of concentric arcuate zones running parallel to the curved upper (distal) margin (Fig. 15C). The wall is very similar to that of the sequenced specimen. Apart from a single agglutinated foraminiferan (*Reophax* sp.), it is composed largely of radiolarian shells of different sizes and a subordinate proportion of sponge spicules, with a patchily developed matrix of fine particles occupying the gaps across some parts of the surface (Fig. 15E). The meshwork of linellae that holds together the surface layer is strongly developed and clearly visible where there are gaps between the radiolarians and near the margin (Fig. 15E). The stercomare can also be seen through these gaps. In more central parts of the test, it forms an interconnected system of irregularly shaped lumps merging into more linear strands that radiate towards the towards the curved upper (distal) margin.

Molecular characterisation

Stannophyllum aff. *granularium* branches next to *S. zonarium* (100%BV). The barcoding fragment of the 18S gene of *S.* aff. *granularium* is 927 nucleotides long and its GC content is 29%. The two sequences obtained for this species are identical.

Remarks

Three of the 15 *Stannophyllum* species included by Tendal (1996) in his synoptic checklist of xenophyophores, *S. granularium* Tendal, 1972, *S. radiolarium* Haeckel, 1889 and *S. zonarium,* have tests composed to some degree of radiolarians (as described by Tendal, 1972). *Stannophyllum zonarium,* is the most widely reported of all xenophyophores (Tendal, 1996). The test is clearly zoned and the strongly developed linellae often project from the lower part in tangled bundles (Tendal, 1972; Gooday et al., 2020a), features are not seen in the species described here. In any case, genetic data indicate that the two species are distinct (Fig. 1).

The other two possible candidates have the following characteristics (Tendal, 1972). In *S. granularium* the test is 1.5–3.0 mm thick, dark brown in colour, sometimes with faint zonations, the surface is ‘granular’, the xenophyae comprise a combination of mineral particles and sponge spicules with a varying proportion of radiolarians and the linellae are strongly developed, often as a surface layer. In *S. radiolarium*, the test is 1–1.5 mm thick, lighter in colour, has a ‘soft consistency’, the surface is ‘smooth’, the xenophyae are mainly radiolarians with occasional sponge spicules, the linellae are sparse and do not form a surface layer.

The three possibly damaged specimens of *S. granularium* illustrated in Pl. 10A–C of Tendal (1972) and Pl. 1.3–1.5 of Tendal (1973) do not closely resemble either of our specimens. Tendal’s (1972) descriptions, however, suggest that our specimens are closer to *S. granularium* than to *S. radiolarium,* although there are differences. Radiolarians are generally a subordinate, rather than dominant, component of the xenophyae in *S. granularium* and may be almost absent. Our specimens are much thinner (<1.0 mm when preserved, compared to 1.5–3.0 mm). With the exception of an anomalous record from the Indonesian region (Banda Sea, 4365 m depth), all specimens of *S. granularium* come from ~5000–6700 m in the NW Pacific (32–54˚ N), some distance from our shallower sampling area in the eastern equatorial Pacific. For these reasons, we cannot confidently assign our specimens to Tendal’s species, but refer it instead to *Stannophyllum* aff. *granularium.*

***Stannophyllum* spp.**

Supplementary Figs S14–S16

Material examined (morphology)

BC014 RC0598

BC015 RC0613

BC001 RC0036

Descriptions

Specimen RC0598. A shipboard photograph shows the test attached to a nodule (Supplementary Fig. S14A). It is 23.2 mm long, 19.5 mm wide, between 530 and 600 µm thick and has a fairly symmetrical and basically subtriangular outline, a semi-circular distal margin and sides that taper down to a relatively narrow attachment point (Supplementary Fig. S14B). A concentric zonation pattern is visible across the entire test and stands out clearly when the specimen is viewed in transmitted light (Supplementary Fig. S14C). The surface layer is greyish and more or less continuous. Compared to *S.* aff. *granularium,* it includes fewer obvious radiolarians and spicules and a considerably larger proportion of fine-grained material (Supplementary Fig. S14D). There is also a scattering of brown particles, many of them globular and cyst-like but a few elongate with one serrated side. Linellae form a dense mesh that is visible in occasional chinks in the surface layer and around the margin (Supplementary Fig. S14E). Granellare strands were not observed.

Specimen RC0613. Shipboard photographs show the specimen attached to a nodule, with the lower part forming a thin layer that spreads across nodule surface (Supplementary Fig. S15A, B). The upper part extends upwards from the nodule surface, at approximately right angles to the attached part (Supplementary Fig. S15C). This upstanding section of the test was about 24 mm long. It comprised a narrower lower section, between 8.0 and 9.5 mm wide with a short lobate lateral protuberance, and a wider, irregularly shaped upper section, 15–16 mm wide. The upper part is clearly marked by rather irregular, approximately concentric furrows in the shipboard photographs (Supplementary Fig. S15A).

The preserved specimen is 985–1300 µm thick, with a thin outer wall ~60 to 100 µm thick. The wall is almost continuous with a rather rough surface and quite similar to that of RC0598, although the overall colour is a rather more greyish shade of brown. It consists basically of a fine-grained matrix with embedded radiolarians. There are few other particles, apart from a number of black grains (presumably micronodules) and one or two protruding spicules. The brownish ‘cysts’ that were a feature of RC0598 are absent. Cross-sections of the main part of the test show the interior occupied largely by stercomare and internal xenophyae, mainly radiolarians.

Detachment of the test from the nodule revealed a nearly circular attachment area, measuring 10.5 mm by 10.0 mm, where the wall was absent, and the test interior was in direct contact with the nodule surface (Supplementary Fig. S15D). Rather featureless stercomare that appeared to be somewhat decayed was attached to the inner surface of this part of the test wall, together with radiolarians. Also present were small pieces of slightly reddish granellare, ~75¬115 µm wide. This detached part of the test was largely excavated in order to remove the sparse granellare, revealing strongly developed masses of linellae. Detached fragments of the wall from the main part of the test are also associated with a meshwork on these organic fibres.

Specimen RC0036. Shipboard photographs show the test attached to a nodule, with the main part projecting up from the surface and the lower part spreading across the surface (Supplementary Fig. S16A). The upper part is a lobate structure, 12.8 mm long, 10.7 mm wide and 930–1030 µm thick, with a semi-circular distal (upper) margin (Supplementary Fig. S16B, C). It is brownish in overall colour with a rather muddy surface layer in which are embedded radiolarians of various sizes and a scattering of dark particles together with a few agglutinated foraminiferal tests (Supplementary Fig. S16D). Although the surface is uneven, the embedded particles do not protrude to any great extent. The muddy layer is not present around the test periphery, where the underlying structure of the test, consisting mainly of small radiolarians, is exposed (Supplementary Fig. S16F). The particles are held in place by linellae, which are visible in places around the margin.

At its base the test extends into a single thin sheet, about 13.6 mm long, that was originally attached to the nodule (Supplementary Fig. S16B). The constituent particles comprise mainly radiolarians, micronodules and fine-grained material, held together by linellae. The muddy layer is not well developed so that the particles protrude to a greater extent than on the main part of the test.

Remarks.

Like *Stannophyllum* aff. *granularium*, these three specimens have a well-developed surface layer of linellae that holds together the test wall. However, in contrast to *S.* aff. *granularium* the surface layer is more or less complete without any significant gaps. They also differ from each other, as well as from *S.* aff. *granularium*, in a number of other respects. 1) RC0589 has a tapered test whereas and RC0036 and RC0613 are more rectangular. 2) The wall of RC0598 includes distinctive brownish particles, in RC0036 it is muddy and rather thick, in RC0613 it is relatively thin. 3) RC0613 is the greyest of the three (a consequence of the thinner wall and interior filling of decayed stercomare), RC0598 is also basically grey but a rather lighter shade than RC0613, whereas RC0036 is brownish. 4) RC0589 has a fairly distinct concentric zonation, RC0036 and RC0613 lack obvious zonation. 5) RC0613 and RC0036 have thicker tests (985–1300 µm and 930–1030 µm, respectively) compared to RC0598 (530–600 µm), which is more similar in thickness to *S.* aff. *granularium* (520–870 µm).

Without genetic data, we cannot determine whether these three specimens represent distinct species or variants of one species, or whether they are related to *S.* aff. *granularium*. RC0589 is most similar morphologically to *S.* aff. *granularium*, but differences in the test shape, agglutination and the relatively strong zonation suggest that it is not the same. This specimen shares some features with *S. zonarium*, but lacks the characteristic bundles of linellae that arise from the base of test in this species (Gooday et al., 2020). Morphologically, RC0613 is quite similar to *S. paucilinellatum* Kamenskaya, Gooday, Tendal, 2017 from the Russian license area in the central CCZ (Kamenskaya et al., 2017). However, linellae are sparsely developed in the Russian species, including within the test wall, so that identification seems unlikely. Granellare fragments taken from the base of RC0613 yielded sequences that do not cluster with those derived from the two undoubted *Stannophyllum* species for which we have genetic data. For this reason, and because other parts of this specimen appear to be dead, we regard these sequences as unreliable.

Discussion

Xenophyophore species ranges in the CCZ

The new material adds to sparse existing evidence that some xenophyophore species have wide geographical ranges across the CCZ (Gooday et al., 2020a). Although our identification of *Psammina multiloculata* is based only on morphology, the specimen is in relatively good condition and we are confident that it represents this species. The new record extends its range from the Russian license area in the central part of the CCZ to the OMS area in the east, a distance of about 1920 km. The genetically supported occurrence of *Abyssalia foliformis* in the OMS area is particularly interesting, since this species was described from the western part of CCZ. It joins two other species, *Aschemonella monilis* and *Moanammina semicircularis*, in spanning a range of some 3,800 km from the western to the eastern CCZ (Gooday et al., 2020a).

Genetic data are particularly valuable for identifying xenophyophores and establishing species ranges, particularly when specimens are fragmented. In our material, *Abyssalia foliformis* is represented by a single fragment that includes only the base of the test attached to a nodule. Although other features, notably wall composition and structure and the internal organisation, are consistent with those of the type specimen, the genetic information was essential for confirming the identification. The new specimen of *Shinkaiyia contorta,* is a fragment that differs in some respects from the holotype, notably the thinner test plate and test wall, making a morphology-based identification at best only tentative. Similarly, Gooday et al. (2020a) described some morphological differences between specimens of *Aschemonella monilis* from the western and eastern CCZ that would have made its identification difficult without genetic support.

Molecular phylogeny

The xenophyophore sequences included in the cladogram cluster in three clades with one species (*P. tenuis*) branching independently (Fig.1). The monophyly of the clades is not sustained by bootstrap values. Species represented by two or more sequences are supported by high bootstrap values (89–100%) except for *S. contorta* and *A. monilis* that are sustained by moderate BV's (74% and 73% respectively).

The first clade contains eight taxa. Within this clade, the branching of *S. zonarium*, *S.* aff. *granularium* and Xenophyophore sp. 1 is highly supported (97%), as is the branching of *Galatheammina* sp. 2 and *S. mollis* (100%). The second clade consists of twelve taxa, among which the grouping of *S. limosa* and *S. corbicula* is highly supported (97%). Another group containing *P. limbata*, *P. rotunda*, *P. tortilis* and *Abyssalia* spp. is moderately supported (75% BV). The third clade comprises fifteen taxa. Within this clade, the branching of *Psammina* sp. 2 and *Galatheammina* sp. 3 is highly supported (100%). Another group with 100% BV consists of *S. lindsayi* and *S. contorta*. Two undescribed species, *Galatheammina* 1A and *Galatheammina* 1B branch with a BV of 89%.

The genus Stannophyllum

We obtained two sequences from a second species of *Stannophyllum.* This is the most species-rich xenophyophore genus and was placed by Haeckel (1889), Schultze (1907), Tendal (1972, 1996), together with a related genus *Stannoma,* in a distinct family, the Stannomidae, characterised by the presence of fine proteinaceous fibres that ramify the test. The new species groups with 100% bootstrap support with sequences from *Stannophyllum zonarium*, confirming that these are genuine *Stannophyllum* sequences. They consistently form a strongly supported (99% BV) group with Xenophyophore sp. 1. This is surprising since the only available material of Xenophyophore sp. 1 comprises tubular fragments that are morphologically completely different from *Stannophyllum* (Supplementary Figure 9c, d in Gooday et al., 2017a). The two sequences of Xenophyophore sp. 1were obtained from one specimen and we would need additional material to examine and confirm its close molecular relationship with *Stannophyllum*.

Conclusions

This new collection builds on previous studies of xenophyophores in the eastern Clarion-Clipperton Zone (Gooday et al., 2017a, b, c, 2018), as well as the central (Kamenskaya 2005; Kamenskaya et al., 2015, 2017) and western part (Gooday et al., 2020a, b) of the CCZ. We recognised a total of 18 species and obtained sequences from eight of them. Three of those that were sequenced were new to science (two assigned to new genera), three were assigned to known species, and two were described under open nomenclature. The ten species from which no sequences were obtained included one that was previously described (*P. multiloculata*) and nine that were left under open nomenclature, four of them previously unknown. The newly described species increases the number of named xenophyophore species found in the CCZ from the current total of 24 (Gooday et al., 2020b) to 27, and the total number in the CCZ, both described and undescribed, from 63 to 70.

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FIGURE LEGENDS

FIGURE 1. PhyML phylogenetic tree based on the 3'end fragment of the SSU rRNA gene, showing the evolutionary relationships of 79 foraminiferal sequences belonging to monothalamids. Specimens marked in bold indicate those for which sequences were acquired during the present study. The tree is unrooted. Specimens are identified by their accession numbers. Numbers at nodes indicate bootstrap values (BVs). Only BVs >70% are shown.

FIGURE 2. *Aschemonella monilis* Gooday & Holzmann 2017. **A–D**, Sequenced specimens. **A,** Dark specimen attached to nodule; RC1056 (BC026). **B,** Interior of test fragment with red granellare (after removal of most pieces for sequencing) and dark stercomare; RC0056 (BC001). **C,** Fragment with two segments; RC0490B (BC010). **D**, **E,** RC1900.1 (BC045). **D**, Fragment with broken segment containing granellare. **E**, Detail of dome and tubular apertural structure. **F, G**, Specimens without cytoplasm; RC1900.2 (BC045). **F,** Complete fragment. **G**, Detail of apertural structures. Scale bars: 5 mm (A), 2 mm (C, D, F), 1 mm (E, G). No scale is available for B.

FIGURE 3. *Aschemonella tani* Gooday & Holzmann sp. nov.; holotype RC1555 (BC036). **A**, Shipboard photograph showing grouping of structures on summit on nodule; numbers 1–3 identify parts illustrated in other photographs. **B–F,** Laboratory photographs. **B,** Part 1 from top of nodule. **C,** Part 2. **D**, **E,** Part 3 viewed from different sides. **F**, Detail of Part 3. Scale bars: 2 mm (A), 1 mm (B–F).

FIGURE 4. *Aschemonella tani* Gooday & Holzmann sp. nov., laboratory photographs of fragments from holotype; RC1555 (BC036). **A**, Detail of Part 1 from summit of nodule showing dark stercomare seen through wall of test. **B,** Part 2 broken open to expose stercomare. **C**, Detail of stercomare in Part 2. **D**, Granellare strands. Scale bars: 1 mm (B), 500 µm (C, D), 200 µm (A).

FIGURE 5. *Abyssalia foliformis* Gooday & Holzmann 2020; RC0612 (BC015). **A**, Shipboard photograph of only test fragment. **B–F**, Laboratory photographs of test fragment; the stercomare had been lost from the central part of the fragment. **C, D**, Details of fragment showing granellare. **E**, Fragments of cytoplasm detached from test; note that the fragments are partly attached to sponge spicules. **F**, Loose stercomare pellets that had fallen out of the test. Scale bars: 5 mm (A, B), 1 mm (C, D), 500 µm (E, F).

FIGURE 6. *Abyssalia* aff. *foliformis*, shipboard photographs; RC0615 (BC011). **A, B**, Two different side views. **C**, Test viewed from above. **D–F**, Details of test; the yellow tube in E is probably part of a *Saccorhiza ramosa* test. Scale bars: 10 mm (A–C), 5 mm (D–F).

FIGURE 7. *Abyssalia* aff. *foliformis*, laboratory photographs; Specimen RC0615 (BC011). **A**, Fragment. **B**, Detail of edge. **C–D**, Broken edge showing granellare embedded in dak stercomare masses. Scale bars: 2.5 mm (A), 1 mm (B–D).

FIGURE 8. *Claraclippia seminuda* Gooday & Holzmann gen. & sp. nov., shipboard photographs; holotype, RC0202 (BC005). **A, B**, Test photographed on the surface of the box core immediately after collection. **C, D**, Test removed from box core. **E, F**, Details of

test; note the small open spaces. Arrows indicate the same feature in A¬D; asterisk indicate point of attachment. Scale bars: 25 mm (C, D), 10 mm (E, F); scales are not available for B and C.

FIGURE 9. *Claraclippia seminuda* Gooday & Holzmann gen. & sp. nov.; holotype, RC0202 (BC005). **A, B**, Laboratory photographs taken in Geneva; details of test surface showing stercomate branches, reddish granellare strands, and the surface veneer of fine particles, which was then still partially intact. **C–F**, Laboratory photographs of fragments consisting mainly of stercomare branches; the photographs were taken in Southampton, by which time the surface veneer of fine particles had largely disappeared. Scale bars: 10 mm (C–F), 2 mm (A–B).

FIGURE 10. *Stereodikyoma mollis* Gooday & Holzmann gen. & sp. nov. **A, B**, Holotype, RC1623 (BC039); shipboard photographs of intact specimen attached to nodule. **C–F**, Paratype, RC1697 (BC040). **C, D**, Shipboard photographs. **E, F,** Laboratory photographs (Geneva) of the two largest fragments. Scale bars: 5 mm (F), 2 mm (A–D).

FIGURE 11. *Shinkaiya contorta* Gooday & Holzmann 2017; Specimen RC0160 (BC004). **A**, Shipboard photograph of fragment. **B–E**, Laboratory photographs. **B**, Collection of fragments. **C**, Broken fragment showing interior. **D**, Detail of broken fragment with exposed interior. **E,** Complete fragment. **E**, Section of test exposed on broken surface. Scale bars: 10 mm (A, B), 5 mm (E), 2 mm (C), 1 mm (D, E).

FIGURE 12. *Shinkaiya contorta* Gooday & Holzmann 2017; Laboratory photographs; specimen RC0160 (BC004). **A**, Exterior of fragment. **B**, Broken edge. **C–E**, Interior surfaces of fragments showing stercomare. **F**, Granellare fragments with attached pieces of stercomare. **G**, Fragment with partially exposed interior. Scale bars: 1 mm. Scales were not available for D and E.

FIGURE 13. *Psammina multiloculata* Kamenskaya, Gooday & Tendal, 2015; specimen RC1019 (BC025). **A–C**, Shipboard photographs showing side views of test and view from above. **D–H**, Laboratory photographs. **D**, Entire specimen; the test had been damaged since it was photographed on the ship. **E**, Detail of damaged side plate. **F**, Detail of surface of main plate showing external expression of internal compartments. **G**, Detail of edge of plate showing stercomare. **H,** Broken edge showing cross sections of compartments. Scale bars: 2 mm (A–F), 500 µm (G, H).

FIGURE 14. *Stanophyllum* aff. *granulatum*; sequenced specimen RC0489 (BC010). **A**, **B** Shipboard photographs **A,** Specimen attached to a nodule. **B.** Side view. **C–F**, Laboratory photographs. **C**, Entire specimen. **D**, **E**, Edge of test showing granellare branches and fringe of radiolarians attached to organic fibres (linellae). **F**, Granellare removed from test. Scale bars: 5 mm (A–C), 1 mm (D–F).

FIGURE 15. *Stanophyllum* aff. *granulatum*; specimen that was not sequenced, RC0608 (BC015). **A**, **B, D** Shipboard photographs **C, E, F**, Laboratory photographs. **A, B**, Specimen attached to a nodule. **C.** Specimen detached. **D**, Base of test showing attachment to nodule. **E,** Detail of surface. **F**, Edge of test showing organic fibres (linellae) Scale bars: 5 mm (A, D), 1 mm (E, F). Scales were not available for A and B.

Supplementary figure captions

FIGURE S1. *Aschemonella monilis* Gooday & Holzmann 2017; shipboard photographs. **A**–**B**, Dark, irregularly segmented specimens on nodule; RC1345 (BC031). **C,** Large dark specimens detached from nodule; RC1042 (BC041). **D,** Large, brownish specimen, dotted with micronodules and with attached tubes; RC1731 (BC040). Scale bars = 10 mm (A, C), 5 mm (B, D)

FIGURE S2. ?*Aschemonella*? sp.; RC1698 (BC040); laboratory photographs. **A, B,** Two fragments. **C**, Detail showing broken wall and interior with decayed stercomare. **D,** Detail of surface dotted with micronodules. Scale bars = 2 mm (A, D), 5 mm (B), 1 mm (C).

FIGURE S3. *Stereodikyoma mollis* Gooday & Holzmann gen. & sp. nov**.** **A,** Shipboard photograph of the remains of a specimen from BC040 attached to nodule; this is probably the base of a test, the upper part of which has been abraded. **B–F,** Laboratory photographs. **B**, Paratype, RC1697 (BC040); fragments of granellare with attached fragments of stercomare and test material. **C–F,** Holotype, RC1623 (BC039). **C–E**, test fragments. **F,** Fragment broken to expose stercomare; RC1623 (BC039). Scale bars = 2 mm (A, C, D), 1 mm (E), 500 µm (B, F)

FIGURE S4. *Psammina* aff. *multiloculata;* RC1830 (BC044). **A,** Shipboard photograph. **B,** Mosaic of more detailed shipboard photographs showing part of test. Scale bars = 10 mm (A), 5 mm (B).

FIGURE S5. *Psammina* aff. *multiloculata*, laboratory photographs*;* RC1830 (BC044). **A,** General view of fragment. **B–D,** Progressively closer views of the same fragment. **E, F.** Broken edge showing cross-sections of compartments. Scale bars = 5 mm (A), 2 mm (B, C, E, F), 500 µm (D).

FIGURE S6. *Psammina* aff. *limbata* form 1 sensu Gooday et al., 2018. **A,** Shipboard photograph; **B–F,** Laboratory photographs. **A, B,** Same specimen photographed using different lighting, the stalk is missing; RC1699 (BC040). **C–F,** RC1558 (BC036). **C,** Part of fan showing growth lines. **D,** Base of test showing broken stem; RC1623 (BC039). **E, F,** Broken cross section showing internal framework of spicules mixed with radiolarians. Scale bars = 2 mm (A, B),

FIGURE S7. *Psammina* aff. *limbata* form 2 sensu Gooday et al., 2018; shipboard photographs. **A**–**C,** RC1337 (BC040). **A, B,** Same specimen photographed from different sides. **C,** Detail of base showing root-like structure attached to nodule. **D,** RC1492 (BC034); second specimen. Scale bars = 5 mm.

FIGURE S8. *Homogammina* sp.. **A,** Shipboard photograph of entire specimen RC1494 (BC034). **B–E,** Laboratory photographs. **B, C,** Broken edge showing solid test ramified by dark stercomare. **D, E,** Loose stercomare. **D,** RC1479 (BC034). **E,** RC1700 (BC040). Scale bars = 5 mm (A), 2 mm (B), 1 mm (C–E).

FIGURE S9. Curved muddy plate, RC1366 (BC032); shipboard photographs. **A, B**, Different views of specimen 1. **C–F,** Different views of specimen 2. **C,** oblique view from above. **D, E**, opposite sides of test. **F**, Base of test partly detached from nodule surface. Scale bars = 5 mm (A–E), 2 mm (F).

FIGURE S10. Curved muddy plate. **A, B** Fragment photographed in Geneva and Southampton, respectively. **C,** Broken edge of fragment. **D,** Second fragment. **E–F,** Broken cross sections showing test interior. Scale bars = 2.5 mm (A, B, D), 1.0 mm (C), 0.5 mm (E, F).

FIGURE S11. Dark complex plate with micronodules, shipboard photographs; RC0372 (BC008). **A–D** Specimen 1; R0373 (BC008). **E, F,** Specimen 2; RC0372 (BC008). These are no scale bars for these images.

FIGURE S12. Dark complex plate with micronodules, laboratory photographs; RC0373 (BC008). **A,** Collection of fragments. **B, C,** Two sides of same fragment. **D, E,** Two different fragments. **F,** Test surface. **G, H**, Broken cross-section of test. Scale bars = 10 mm (A), 5 mm (B–E), 2 mm (F), 1 mm (G, H).

FIGURE S13. Dark plate with radiolarians; specimen RC1019 (BC025). **A–B**, Shipboard photographs of complete fragment and detail of surface. **C, D**, Fragments of granellare. Scale bars: 10 mm (A), 2 mm (B). Scales were not available for D and E.

FIGURE S14. *Stannophyllum* sp.; RC0598 (BC014). **A,** Shipboard photograph of entire specimen. **B–E,** Laboratory photographs. **B,** Entire specimen. **C,** Specimen photographed using transmitted light showing ‘growth lines’ **D,** Detail of test surface. **E,** Detail of test margin including organic fibres (linellae). Scale bars = 5 mm (A, B), 2.5 mm (D), 2 mm (C), 1 mm (E).

FIGURE S15. *Stannophyllum* sp.; RC0613 (BC015). **A–C,** Shipboard photograph of entire specimen attached to nodule. **D,** Laboratory photograph of entire specimen removed from nodule and showing underside of attached area. Scale bars = 5 mm.

FIGURE S16. *Stannophyllum* sp.; RC0036 (BC001). **A, B,** Shipboard photographs of entire specimen attached nodule and following its removal. **C–F,** Laboratory photograph. **C,** Entire sp6ecimen. **D,** Test surface. **E,** Side view of test edge. **F,** Test margin. Scale bars = 2 mm (A, B).

Table 1. Locality and specimen data for the xenophyophores collected. There were no formal station numbers and so the localities are identified by box core (BC) numbers. OMS = Ocean Mineral Singapore exploration license area. UK-1 = United Kingdom 1 exploration license area.

Box core	**Specimen**	**Area**	**Latitude**	**Longitude**	**Depth (m)**	**Species**	**Sequences**
BC001	RC0056	OMS	14°01'08.0"N	116°18'22.4"W	4111	*Aschemonella monilis*	Yes
BC010	RC049B	OMS	14°02'52.0"N	116°26'38.7"W	4034	*Aschemonella monilis*	Yes
BC025	RC1042	UK-1	13°30'02.5"N	117°09'49.2"W	4075	*Aschemonella monilis*	No
BC026	RC1056	UK-1	13°21'54.0"N	117°01'22.0"W	4123	*Aschemonella monilis*	Yes
BC031	RC1345	UK-1	12°22'18.4"N	116°38'03.5"W	4167	*Aschemonella monilis*	No
BC040	RC1689	OMS	12°22'05.1"N	117°33'01.0"W	4157	*Aschemonella monilis*	Yes
BC040	RC1731	OMS	12°22'05.1"N	117°33'01.0"W	4157	*Aschemonella monilis*	No
BC045	RC1900	OMS	12°23'06.3"N	117°25'13.9"W	4131	*Aschemonella monilis*	Yes
BC036	RC1555	OMS	12°26'45.5"N	117°49'41.1"W	4196	*Aschemonella tani* sp. nov	Yes
BC040	RC1698	OMS	12°22'05.1"N	117°33'01.0"W	4157	*Aschemonella*? sp.	No
BC015	RC0612	OMS	14°07'34.9"N	116°31'20.4"W	4116	*Abyssalia foliformis*	Yes
BC011	RC0520	OMS	14°07'02.3"N	116°27'39.9"W	4148	*Abyssalia* aff. *foliformis*	Yes
BC005	RC0202	OMS	14°06'38.2"N	117°13'54.2"W	4200	*Claraclippia seminuda* gen & sp. nov.	Yes
BC039	RC1623	OMS	12°20'37.4"N	117°28'50.6"W	4174	*Stereodiktyoma mollis* gen & sp. nov.	Yes
BC040	RC1697	OMS	12°22'05.1"N	117°33'01.0"W	4157	*Stereodiktyoma mollis* gen. & sp. nov.	No
BC004	RC0160	OMS	14°17'31.0"N	117°12'17.7"W	4155	*Shinkaiya contorta*	Yes
BC025	RC1019	UK-1	13°30'02.5"N	117°09'49.2"W	4075	Dark plate with radiolarians	No
BC010	RC0489	OMS	14°02'52.0"N	116°26'38.7"W	4034	*Stannophyllum* aff. *granularium*	Yes
BC010	RC0608	OMS	14°02'52.0"N	116°26'38.7"W	4034	*Stannophyllum* aff. *granularium*	No
BC001	RC0036	OMS	14°01'08.0"N	116°18'22.4"W	4111	*Stannophyllum* spp.	No
BC014	RC0598	OMS	14°01'39.0"N	116°33'46.1"W	4125	*Stannophyllum* spp.	No
BC015	RC0613	OMS	14°07'34.9"N	116°31'20.4"W	4116	*Stannophyllum* spp.	No
BC036	RC1588	OMS	12°26'45.5"N	117°49'41.1"W	4196	*P.* aff. *limbata* form 2 sensu Gooday et al., 2018	No
BC040	RC1699	OMS	12°22'05.1"N	117°33'01.0"W	4157	*P.* aff. *limbata* form 2 sensu Gooday et al., 2018	No
BC040	RC1337	OMS	12°22'05.1"N	117°33'01.0"W	4157	*P.* aff. *limbata* form 2 sensu Gooday et al., 2018	No
BC034	RC1492	UK-1	12°10'47.9"N	117°03'55.0"W	4117	*P.* aff. *limbata* form 2 sensu Gooday et al., 2018	No
BC042	RC1743	OMS	12°24'23.2"N	117°29'21.4"W	4163	*P.* aff. *limbata* form 2 sensu Gooday et al., 2018	No

BC010	RC0490	OMS	14°02'52.0"N	116°26'38.7"W	4034	*P. multiloculata*	No
BC044	RC1830	OMS	12°14'13.5"N	117°38'34.7"W	4053	*P.* aff. *multiloculata*	No
BC034	RC1494	UK-1	12°10'47.9"N	117°03'55.0"W	4117	*Homogammina* sp.	No
BC034	RC1495	UK-1	12°10'47.9"N	117°03'55.0"W	4117	*Homogammina* sp.	No
BC040	RC1700	OMS	12°22'05.1"N	117°33'01.0"W	4157	*Homogammina* sp.	No
BC032	RC1366	UK-1	12°22'44.7"N	116°33'27.6"W	4196	Curved muddy plate	No
BC008	RC0372	UK-1	13°59'13.1"N	116°28'35.9"W	4059	Dark complex plate with micronodules	No
BC008	RC0373	UK-1	13°59'13.1"N	116°28'35.9"W	4059	Dark complex plate with micronodules	No

Table 2. Summary of isolate and accession numbers for xenophyophres included in the cladogram. Species described in this paper are in bold.

Species	**Isolate**	**Accession number**	**Sample**	**Specimen**	**Figure**
Abyssalia* aff. *foliformis	**21429**	**OQ304628**	**BC011**	**RC0520**	**Fig. 6, 7**
Abyssalia foliformis	19733	MK748285			
Abyssalia foliformis	19734	MK748286			
Abyssalia foliformis	19735	MK748287			
Abyssalia foliformis	**21442**	**OQ304627**	**BC015**	**RC0612**	**Fig. 5**
Abyssalia sphaerica	19725	MK748288			
Abyssalia sphaerica	19726	MK748289			
Aschemonella aspera	18264	LT796817, LT796818			
Aschemonella monilis	18236	LT796811			
Aschemonella monilis	18277	LT796784			
Aschemonella monilis	**21108**	**OL772069**	**BC026**	**RC1056**	**Fig. 1A**
Aschemonella monilis	**21431**	**OQ304630**	**BC010**	**RC049B**	**Fig. 2C**
Aschemonella monilis	**21439**	**OR283242**	**BC001**	**RC0056**	**Fig. 2B**
Aschemonella monilis	**21444**	**OQ304632**	**BC045**	**RC1900.1**	**Fig. 2D, E**
Aschemonella ramuliformis	9340	LT576134			
Aschemonella ramuliformis	9373	LT796828			
Aschemonella sp.3	18454	LT576133			
Aschemonella sp.3	18458	MK748318			
Aschemonella tani	**21430**	**OQ304629**	**BC036**	**RC1555**	**Figs 3, 4**
Bizarria bryiformis	18256	LT854207 , LT854208			
Claraclippia seminuda	**21436**	**OQ304625**	**BC005**	**RC0202**	**Figs 8, 9**
Claraclippia seminuda	**21437**	**OQ304626**	**BC005**	**RC0202**	**Figs 8, 9**
Galatheammina 1A	18428	MK748323,			

		MK748324			
Galatheammina 1B	18426	MK748321, MK748322			
Galatheammina interstincta	18278	LT576131			
Galatheammina interstincta	18279	LT854193			
Galatheammina sp. 3	18250	OQ304611			
Galatheammina sp. 3	18251	LT576123			
Galatheammina sp.2	18092	LT576121, MK753025			
Moanammina semicircularis	18461	MK748319			
Moanammina semicircularis	18462	OQ304615			
Psammina limbata	18230	MF441523			
Psammina limbata	18235	MF441528			
Psammina rotunda	18267	MF441544			
Psammina rotunda	18269	MF441541			
Psammina sp. 1	18434	LT576122			
Psammina sp. 1	18435	MK748327			
Psammina sp.2	18262	MK748325			
Psammina sp.2	18261	OQ304612			
Psammina tenuis	19705	MK748294			
Psammina tenuis	19706	MK748295			
Psammina tortilis	18242	MF441536			
Psammina tortilis	18243	MF441539			
Reticulammina cerebriformis	9356	LT839028			
Reticulammina cerebriformis	9357	LT839029			
Semipsammina mattaeformis	18239	LT576127			
Semipsammina mattaeformis	18265	LT854196			
Shinkaiya contorta	18253	LT854189, LT854190			
Shinkaiya contorta	**21448**	**OQ304623**	**BC004**	**RC0160**	**Fig. 12**
Shinkaiya contorta	**21449**	**OQ304624**	**BC004**	**RC0160**	**Fig. 12**

Shinkaiya lindsayi	19840	OQ304619			
Shinkaiya lindsayi	n.a.	EU649778			
Stannophyllum* aff. *granularium	**21445**	**OQ304621**	**BC010**	**RC0489**	**Figs 15, 16**
Stannophyllum* aff. *granularium	**21446**	**OQ304620**	**BC010**	**RC0489**	**Figs 15, 16**
Stannophyllum zonarium	18447	LT576118			
Stannophyllum zonarium	18448	MK748331			
Stereodictyoma mollis	**21433**	**OQ304622**	**BC039**	**RC1623**	**Figs. 10, S3**
Syringammina corbicula	2270	AJ514856			
Syringammina limosa	X6	MG132678			
Syringammina limosa	X7	MG132682			
Tendalia reteformis	18231	LT576120			
Tendalia reteformis	18438	LT854202			
Toxisarcon alba	WC18H	AJ307750			
Toxisarcon synsuicida	1370	AJ315955			
Toxisarcon taimyr	14533	KF931124			
Xenophyophora sp. 3	18487	OQ304613, OQ304614			
Xenophyophora sp.1	18248	LT576119			
Xenophyophora sp.1	18249	MK748330			
Xenophyophora sp.2	18488	LT576128, MK753024			
Xenophyophora sp.4	19719	MK748282			
Xenophyophora sp.4	19720	MK748283			

Fig.1

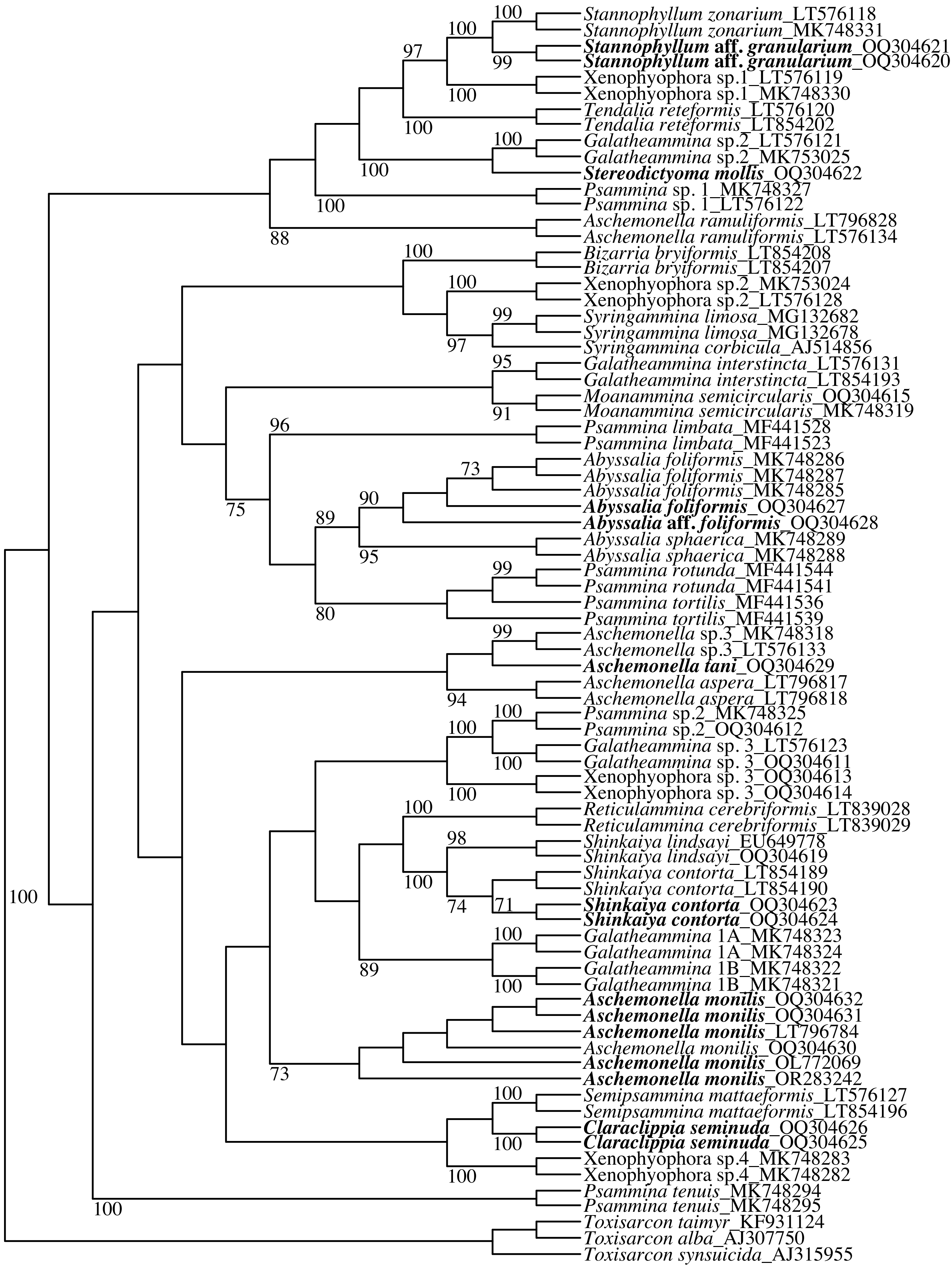

Stannophyllum zonarium_LT576118
Stannophyllum zonarium_MK748331
Stannophyllum aff. granularium_OQ304621
Stannophyllum aff. granularium_OQ304620
Xenophyophora sp.1_LT576119
Xenophyophora sp.1_MK748330
Tendalia reteformis_LT576120
Tendalia reteformis_LT854202
Galatheammina sp.2_LT576121
Galatheammina sp.2_MK753025
Stereodictyoma mollis_OQ304622
Psammina sp. 1_MK748327
Psammina sp. 1_LT576122
Aschemonella ramuliformis_LT796828
Aschemonella ramuliformis_LT576134
Bizarria bryiformis_LT854208
Bizarria bryiformis_LT854207
Xenophyophora sp.2_MK753024
Xenophyophora sp.2_LT576128
Syringammina limosa_MG132682
Syringammina limosa_MG132678
Syringammina corbicula_AJ514856
Galatheammina interstincta_LT576131
Galatheammina interstincta_LT854193
Moanammina semicircularis_OQ304615
Moanammina semicircularis_MK748319
Psammina limbata_MF441528
Psammina limbata_MF441523
Abyssalia foliformis_MK748286
Abyssalia foliformis_MK748287
Abyssalia foliformis_MK748285
Abyssalia foliformis_OQ304627
Abyssalia aff. foliformis_OQ304628
Abyssalia sphaerica_MK748289
Abyssalia sphaerica_MK748288
Psammina rotunda_MF441544
Psammina rotunda_MF441541
Psammina tortilis_MF441536
Psammina tortilis_MF441539
Aschemonella sp.3_MK748318
Aschemonella sp.3_LT576133
Aschemonella tani_OQ304629
Aschemonella aspera_LT796817
Aschemonella aspera_LT796818
Psammina sp.2_MK748325
Psammina sp.2_OQ304612
Galatheammina sp. 3_LT576123
Galatheammina sp. 3_OQ304611
Xenophyophora sp. 3_OQ304613
Xenophyophora sp. 3_OQ304614
Reticulammina cerebriformis_LT839028
Reticulammina cerebriformis_LT839029
Shinkaiya lindsayi_EU649778
Shinkaiya lindsayi_OQ304619
Shinkaiya contorta_LT854189
Shinkaiya contorta_LT854190
Shinkaiya contorta_OQ304623
Shinkaiya contorta_OQ304624
Galatheammina 1A_MK748323
Galatheammina 1A_MK748324
Galatheammina 1B_MK748322
Galatheammina 1B_MK748321
Aschemonella monilis_OQ304632
Aschemonella monilis_OQ304631
Aschemonella monilis_LT796784
Aschemonella monilis_OQ304630
Aschemonella monilis_OL772069
Aschemonella monilis_OR283242
Semipsammina mattaeformis_LT576127
Semipsammina mattaeformis_LT854196
Claraclippia seminuda_OQ304626
Claraclippia seminuda_OQ304625
Xenophyophora sp.4_MK748283
Xenophyophora sp.4_MK748282
Psammina tenuis_MK748294
Psammina tenuis_MK748295
Toxisarcon taimyr_KF931124
Toxisarcon alba_AJ307750
Toxisarcon synsuicida_AJ315955

Fig.2

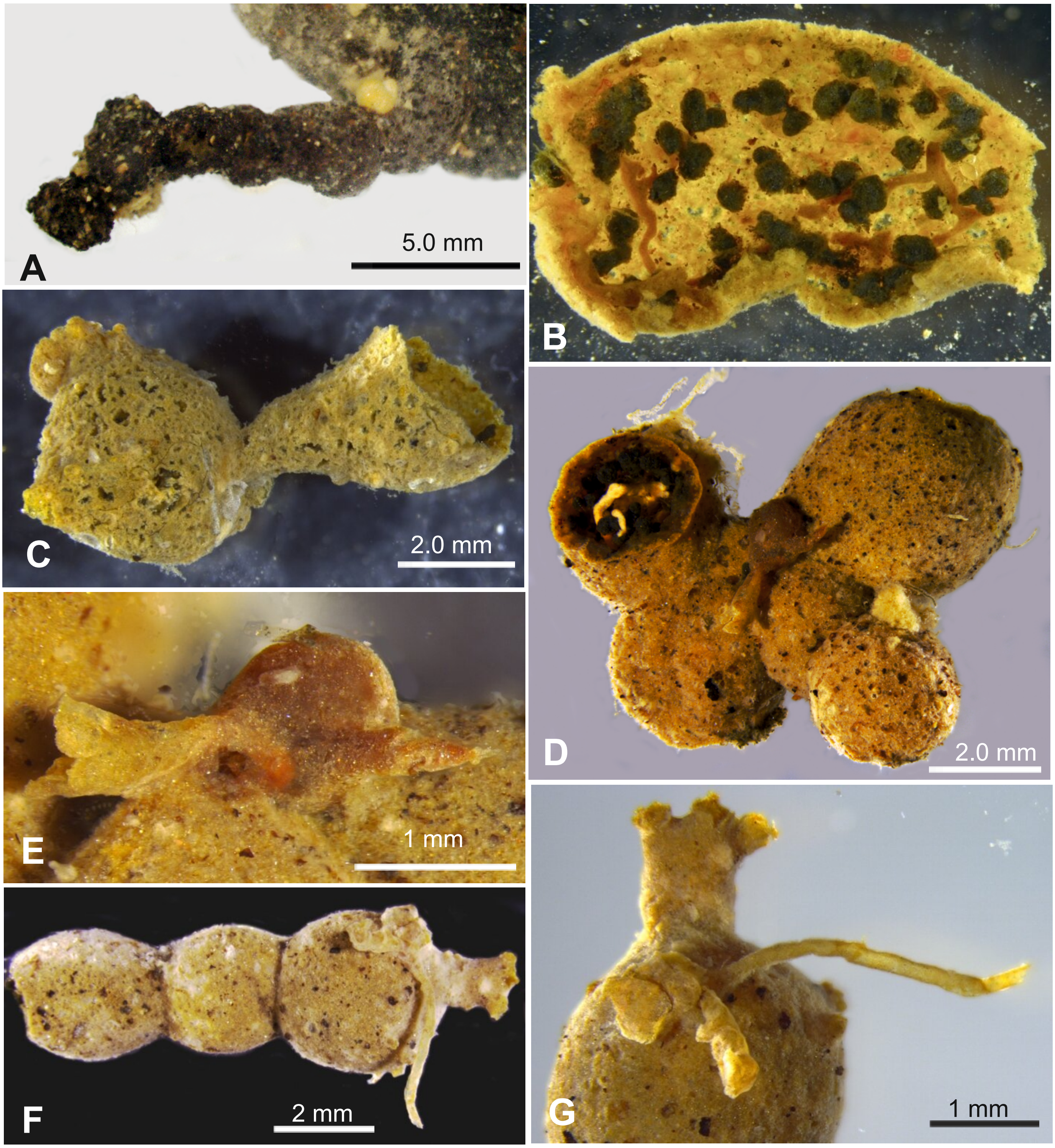


Fig.3

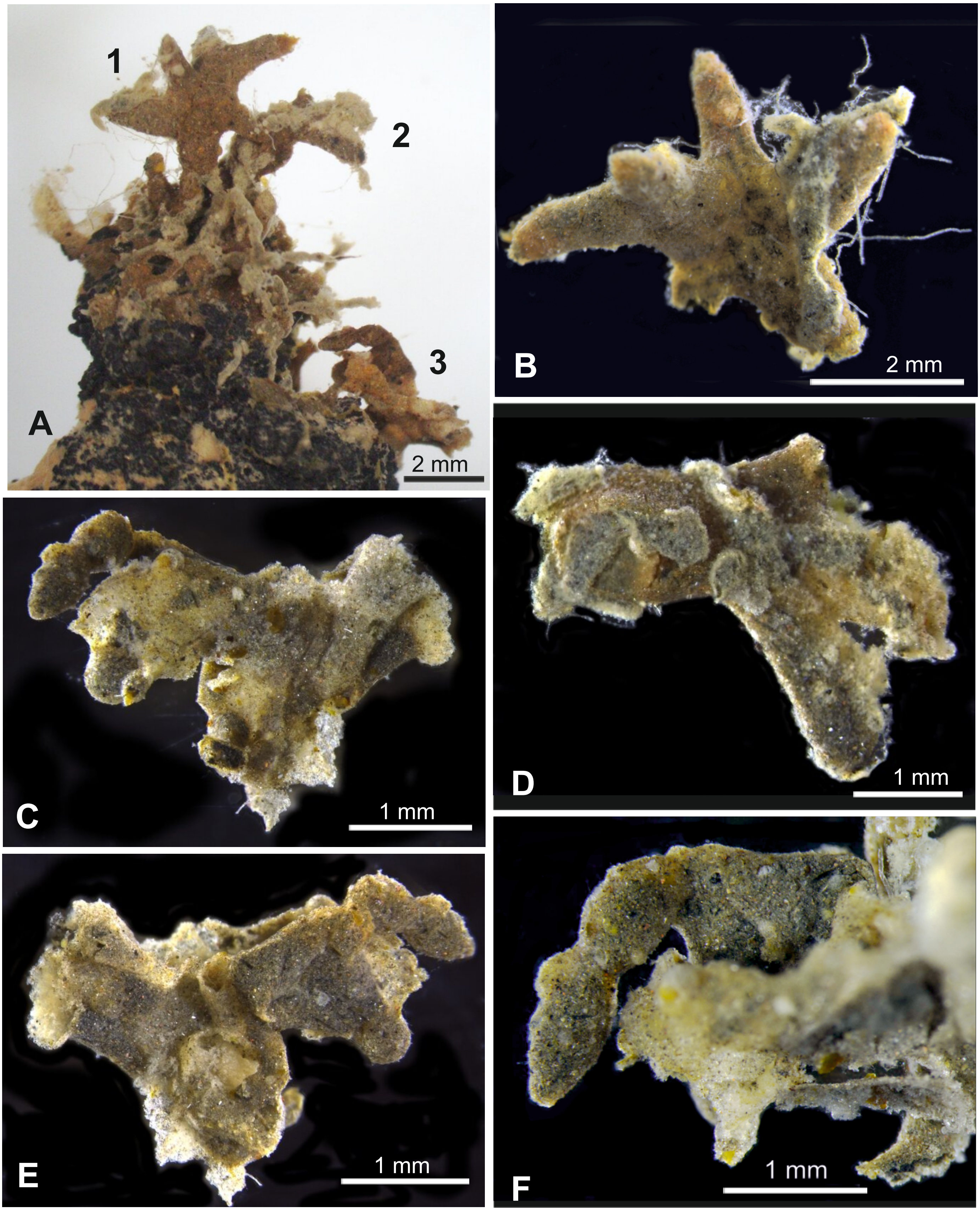


Fig.4

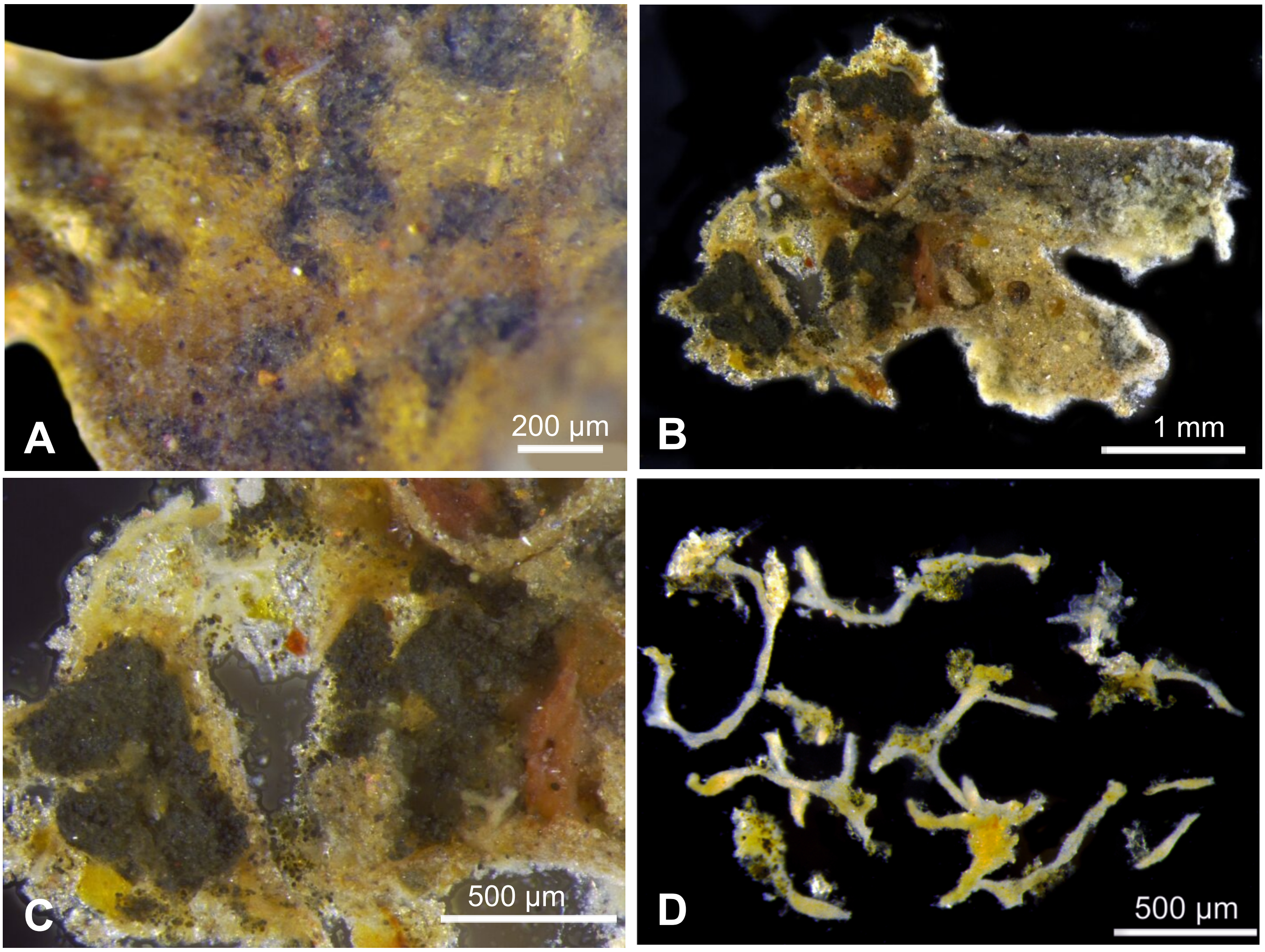
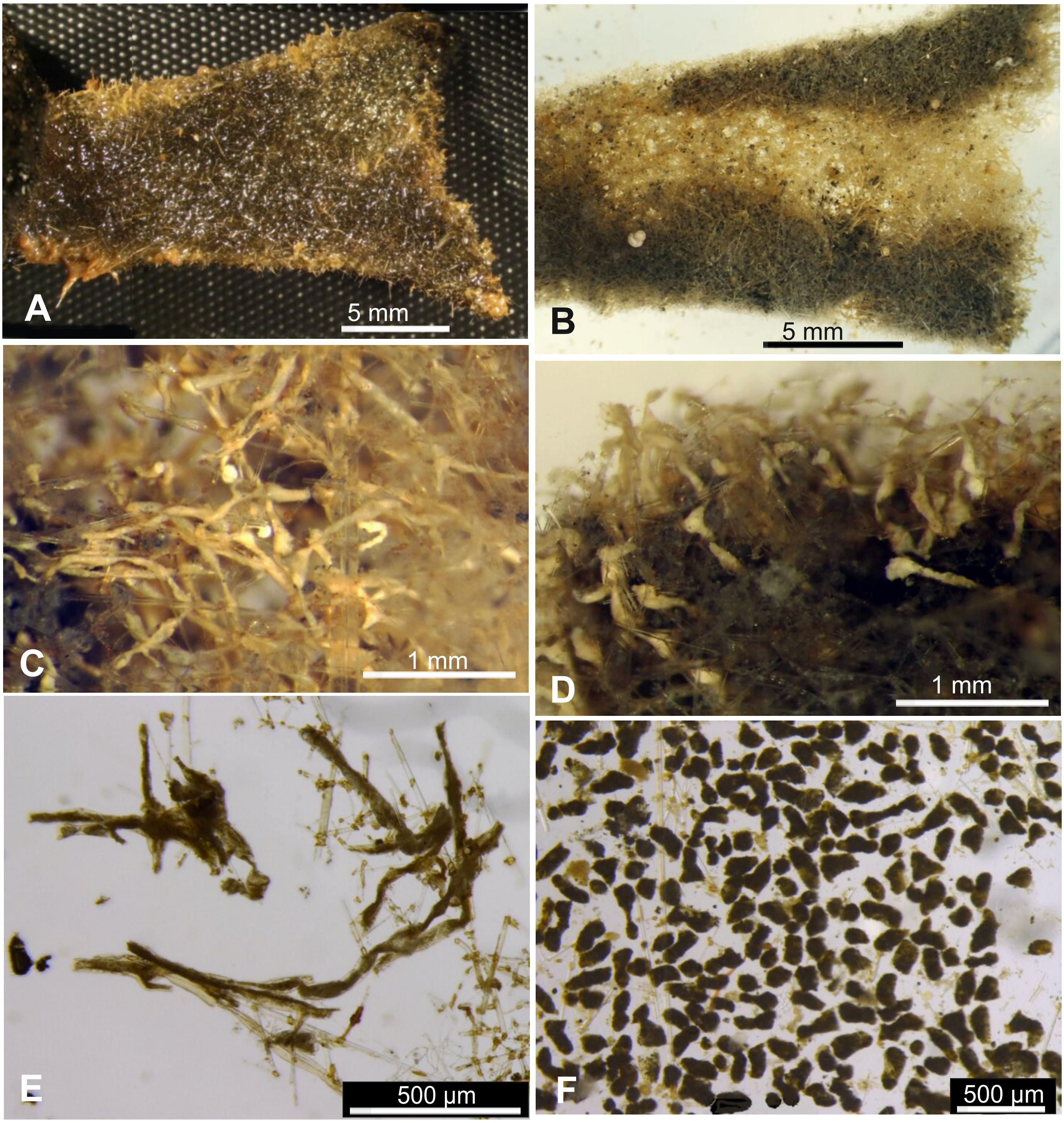


Fig.5



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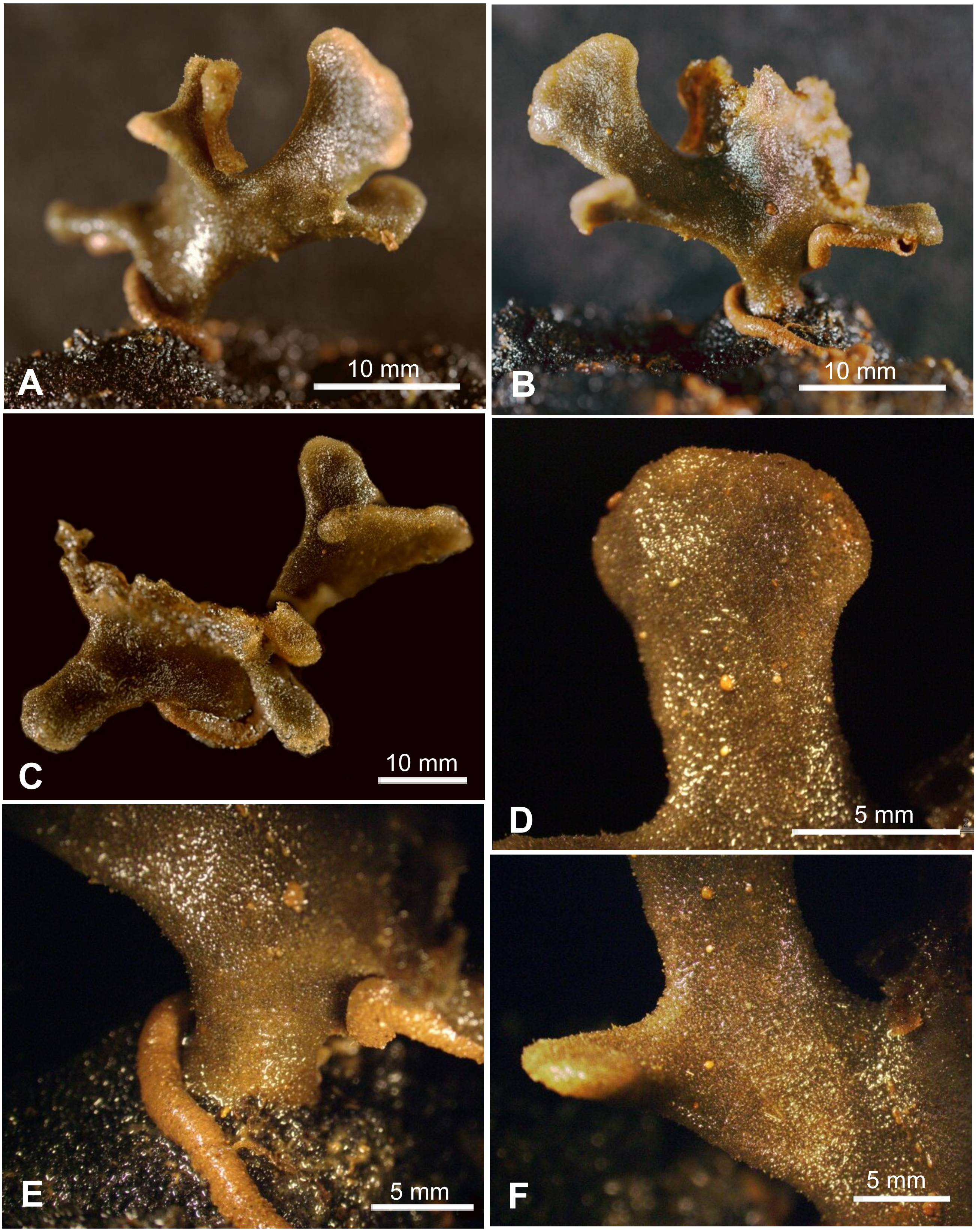

Fig.7

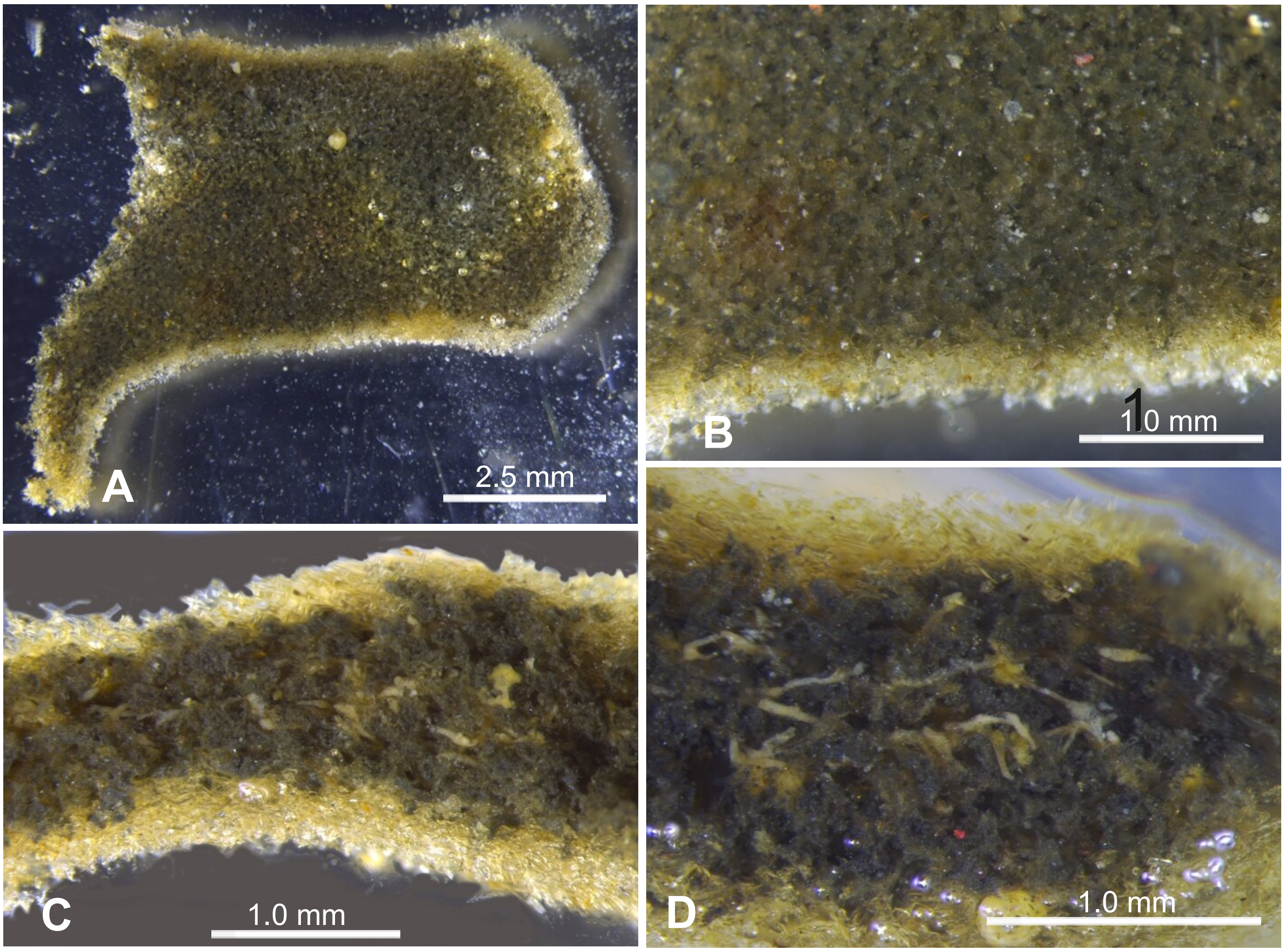

Fig.8

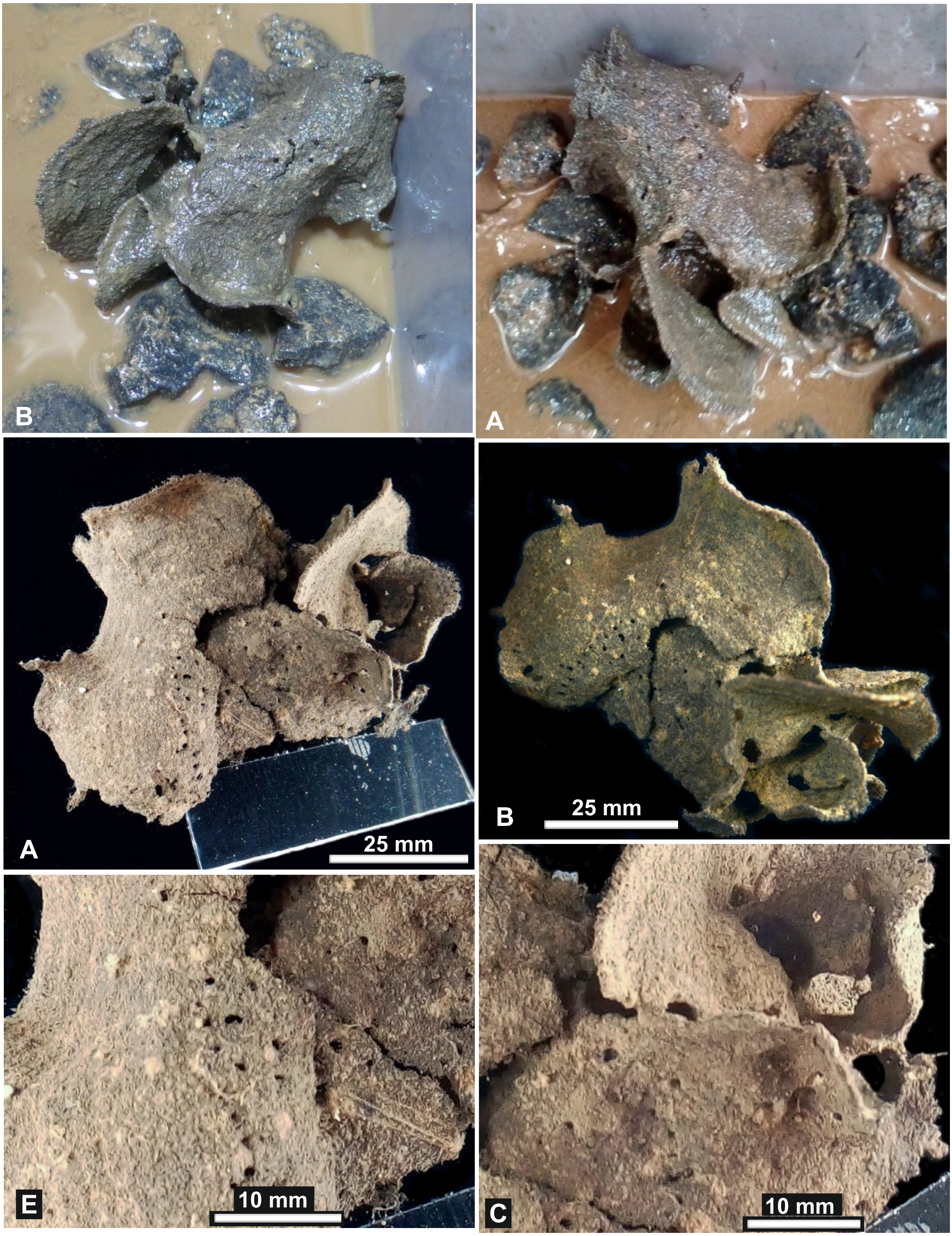

Fig. 9

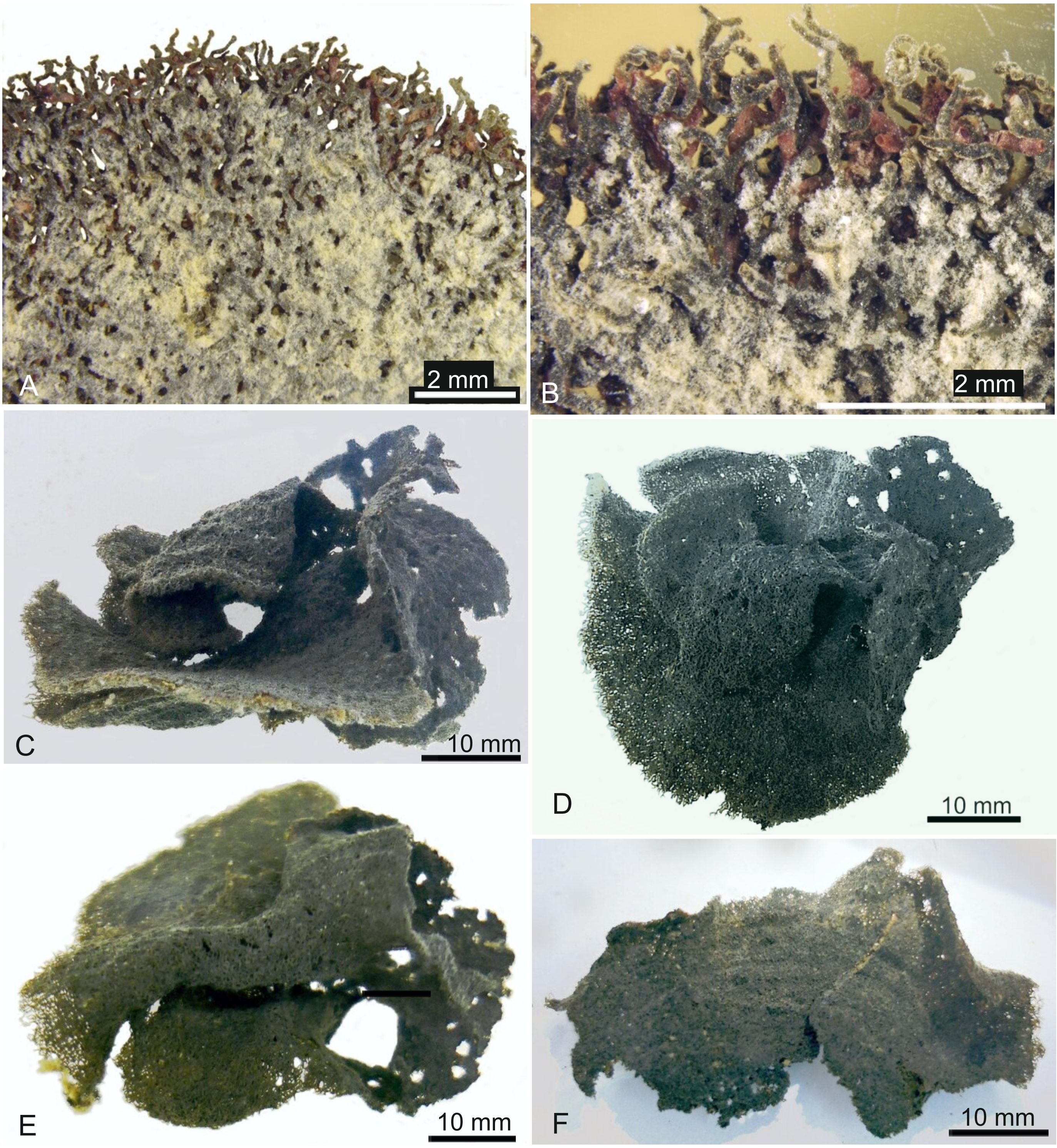

Fig.10

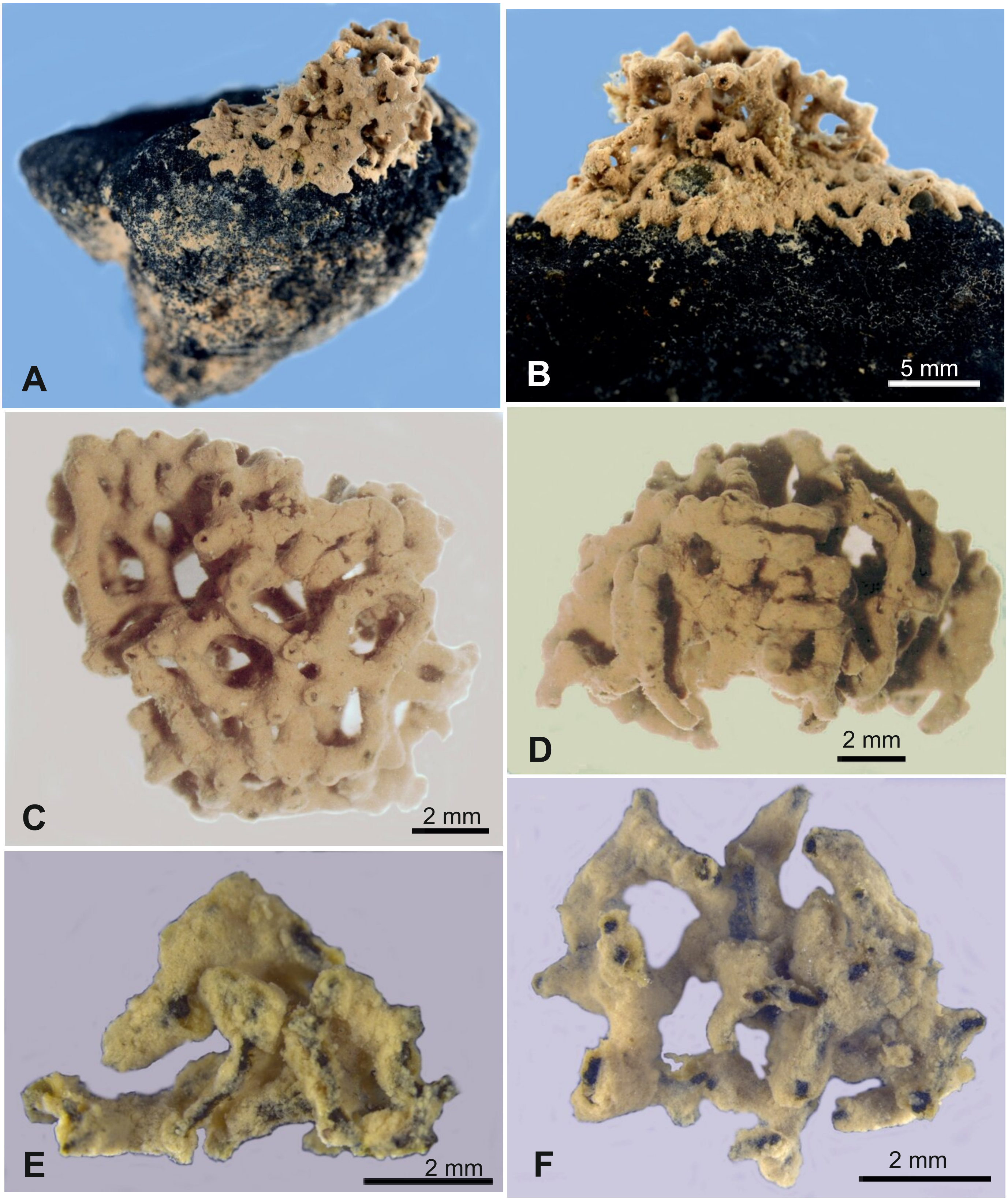

Fig.11

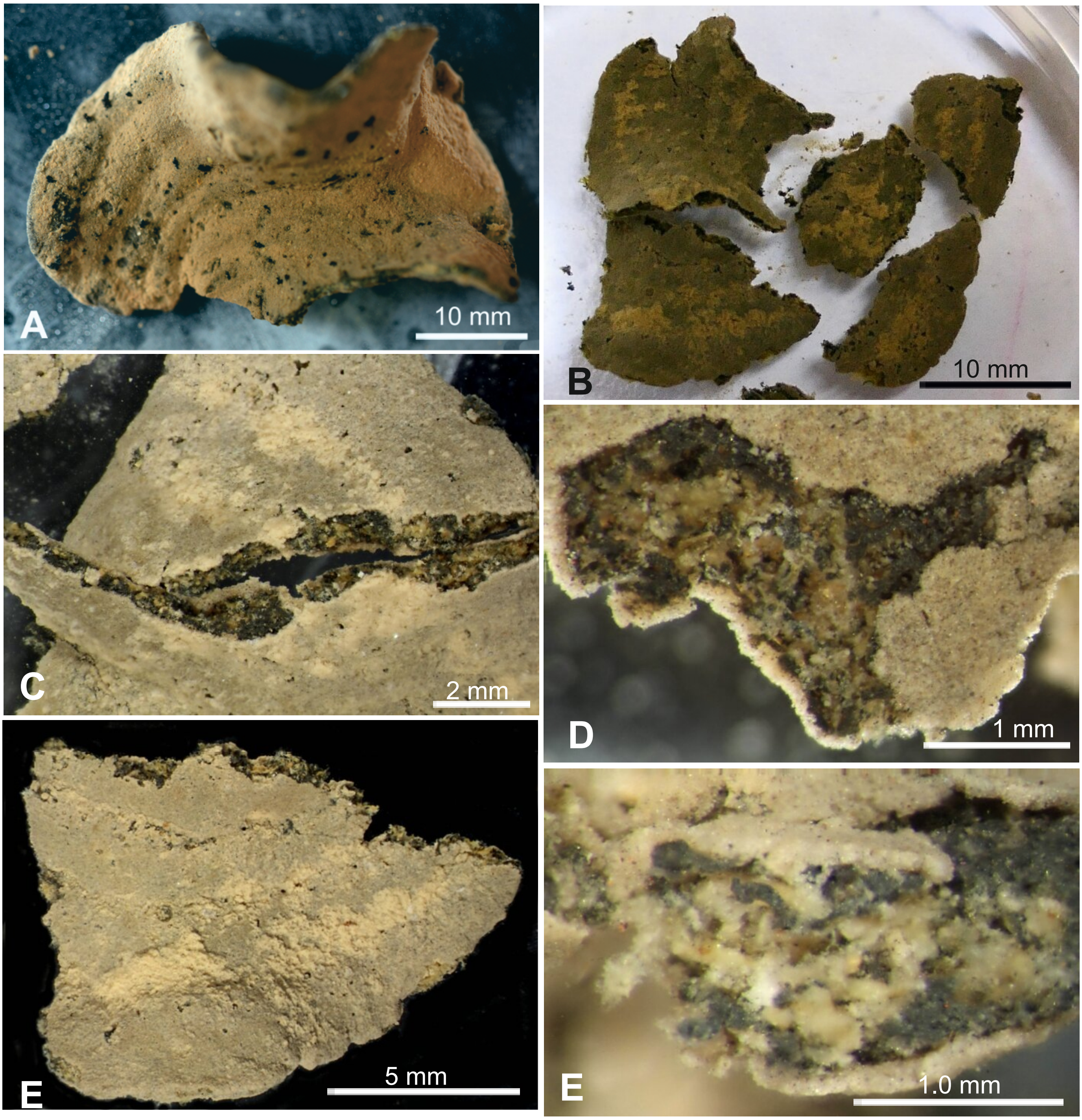

Fig.12

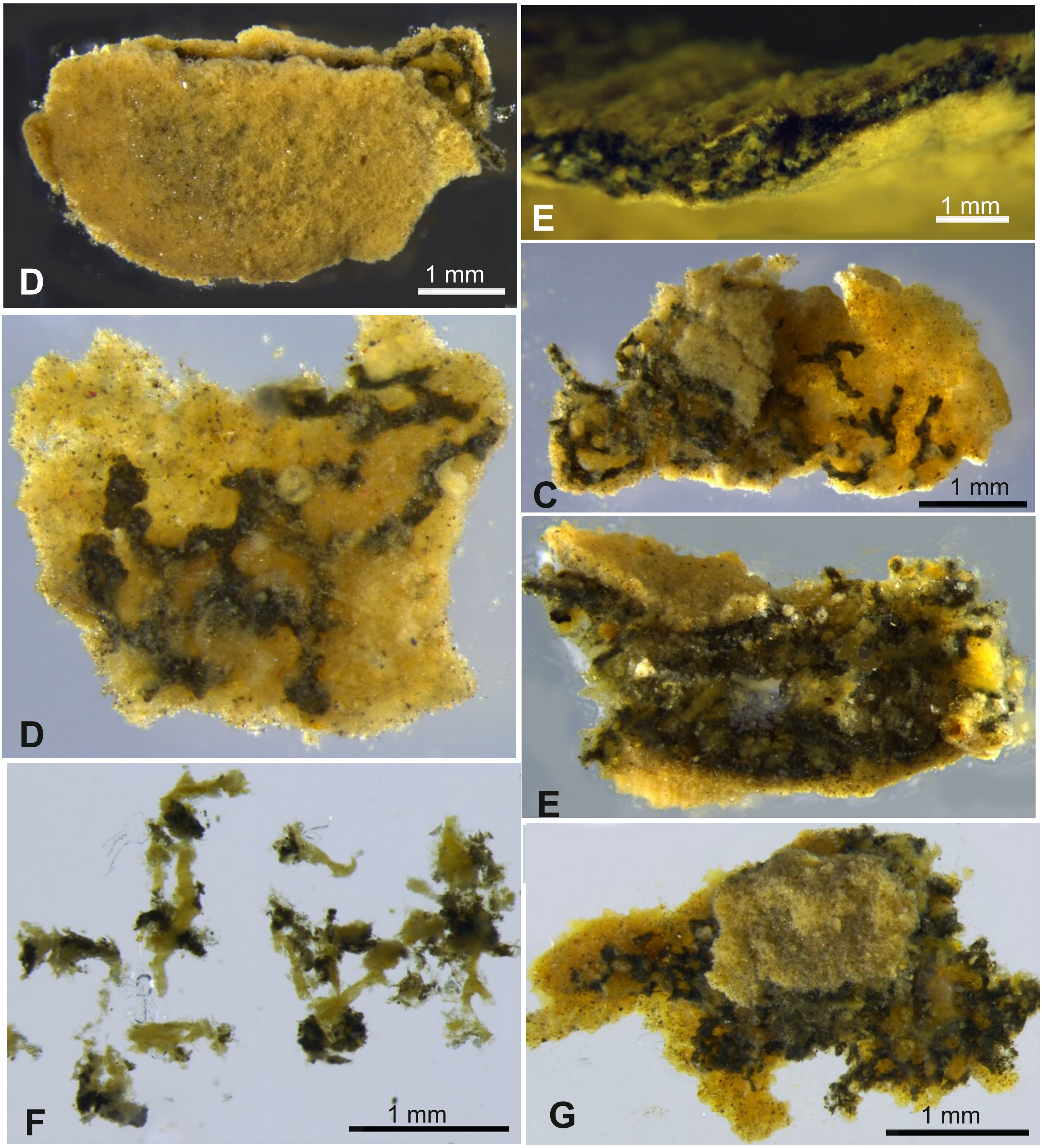

Fig.13

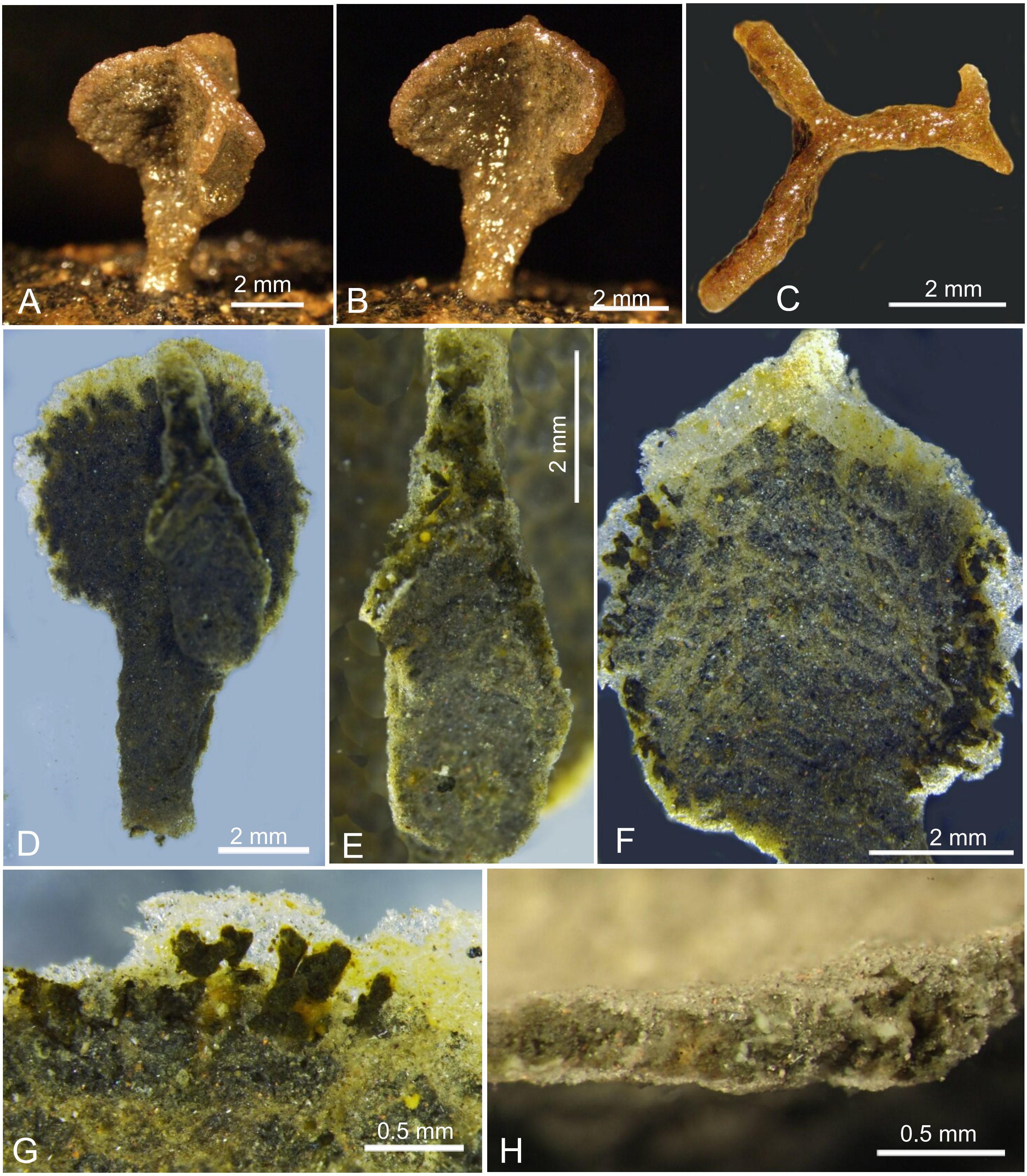

Fig.14

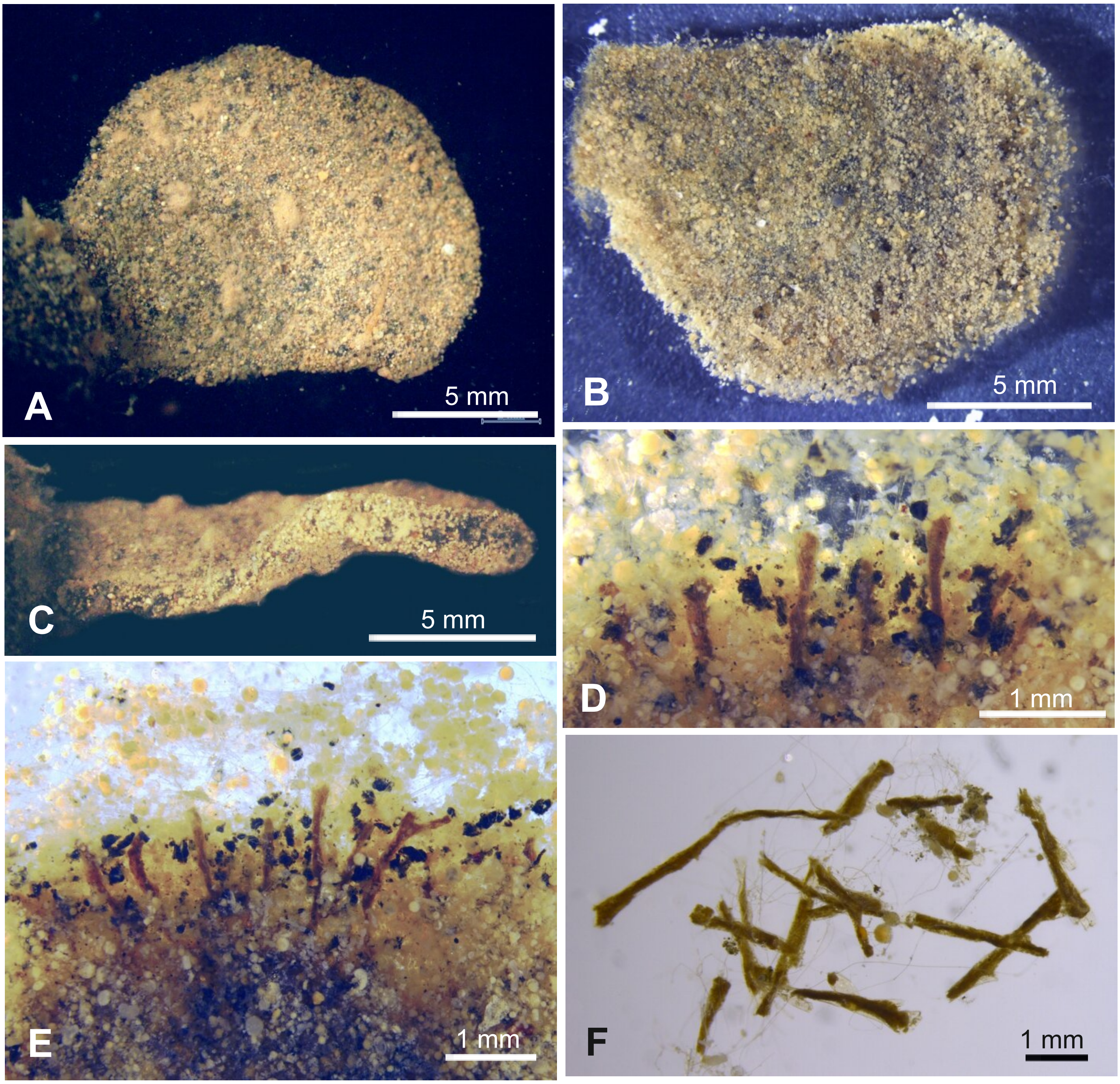

Fig.15