Xenophyophores (Protista, Foraminifera) from the Clarion-Clipperton Fracture Zone with description of three new species

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Introduction

Xenophyophores are giant agglutinated deep-sea protists (Tendal, 1972, 1996) that are confined to regions below about 500 m water depth. Since the first species were described in the 1880s, (Brady, 1883; Haeckel, 1889), they have been variously classified as foraminifera, sponges or as a distinct prosistan group (Tendal, 1972). However, recent molecular analyses place at least some species within the monothalamous foraminifera ("monothalamids") (Pawlowski et al., 2003; Lecroq et al., 2009; Gooday et al., 2011). Xenophyophores are particularly abundant in areas where the food flux is enhanced, for example, on seamounts and ridges, in submarine canyons and under productive surface waters, including the eastern equatorial Pacific (Tendal, 1972; Tendal and Levis, 1978; Levin and Thomas, 1988; Levin, 1994).

Interest in xenophyophores has been heightened recently by their abundance in the Clarion-Clipperton Fracture Zone (CCFZ), a large tract of the equatorial Pacific where polymetallic nodules ('manganese nodules') are particularly abundant. The International Seabed Authority (ISA) has awarded contracts to countries and companies to exploit nodules in designated claim areas within the CCFZ. Our previous investigations have revealed that xenophyophores are a key megafaunal group within the Russian claim area in the central part of the Clarion-Clipperton nodule field (Kamenskaya et al., 2013). They were seen in 70% of sea-floor photographs and were found in 30% of box-cores samples collected during a 2007 cruise of Research Vessel *Yuzhmorgeologia*. Their average density was 1,600 specimens per hectare, with a maximal value of 120,000 specimens per hectare (= 12 specimens per m^2); the next most common group, the Actiniaria, did not exceed a density of 170 specimens per hectare. According to earlier studies on eastern equatorial Pacific seamounts, the abundance and species diversity of macro- and meiobenthos is elevated in sediments beneath and close to xenophyophore tests compared to sediments where no xenophyophores are present (Levin et al.,1986; Levin and Thomas, 1988). Diverse assemblages of metazoans and foraminifera also inhabit the cavities and interstices of xenophyophore tests (Levin and Thomas, 1988; Levin 1994; Hughes and Gooday, 2004). Therefore, in the areas where these giant protists dominate, they probably play the important role in structuring of benthic communities. Their study is especially important in the light of likely future polymetallic nodule mining within the CCFZ.

Following Tendal (1972), we recognize two main xenophyophore groups: stannomids (order Stannomida of Tendal, 1972) and psamminids (order Psamminida of Tendal 1972). Both groups are present in the central part of the Clarion-Clipperton nodule field, either attached to the nodules (species of the genera *Psammina*, *Semipsammina*, *Stannophyllum* and *Spiculammina*) or living on soft sediment between the nodules (species of *Psammina* and *Reticulammina*). About 60% of these xenophyophores have a leaf-like test shape and probably belong to genera *Psammina* and *Stannophyllum*. The tree-like species *Spiculammina delicata* was seen in 10% of bottom photographs. Here, we analyze the taxonomic composition of xenophyophores attached to the nodules from central part of the CCFZ and describe three new species in the genera *Psammina* and *Semipsammina*. In the absence of material suitable for molecular analyses, our descriptions are based on morphological characters.

Material and methods

The material was obtained using a box corer (cross-sectional area 0.25 cm^2) from different parts of the Russian claim area of the Clarion-Clipperton nodule field during four cruises of the Research Vessel *Yuzhmorgeologia* in 2003, 2006, 2009 and 2010 (Table 1). Nodules with xenophyophores were collected from the surface of the box-core samples. Xenophyophores were carefully removed from the nodules and preserved in 70% ethanol. For SEM study fragments of specimens were mounted on aluminium stubs and coated with Au. Analysis of chemical constituents (Ba) was performed with an energy-dispersive X-ray spectrographic analyzer (EDS) connected to a scanning electron microscopes (CamScan and Zeiss EV050). The holotypes are deposited in the collection of the Zoological Museum of the Moscow State University.

Systematics

Recent molecular analyses place several xenophyophore species within the monothalamous foraminifera (Pawlowski, et al., 2003, 2013; Lecroq et al., 2009; Gooday et al., 2011). Unfortunately, DNA sequences are not available for most xenophyophores, and the higher-level taxonomy of monthalamids generally is in a state of flux (Pawlowski et al., 2013). We, therefore, avoid assigning our species to taxa beyond genus level and simply divide them into psamminids and stannomids.

Supergroup Rhizaria Cavalier-Smith 2002
Phylum Foraminifera d'Orbigny 1826
"Monothalamids" Pawlowski et al. 2003

Psamminid group of species:

***Semipsammina licheniformis* sp. nov. Kamenskaya. Gooday, Tendal**
(Fig. 1)

Semipsammina sp. Kamenskaya, Melnik, Gooday 2013: 391-392, Fig. 6d

Material examined The holotype was from St 60-1 , R/V *Yuzhmorgeologia*, cruise 4-06, 13.26° N, 134.41° W; depth 4,777 m; collected using a box-corer. The holotype is deposited under registration number F-16.

Diagnosis Encrusting test covering part of nodule surface. Outline more or less rounded with irregular margin that forms occasional elongate extensions. Test surface with concentric pattern of linear, step-like features. Maximum test dimension up to ~ 6 cm; thickness decreasing from ~3 mm in central part to ~1 mm near margin. Agglutinated test wall composed of radiolarian skeletons with occasional diatom and sponge spicules fragments; test wall covers interior that contains strings of granellare and stecomare lying directly adjacent to nodule surface.

Description of holotype The test of the single available specimen is light greyish in colour and forms a flattened structure that encrusts the surface of a polymetallic nodule. It has an approximately circular outline, measuring 6.1 x 4.9 cm, and covers about half of the nodule surface, following the curved contours of the substrate (Fig. 1a). The thickness in the central part is about 3 mm, decreasing to 1 mm near the margins. The surface of the test is has distinct, concentric step-like features, most clearly developed in the central part and probably reflecting episodic growth. The margin of the test is irregularly rounded and often displays small lobes. Several long narrow extensions of the margin, having the form of a flattened tube, are also developed; they are up to 1 cm long, sometimes branching, and consist of either naked granellare or granellare covered with xenophyae.

The test covers the granellare and stercomare. The xenophyae (agglutinated particles) comprise a jumble of complete and fragmentary radiolarian skeletons, with scattered micronodules and occasional diatoms and small fragments of sponge spicules, creating a fairly rough surface texture (Figs. 1b, c). There are some internal xenophyae. The granellare and stercomare lie directly adjacent to the nodule surface; some parts are also attached to the inner surface of the test wall, as seen when parts of the test wall are detached (Fig. 1d). The granellare are light in colour and forms strands, 50 to 100 μm in diameter, which branch but do not anastomose (Fig. 1d). The strands contain numerous granellae, 3-4 μm in length with the ovate shape typical of xenophyophore barite crystals (Fig. 1e). The stercomare masses form branched structures, ranging from less than 50 μm to more than 100 μm in diameter, containing stercomata with a diameter <10 μm (Fig. 1f).

Etymology From Latin and English “lichen”

Distribution Currently known only from one site in the Russian license area of the Clarion-Clipperton Fracture Zone, Eastern Pacific, depth 4777 m (Table 1)

Remarks The only previously described species of the genus, *Semipsammina fixa* Tendal 1975, is known from two specimens and some fragments attached to turtle grass rhizomes from the Puerto Rico Trench (depth 6,000-5,890 m). The plate-like body of *S. fixa* is irregularly rounded in outline, up to 5.5 mm in diameter and ~ 0.5 mm in thickness. The xenophyae comprise sponge spicules and mineral particles. Our new species differs from *S. fixa* mainly in the much larger size of the test and the nature of the xenophyae. There also appear to be differences in the shape of stercomare system.

Mullineaux (1987) reported two species (designated 'sp. a' and 'sp. b') of *Semipsammina* living on the surfaces of polymetallic nodules from the equatorial North Pacific (5°N, 125°W; 4,500 m depth) and the central North Pacific (30°N, 157°W; 5,800 m depth). *Semipsammina* sp. a occurred at the equatorial site while *S.* sp. b occurred at both sites. These represent the first records of *Semipsammina* in the Pacific Ocean. No further information is available about these species.

Genus *Psammina* Haeckel 1889

Remarks The genus was established by Haeckel (1889) based on three species, *Psammina nummulina, P. globigerina* and *P. plankina.* According to the diagnosis given in Tendal (1972), the main features of *Psammina* are 1) a discoidal test with large pores around the margin, 2) firmly cemeted xenophyae comprising hard, upper and lower plates, 3) internal xenophyae forming pillar-like structures between the two plates, and 3) granellare branches and stercomare strings strongly developed around the pillars. Gooday and Tendal (1988) added three further species, *P. delicata, P. fusca*, and *P. sabulosa*. These confirm more or less to the diagnosis of Tendal (1972), although none has a clearly discoidal shape, marginal pores are evident only in *P. sabulosa*, and *P. fusca* lacks internal pillars as well as pores. Tendal (1994) described *P. zonaria,* a bathyal species from the western Pacific with an elongate test that widens towards its distal end and is subdivided internally into transverse compartments. Finally, Kamenskaya and Saidova (1998) redescribe *Psammina planata* Saidova 1970, a hadal species from the western Pacific that was originally placed in the genus *Astrorhizinella*.

Here, we assign two additional species to the genus *Psammina*. They also deviate from the original concept of *Psammina* in certain respects. In the future it may be necessary to divide this now rather heterogenous group of species into two or more distinct genera.

Psammina multiloculata sp. nov. Kamenskaya, Gooday, Tendal

(Figs. 2, 3)

Material examined The holotype was from St. 28, R/V *Yuzhmorgeologia* cruise 4-06, 13.28^0 N, 134.41^{0}W, depth 4,843 m. The holotype deposited under registration number F-17. Other material: one specimen from St. 8726, one specimen from St. 8655, one specimen from St. 204.

Diagnosis More or less semicircular, plate-like test, sometimes with additional side plate, attached to hard substrate by short wide basal stalk. Outer layer of test consisting of small fragments of radiolarian skeletons, sponge spicules and mineral grains. Surface is granular at base and with weakly developed concentric zonation most evident close to margin. Inner space divided into numerous compartments containing stercomare and granellare.

Etymology From Latin “loculata”, meaning divided into small volumes.

Description Holotype (Fig. 2a-c): The test is flat, plate-like, and was attached upright to a nodule by its longest side without the development of a stalk. The dimestion of the intact specimen is 24x18 mm but the test was broken into several fragments during preparation. One of these fragments includes the base of a side plate (Fig. 2c). The surface of the test is noticably granular at the base and shows concentric zones, which are most clearly visible near the outer margin (Fig. 2a, b). The outer layer of the test is composed of small fragments of radiolarian skeletons, sponge spicules and mineral grains (external xenophyae). The test interior is divided into compartments by the partitions consisting of internal xenophyae; along the abraided margin the compartments appear as open spaces filled with dark stercomata. (Fig. 2c).

Specimen from St. 204 (Figs 2d, 3a-g): The specimen broke into fragments during preparation (Fig.2d). The undamaged test formed a more or less flat structure with a relatively smooth, semi-circular outline, 31 mm wide and 24 mm high, originally attached to the host nodule by a short flattened stalk about 9 mm wide. The thickness varied from 3 mm at the basal part of the test to 2 mm close to margins. As in the holotype, the test surface is granular near the base, becoming more smooth towards the margin, and the xenophyae are small fragments of

radiolarian skeletons, sponge spicules and mineral grains (Fig. 3 a, b). The inner space of the test is divided into numerous small compartments, each measuring about 600 x 400 μm (Fig. 3c). These spaces are occupied by stercomare and granellare. The stercomare masses may be oval in shape and occupy one chamber (Fig.3d) or arranged in strings and extend between several compartments (Fig. 3e). The oval masses typically measure 400-500 μm long and ~200 μm wide (Figs. 3c-d). They consist of small stercomes with maximum dimensions of ~10-15 μm. The granellare branches are up to 150-200 μm wide and extend through several compartments (Fig. 3c, f). They contain numerous barite crystals (granellae), no more than 2 μm in length. (Fig. 3g, h).
Other material (Fig. 2e-f): Two more or less intact tests have differing morphologies. The specimen from St. 8655 was originally attached to a nodule. It measures 23 by 13 mm and consists of three well-developed plates, the angles between them varying from ~90° to ~170° (Fig. 2f). The test surface exhibits a clear concentric zonation and the internal compartments are clearly visible in places through the test wall. The specimen from St. 8726 is smaller, measuring 15 by 11 mm (Fig. 2g). The test is fan-like with a short (~2 mm), wide (~5 mm) stalk that was originally attached to the surface of a nodule. Concentric zones and internal compartments are visible chambers close to the margin. (Fig. 2g, h)..

Etymology From Latin “loculata”, meaning divided into small volumes.

Distribution Currently known from four sites in the Russian license area of the Clarion-Clipperton Fracture Zone, Eastern Pacific, depth 4,841-4,936 m (Table 1).

Remarks Psammina multiloculata differs from other species of the genus in the presence of an elaborate system of small internal compartments. In *Psammina zonaria* the test interior is also partitioned into compartments, but these spaces are relatively large and are delimited by transverse bars that occupy the entire width of the test, rather than the tiny cell-like spaces that characterise the new species. In both of these species, the internal structure of the test probably represents an elaboration of the pillars present in species such as *P. nummulina, P. globigerina, P. plankina.*

The basically plate-like test of *P. multiloculata* shows some variability, particularly regarding the degree of development of side plates. The shape is somewhat reminiscent of the foraminiferal genus *Jullienella,* particularly *J. foetida* Schlumberger, 1890 in which the test interior is partly subdivided by parallel ridges. However, these are not sufficiently developed to create internal compartments (Buchanan 1960; Nørvang 1961; Hayward and Gordon 1984). Moreover, *Julienella foetida* and *J. zealandica* are not xenophyophores, lacking the typical granellare and stercomare systems, and are confined to sublittoral and to upper bathyal depths.

Psammina limbata **sp.nov. Kamenskaya, Gooday, Tendal**

(Fig.4)

Psammina sp. Kamenskaya, Melnik, Gooday 2013: 391-392, Fig. 6 b

Material examined The holotype was from St. 25, R/V *Yuzhmorgeologia*, $13^0$28 N; $134^0$45 W, depth 4,724 m. The holotype is deposited under registration number F-18.

Etymology From Latin “limbata”, meaning bordered.

Diagnosis Flattened, plate-like semi-circular test attached to nodule surface by basal stalk and root-like structures. Outer layer of test composed of firmly cemented fragments of radiolarian skeletons, mineral grains and small sponge spicule fragments with weakly developed concentric zonation. Curved outer margin distinctly lighter than other parts of test. Interior friable with mass of stercomare and strings of granellare interwoven with loosely-agglutinated spicule fragments; stercomare absent from outer margin. Weaklydeveloped concentric ridges on inner surface of outer test layers.

Description of holotype The single collected specimen has a curved, approximately semi-circular, plate-like test that was attached to the surface of a nodule by a basal stalks and several long, branched, root-like structures (Fig. 4a, b). It is ~ 40 mm wide, ~31 mm high and ~1 mm thick. The external xenophyae that form the outer test layer consists of firmly cemented fragments of radiolarian skeletons, small mineral grains and small fragments of sponge spicules (Fig. 4c). A weakly-developed concentric zonation on the surface of the test presumably reflects episodic growth (Fig. 4b). A narrow zone around the outer margin comprise only transparent sponge spicule fragments and appears lighter than other parts of the test, Small concentric ridges are developed on the inner surface of the outer test layers (Fig. 4g), but they do not partition the interior space into compartments. (Fig. 4h). The interior of the test has a friable consistency and contains larger, loosely organised spicule fragments (Fig. 4d) between which are situated masses of stercomare, up to 300 x 600 μm in size and granellare branches, 50-100 μm diameter (Fig. 4e). The absence of dark stercomare from the marginal zone of the test is responsible for its ligher colour (Fig. 4 i). Stercomes range in size from 7 to 20 μm (Fig. 4e) and the granellae crystals are typically 3 μm long (Fig. 4f).

Etymology From Latin “limbata”, meaning bordered.

Distribution Species was found in the Russian license area of the Clarion-Clipperton Fracture Zone, Eastern Pacific, depth 4,724 (Table 1).

Remarks Psammina limbata sp. nov. resembles *P. multiloculata* in the general shape and composition of the test but is not divided intocompartments internally, and it has basal root-like structures that are not present in *P. multiloculata.* The new species resembles *P. zonaria* in the zonation of outer and inner surfaces of the outer test layers, but this zonation does not affect the test interior. The two species also have different test shapes as well as different kinds of xenophyae, namely planktonic foraminiferal shells in *P. zonaria* and siliceous particles in *P. limbata*.

The pale outer margin of the new species is a distinctive feature that, together with its plate-like form, makes it easily recognisable in bottom photographs from the CCFZ. Based on photographic surveys, it appears to be one of the most common species in this region.

Spiculammina delicata **Kamenskaya 2005**

(Fig.5, 6)

Spiculammina delicata Kamenskaya 2005: 23-27, Fig. 1-2
Spiculammina delicata Kamenskaya, Melnik, Gooday 2013: 391- 393, Fig. 6 c

Material examined A total of 19 specimens collected during R/V *Yuzhmorgeologia* cruise 4-06, Stns 25, 34, 39, 43, 49, 52, 85, 94, 95, 118, 119, 122, 133, 150, 151, 159, 164, 166, 167.

Remarks Spiculammina.delicata was described by Kamenskaya (2005) based on a single specimen from the central part of the Clarion-Clipperton Fracture Zone (11° 52' N, 136° 06' W). Our new material demonstrates the wide distribution of this species within the Russian CCFZ claim area (Table 1). The test varies from several mm to 5-6 cm in size and exhibits considerable morphological variation (Fig. 5). Some specimens have a relatively simple tubular form (Fig. 5d) but in most cases the test is tree-like with a basal trunk giving rise to variable numbers of branches that range from long and relatively slender to short and relatively wide. The test is composed almost exclusively of sponge spicule fragments (Fig. 6 a,b). Although in some respects it resembles members of the family Syringamminidae (e.g. the genus *Aschemonella*), Kamenskaya (2005) assigned *Spiculammina* to the family Psamminidae Haeckel, 1889, based on the presence of sparse xenophyae in the lumen of the tubular test. This placement is supported by examination of the new material, which has revealed that the test interior is occupied by numerous internal xenophyae, creating a rigid framework (Fig. 6c). Kamenskaya (2005) suspected that the original specimen, which was fragmented, had been attached to a hard substrate. The new specimens were all growing on polymetallic nodules, confirming the sessile nature of this species.

Spiculammina delicata is easily recognisable in bottom photographs. It was visible in 10% of the images from the Russian claim area and was collected in many box corer samples (Kamenskaya et al. 2013).

Distribution In the present study the species was found at 19 stations in the Russian license area of the Clarion-Clipperton Fracture Zone, Eastern Pacific, depth range 4,716-5,400 m. It was previously known from a single specimen obtained at 11.52^{0}N, 136.06^{0}W, depth 5,400 m (Kamenskaya, 2005).

Stannomid group of species:

***Stannophyllum radiolarium* Haeckel, 1889**

(Fig. 7)

Stannophyllum radiolarium Haeckel 1889: 65, pl. I, 2A-C; 9, 53, 61, 66, 68, 70
Stannophyllum radiolarium Schulze 1907a: 36, 41, 42, 49, 50, 52, 53, 54
Stannophyllum radiolarium Schulze 1907b: 160, 162
Stannophyllum radiolarium Schepotieff 1912: 277
Stannophyllum radiolarium Laubenfels 1948: 185
Stannophyllum radiolarium Tendal 1972: 13, 15, 44, 45, 54-55, 57, 61, 62, 69, 70, 74, 76, 77, 81, 85, 90, pl. 10F;
Stannophyllum radiolarium Tendal 1973: 26, 28-29
Stannophyllum radiolarium Tendal 1994: 91
Stannophyllum radiolarium Kamenskaya, Melnik, Gooday 2013:392, Fig.6a

Material examined R/V *Yuzhmorgeologia* cruise 4-08, St.8639, depth 4,750 m (specimen 1); R/V *Yuzhmorgeologia* cruise 4-06, St. 31, depth 4,785 m (specimen 2) (Table 1)

Remarks Both specimens were originally attached to nodules. Specimen 1 from St. 8639 (Fig. 7a) has a fan-like test, measuring 22 x 15 mm, with long and thin tubular processes developed at the base. Specimen 2 from St. 31 (Fig. 7b) has a more elongate, drop-like test measuring 32 x 25 mm. Both have a concentric surface zonation, more pronounced in the case of specimen 1. The colour is brownish and the consistency is soft. The xenophyae are

radiolarian tests (Fig. 7c). The linellae have a diameter of 1-2 μm and do not anastomose (Fig. 7d, e). The stercomare are sparsely developed but are sometimes visible as oval masses up to 200 μm in length (Fig. 7d). The granellare branches are up to 40 μm in diameter and the granellae crystals 1-3 μm long (Fig. 7f).

The features of these two tests are generally consistent with the description of *Stannophyllum radiolarium* given by Tendal (1972), which was based on a re-examination of the original *Challenger* material supplemented by two additional specimens collected during the *Galathea* Expedition and a *Vityaz* cruise. However, our specimens (particularly #1) have a clearly developed surface zonation, a feature not evident in the material examined by Tendal (1972). The *Challenger* and *Galathea* specimens were also whitish in colour compared to the brownish appearance of our material, although the *Vityaz* specimen is described as 'yellow-brown'.

Distribution Northern, eastern, western and central areas of the Pacific Ocean. Depth 3,570-5,515 m. In the present study it was recorded at two sites in the Russian license area of the Clarion-Clipperton Fracture Zone, Eastern Pacific, depth 4,750-4,785 (Table 1)

***Stannophyllum* sp.**

(Fig. 8)

Material examined Single specimen from R/V *Yuzhmorgeologia*, cruise 18-01, St. 197, depth 4,845 m.

Description The single specimen, originally attached to a nodule, was approximately semicircular in shape, resembling bracket fungus and measured approximately 6 by 3 cm (Fig. 8a). The width was about 1 mm near the outer margin, increasing towards the base. Unfortunately, the test was damaged during collection and lost much of its original morphology when placed in a Petri dish (Fig. 8b). The colour is brownish and the consistency is flexible. The xenophyae consists largely of complete and fragmentary radiolarian skeletons (Fig. 8c). The test interior is penetrated by numerous dichotomously branching granellare strands (Fig. 8d, e), about 20μm in diameter and full of granellae crystals about 2 μm in length (Fig. 8f, g). Stercomata are quite small (about 5 μm) and organized in oval masses of stercomare covered with organic sheath (Fig. 8h). Linellae are simple, not anastomosed, 2 μm in diameter and form a distinct layer (Fig. 8i).

Remarks Our specimen shares some characters with other *Stannophyllum* species (Tendal, 1972), although it differs in certain respects from all of them. It resembles *S. zonarium* in the type of xenophyae, but lacks the surface zonation of the test typical of this species. The test is soft and flexible as in *S. mollum,* but the linellae are simple rather than anastomosing. It has the same type of xenophyae (radiolarians) as *S. radiolarium*, but differs from this species in possessing a distinct layer of linellae. The closest match to a known species appears to be with *S. granularium.* The shape and consistence of the test are similar*,* but in contrast to *S. granularium*, the xenophyae consist almost entirely of radiolarians rather than a mixture of mineral grains and sponge spicules, with a varying proportion of radiolarians (Tendal, 1972).

Distribution Recorded at one site in the Russian license area of the Clarion-Clipperton Fracture Zone, Eastern Pacific, depth 4,845 m (Table 1).

Concluding remarks

Our relatively small collection of xenophyophores obtained at depths between 4,716 and 4, 936 m in the central part of the CCFZ (13-14^{0}N, 130-135^{0}W) reveals the occurrence of at least six species, three new and one poorly known species belonging to the order Psamminida and two species belonging to the order Stannomida. All of the specimens were found attached to polymetallic nodules. Previous studies have demonstrated that some xenophyophores are sessile on hard substrates, including rocks and plant material (Pearcey, 1914; Tendal 1975; Levin and Thomas 1988), as well as on and in soft sediments. Mullineaux (1987) reported the genera *Semipsammina, Stannoma, Stanophyllum* and *Syringammina* living on nodules from the central (30^{0}N, 157^{0}W) and equatorial (5^{0}N, 125^{0}W, North Pacific. Similarly, Vielette et al. (2007) found two xenophyophore-like organisms, one a fan-shaped morphotype and the other lacking agglutinated particles, in the western (9^{0}N, 150°W) and more central (14^{0}N, 130°W) parts of the CCFZ. We anticipate that additional undescribed species will be discovered in this part of the Pacific Ocean.

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Figure captions

Fig. 1. *Semipsammina licheniformis* sp. nov., Stn.60-1, cruise 4-06, holotype, registration number F-16; a,b,d light micrographs; c,e,f scanning electron micrographs.

a- Intact specimen on the surface of the host nodule
b- Fragment of the surface of the test
c- Surface of test showing xenophyae (mainly radiolarian skeletons)
d- Underside of outer test layer showing granellare branches and dark masses of stercomare
e- Granella (barite crystal) on the surface of a granellare branch
f- Strings of stercomare composed of stercomes

Scale bar: a 1 cm; b 1 mm; c 100 µm, d 1 mm; e 10 µm; f 30 µm

Fig. 2. *Psammina multiloculata* sp.nov.; light micrographs.

a- Holotype from Stn. 28, cruise 4-06, registration number F-17
b- Fragment of holotype
c- Fragment of holotype with base of secondary plate
d- Fragments of specimen from Stn. 204, cruise 18-01
e- Specimen from Stn. 8655, cruise 4-09, side view
f– Specimen from Stn. 8655, cruise 4-09, top view
g- Specimen from Stn.t.8726, cruise 4-09, side view
h- Specimen from Stn. 8726, cruise 4-09, margin of the test showing internal compartments.

Scale bar: a, e, g 10 mm, b 5 mm, c 1,5 mm

Fig. 3. *Psammina multiloculata* sp.nov., specimen from Stn.204, cruise 18-01; scanning electron micrographs.

a- Surface of the test
b- Detail of surface showing xenophyae (fragments of sponge spicules and radiolarians)
c- Test interior showing compartments
d- Oval stercomare mass within compartment
e- Stercomare strings (left) and granellare branch (right)
f- Granellare branch
g- Detail of granellare branch containing numerous granellae (barite crystals)
h- Single granella

Scale bar: a, c 1000 µm, b, d, f 100 µm, e 30 µm, g 10 µm, h 3 µm

Fig. 4. *Psammina limbata* sp.nov., Stn. 25, cruise 4-06, 4,724 m, holotype, registration number F-18.

, a- Intact test attached to host nodule.
b- Test detatched from nodule showing concentric zonation.
c- Surface of the test showing xenophyae.
d- Outer layer of test underlain by internal xenophyae (mainly sponge spicules), stercomare and granellare
e- Stercomare mass
f- Single granella (barite crystal)
g- Small ridge on underside of outer test layer

h- Weakly developed zonation on underside of outer test layer inside test
i- Margin of test consisting of sponge spicules
Scale bar: a, b 1 cm, g 1 mm, d, i-200µm, c, h- 100µm, e 20µm, f– 3 µm

Fig. 5. *Spiculammina delicata,* variation in test morphology of specimens attached to nodules (cruise 4-06).
a- Stn. 118
b- Stn. 166
c- Stn. 159
d- Stn. 43
e- Stn. 119
f- Stn. 164

Fig. 6. Test structure of *Spiculammina delicata,* from Stn. 25, cruise 4-06*;* scanning electron micrographs.
a - Surface of the test
b - Detail of test wall showing xenophyae (sponge spicules)
c - Test interior containing stercomare, granellare and xenophyae
d – Strings of stercomare between inner xenophyae
Scale bar: a 200 µm; b 100 µm; d 20 µm; c 10 µm

Fig. 7. *Stannophyllum radiolarium;* a,b, light micrographs; c - f, scanning electron micrographs.
a- Specimen from Stn. 8639; dimensions 22x15 mm
b- Specimen from Stn.31 attached to host nodule; dimensions 32x25 mm
c- Surface of the test showing xenophyae (radiolarians).
d- Linellae and stercomare mass
e- Detail of linellae
f- Granellare branch with granellae
Scale bar: c,d 100 µm; e, f, 10 µm

Fig. 8. *Stannophyllum* sp. from Stn 197, cruise 18-01; a,b, light micrographs; c - i, scanning electron micrographs.
a- Specimen as originally found in box core, attached to a nodule
b- Damaged fragment in Petri dish
c- Test surface showing xenophyae (radiolarians)
d, e- Test interior with granellare branches and internal xenophyae
f- Mass of granellae within granellare branch
g- Single granella (barite crystal)
h- Stercomare
i- Layer of linellae
Scale bar: b 1 cm; d 300 µm; c, e 100 µm; i-30 µm; h 10 µm; f, g 3 µm

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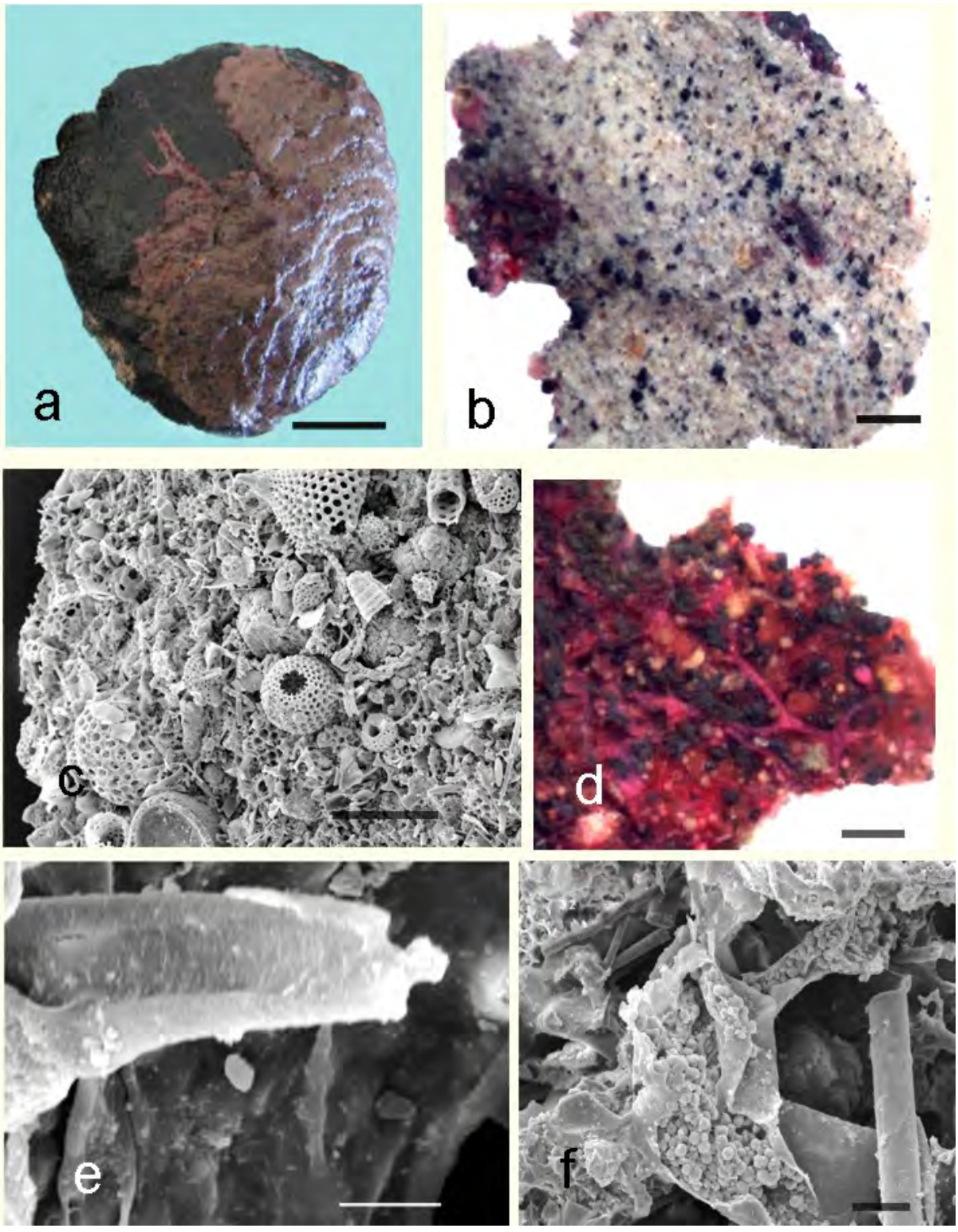

Fig. 1

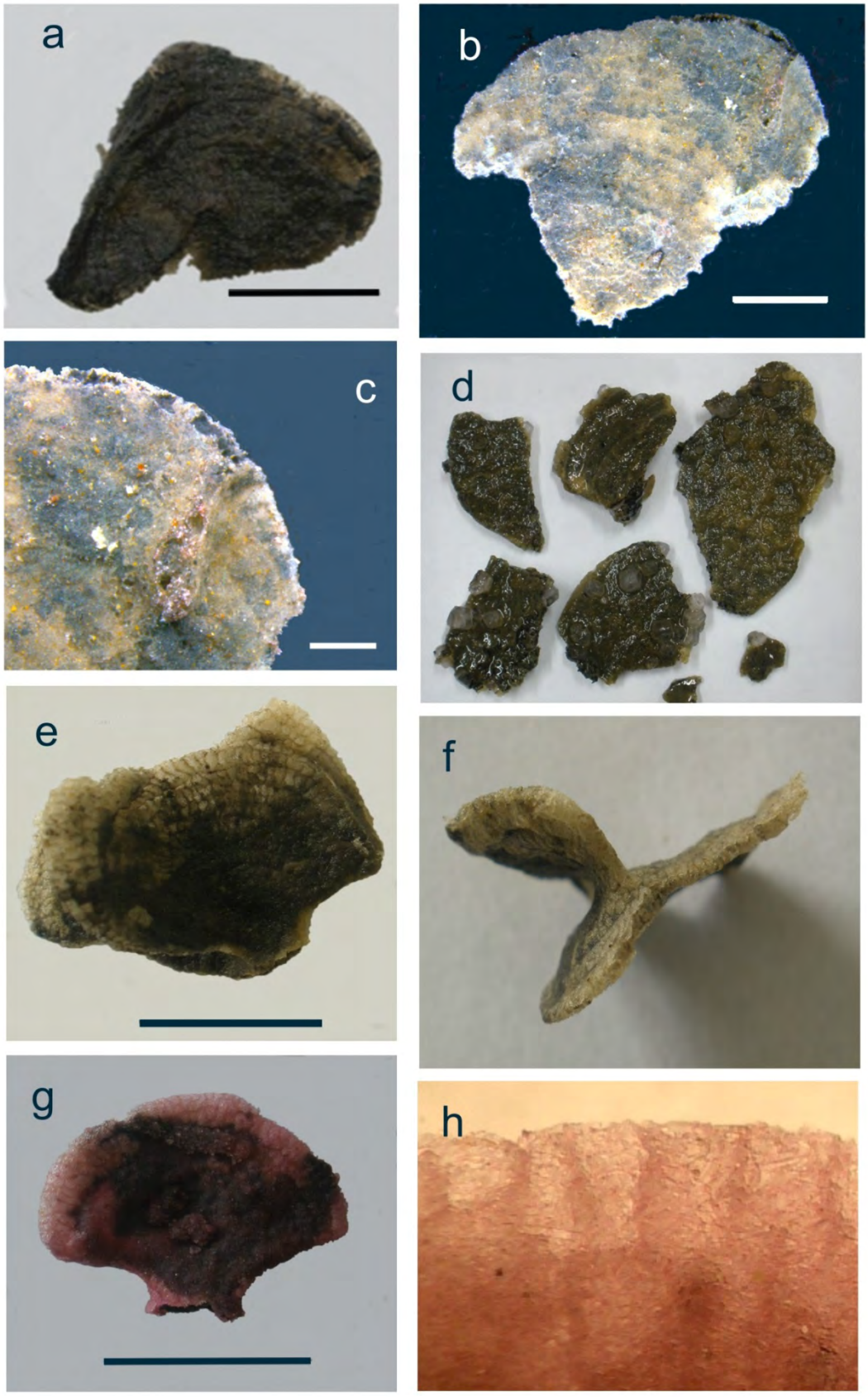

Fig. 2

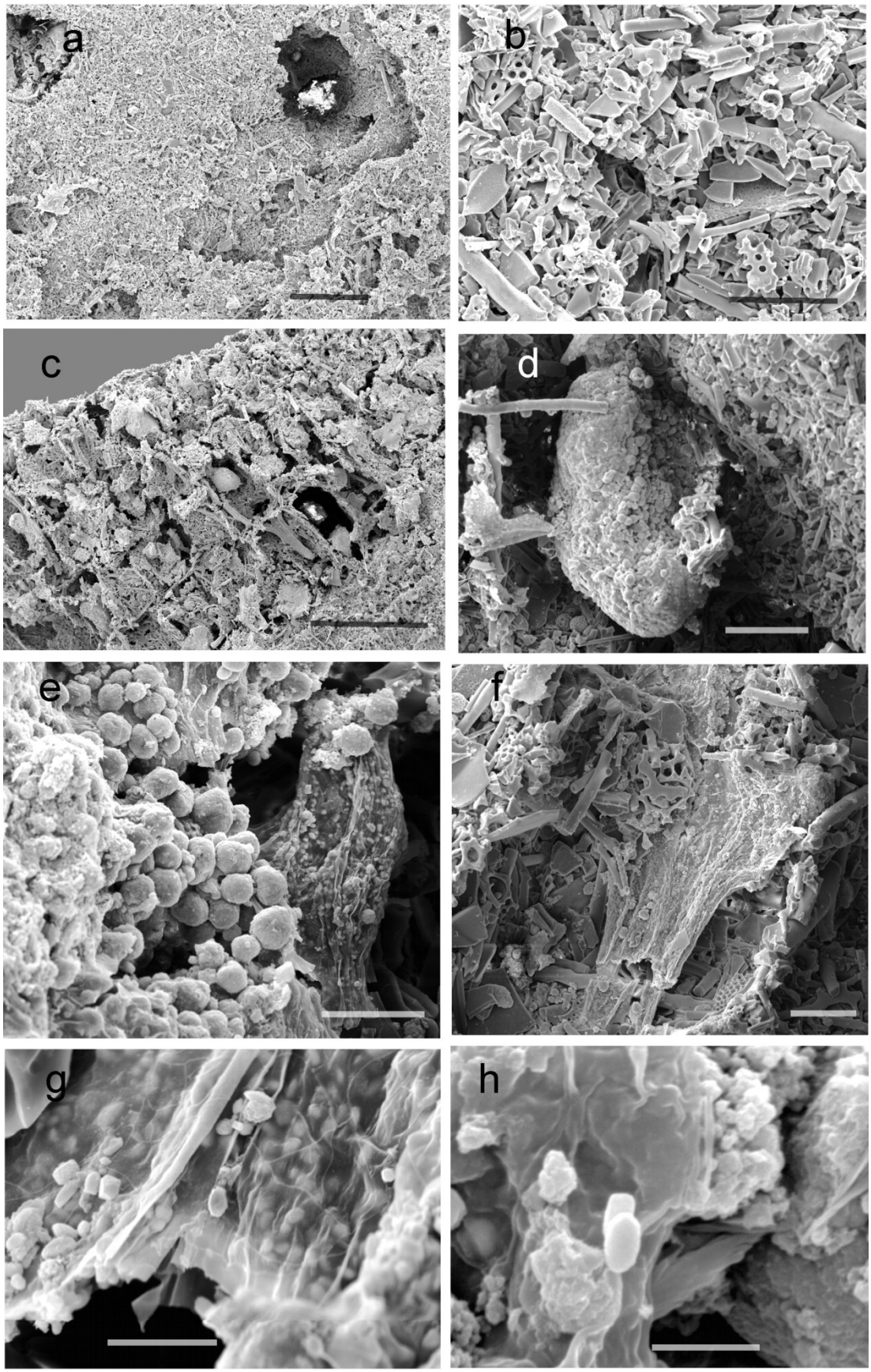

Fig. 3

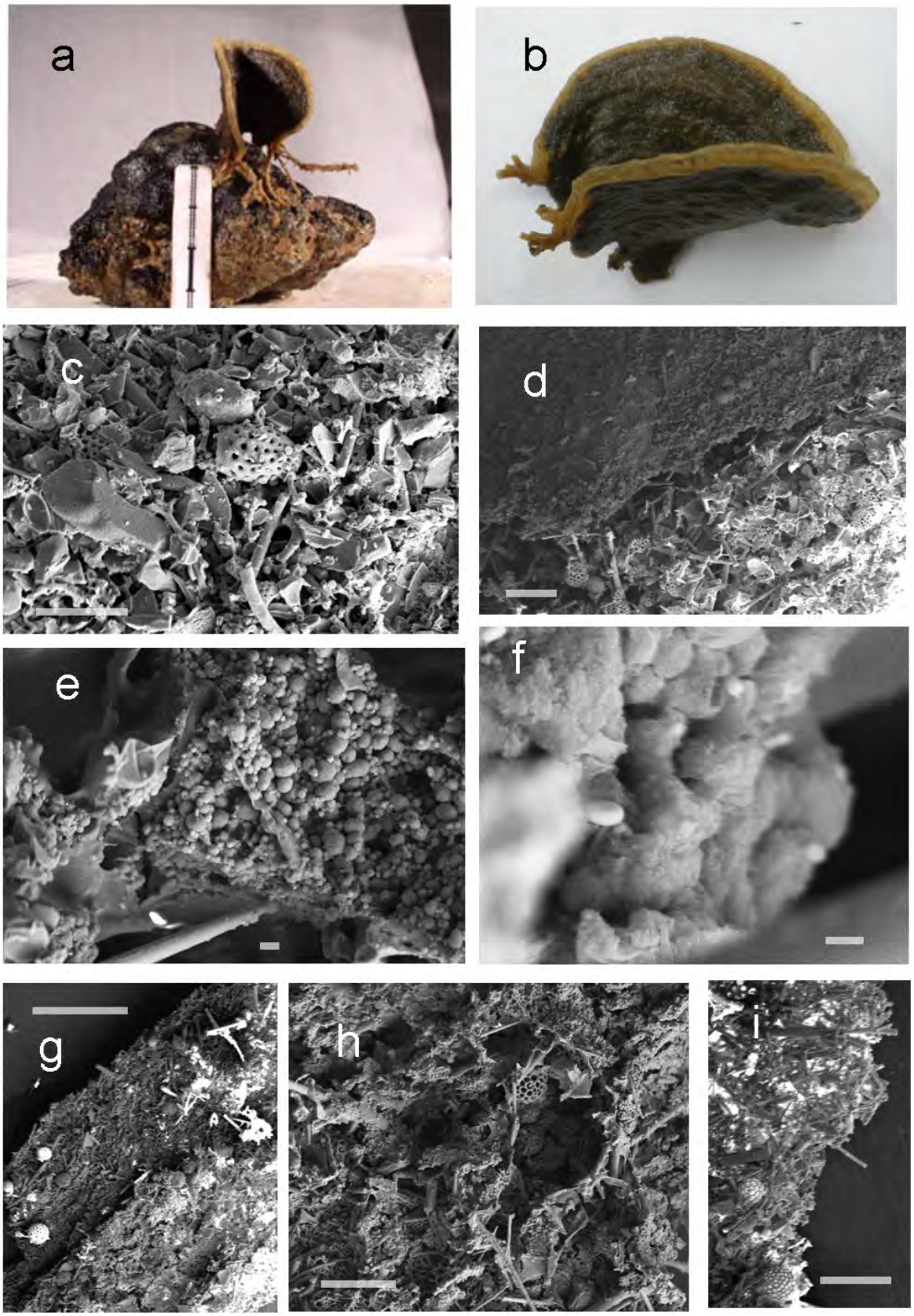

Fig. 4

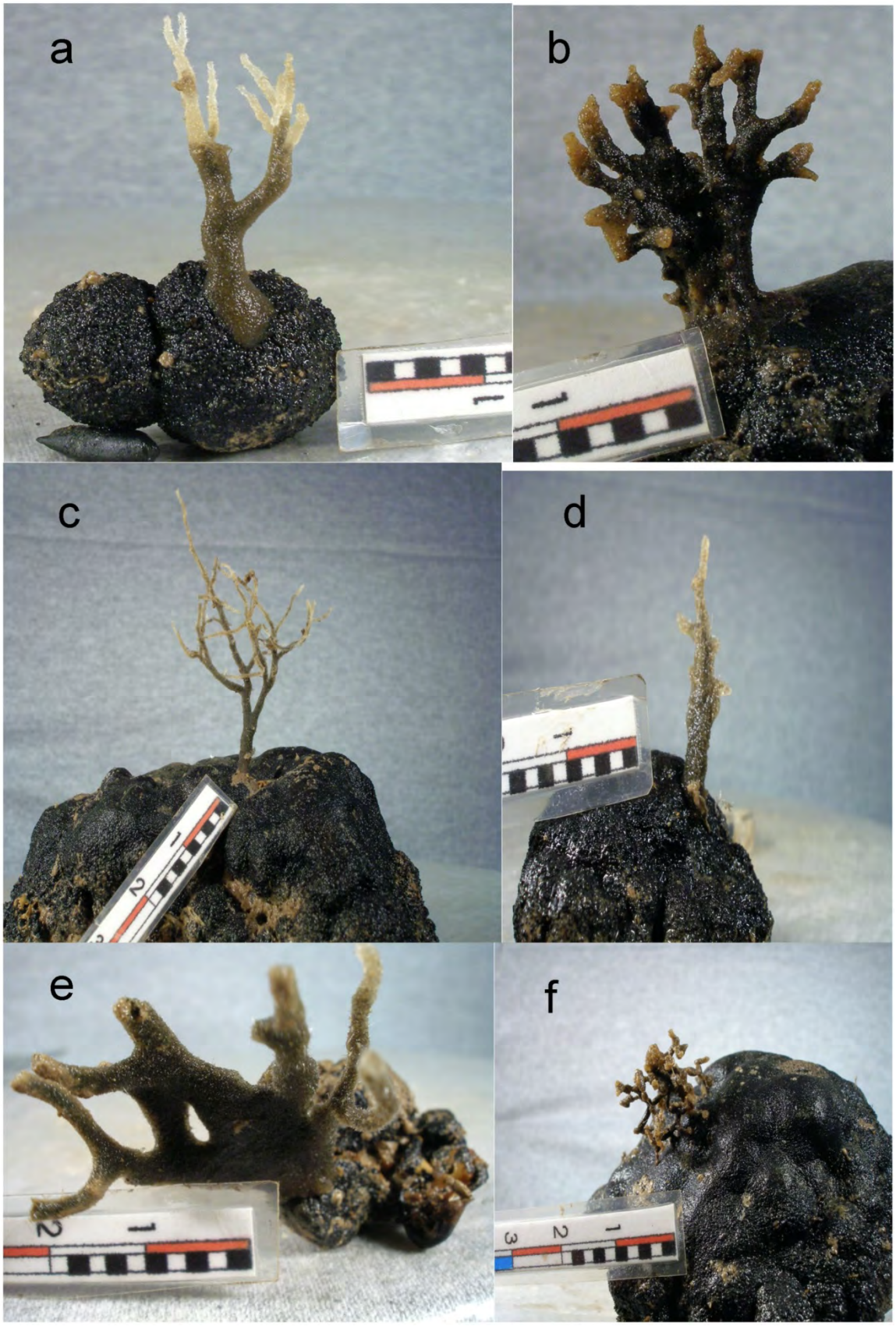

Fig.5

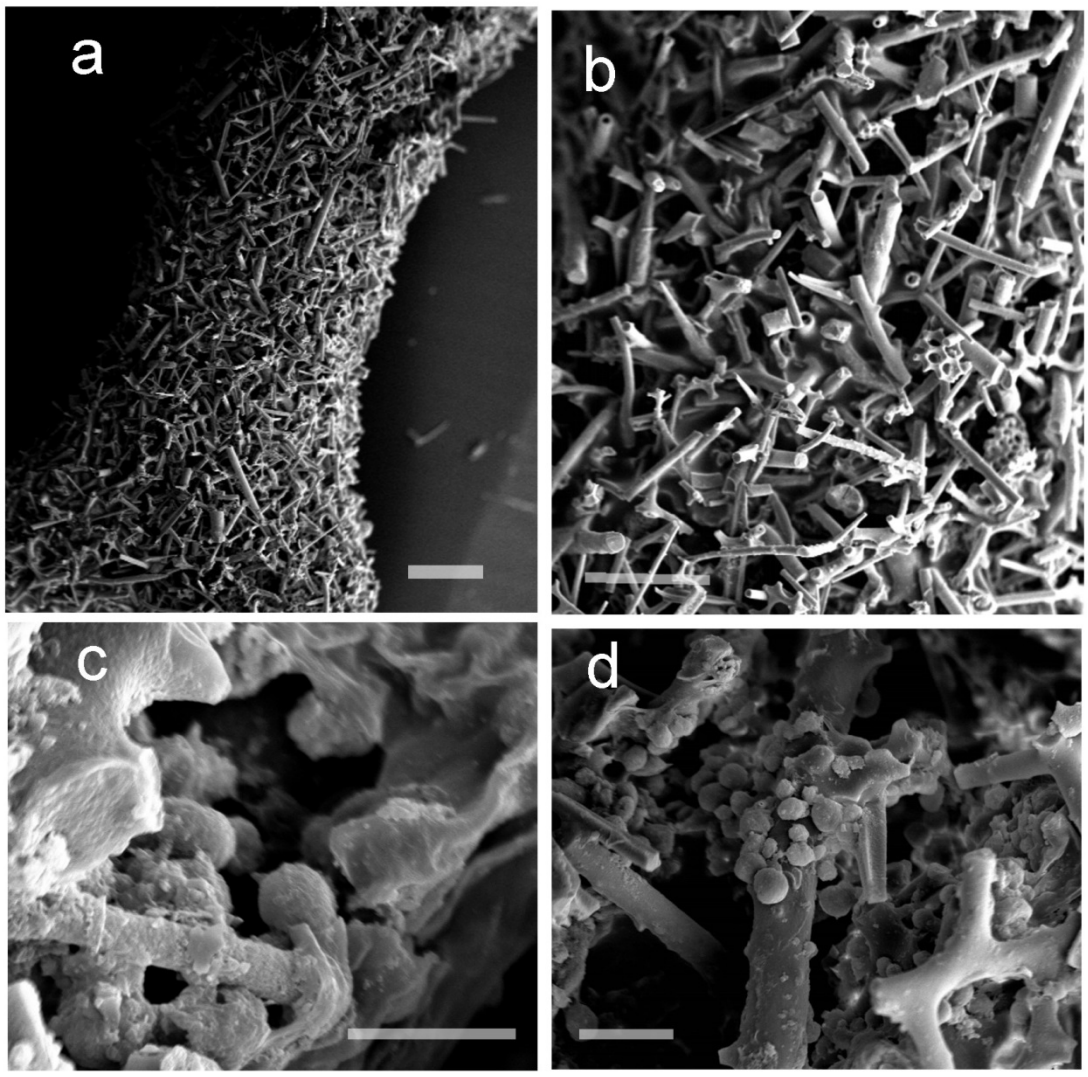

Fig. 6

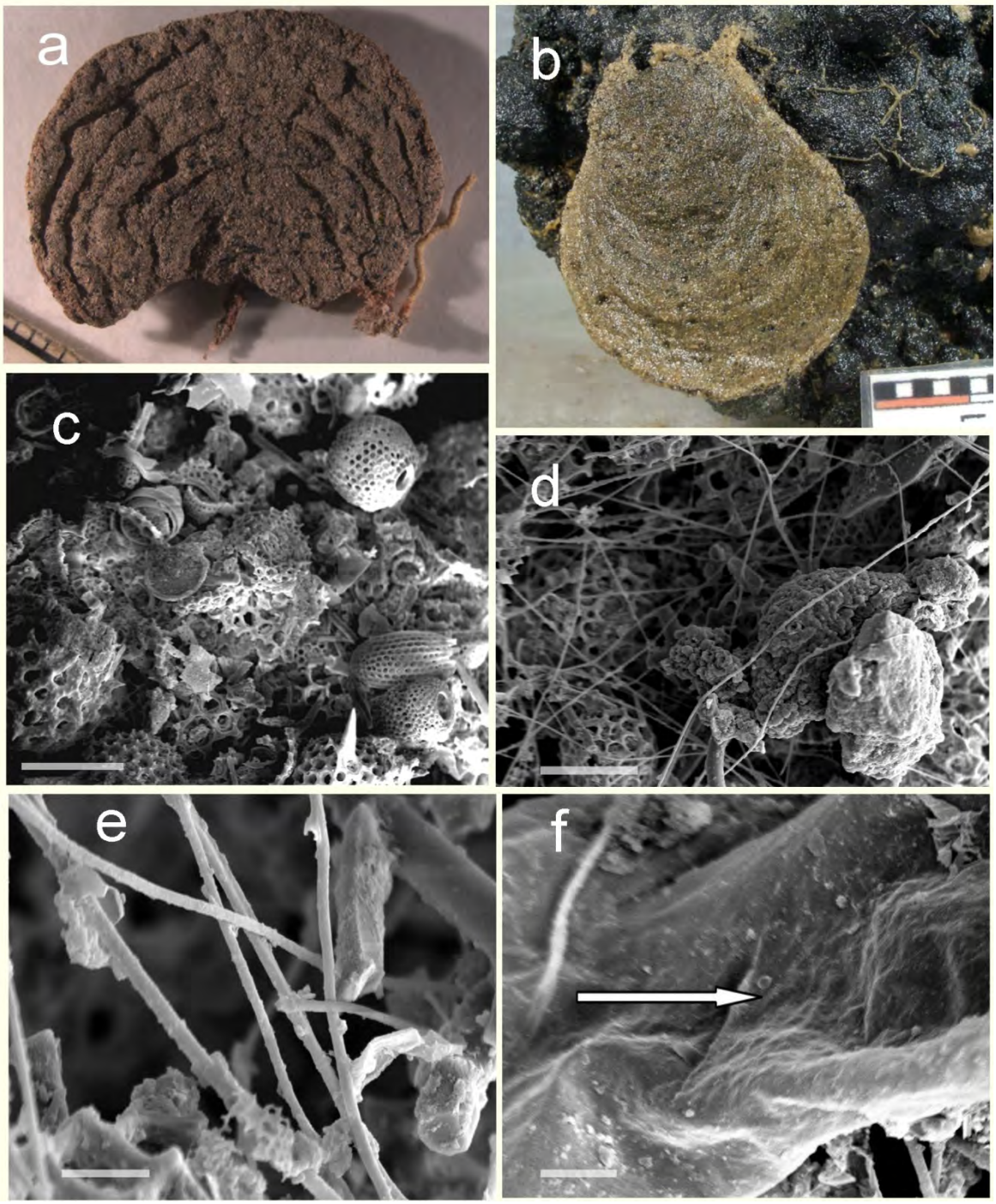

Fig. 7

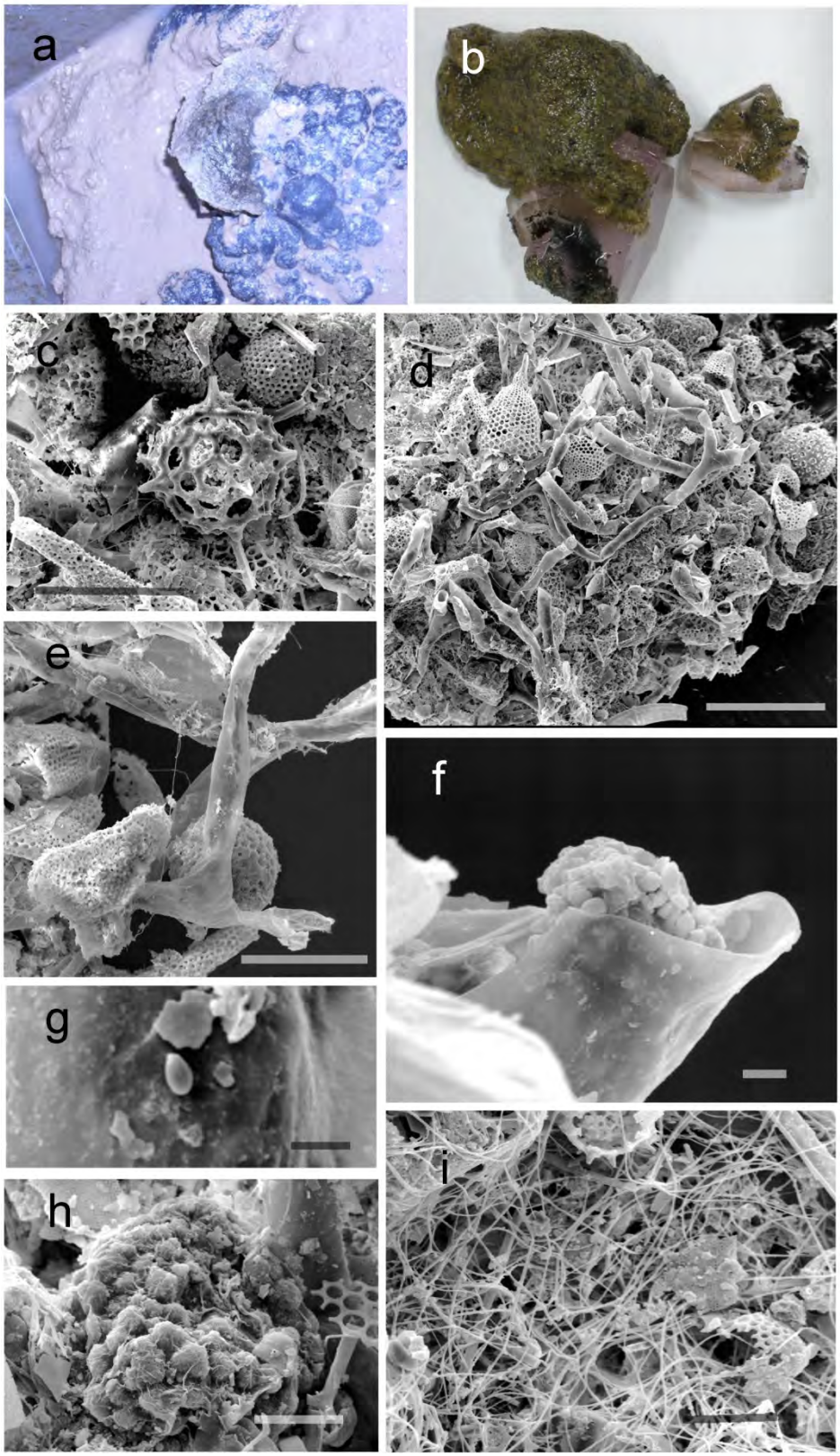

Fig. 8

Table 1. List of stations from cruises of R/V *Yuzhmorgeologiya* with xenophyophores from the Clarion-Clipperton nodule field.

Station N	Cruise	Year	Coordinates N, W	Depth m	Species
25	4-06	2006	$13,28^0$ $134,45^0$	4724	*Psammina limbata, Spiculammina delicata*
28	4-06	2006	$13,29^0$ $134,41^0$	4843	*Psamina multiloculata*
31	4-06	2006	$13,31^0$ $134,41^0$	4785	*Stannophyllum radiolarium*
34	4-06	2006	$13,31^0$ $134,32^0$	4742	*Spiculammina delicata*
39	4-06	2006	$13,26^0$ $134,47^0$	4716	*Spiculammina delicata*
43	4-06	2006	$13,28^0$ $134,42^0$	4753	*Spiculammina delicata*
49	4-06	2006	$13,29^0$ $134,34^0$	4755	*Spiculammina delicata*
52	4-06	2006	$13,24^0$ $134,53^0$	4787	*Spiculammina delicata*
60-1	4-06	2006	$13,26^0$ $134,42^0$	4777	*Semipsammina licheniformis*
85	4-06	2006	$13,27^0$ $134,32^0$	4820	*Spiculammina delicata*
94	4-06	2006	$13,23^0$ $134,44^0$	4772	*Spiculammina delicata*
95	4-06	2006	$13,23^0$ $134,43^0$	4786	*Spiculammina delicata*
118	4-06	2006	$13,24^0$ $134,34^0$	4778	*Spiculammina delicata*
119	4-06	2006	$13,24^0$ $134,33^0$	4825	*Spiculammina delicata*
122	4-06	2006	$13,19^0$ $134,51^0$	4820	*Spiculammina delicata*
133	4-06	2006	$13,22^0$ $134,37^0$	4788	*Spiculammina delicata*
150	4-06	2006	$13,27^0$ $134,43^0$	4778	*Spiculammina delicata*
151	4-06	2006	$13,27^0$ $134,43^0$	4776	*Spiculammina delicata*
159	4-06	2006	$13,26^0$ $134,45^0$	4755	*Spiculammina delicata*
164	4-06	2006	$13,26^0$ $134,43^0$	4769	*Spiculammina delicata*
166	4-06	2006	$13,26^0$ $134,42^0$	4777	*Spiculammina delicata*
167	4-06	2006	$13,26^0$ $134,42^0$	4789	*Spiculammina delicata*
197	18-01	2003	$13,55^0$ $129,02^0$	4845	*Stannophyllim sp.*
204	18-01	2003	$13,90^0$ $129,14^0$	4896	*Psammina multiloculata*
8639	4-08	2009	$12,77^0$ $133,41^0$	4750	*Stannophyllum radiolarium*
8655	4-09	2010	$12,72^0$ $133,59^0$	4841	*Psammina multiloculata*
8726	4-09	2010	$13,54^0$ $133,42^0$	4936	*Psammina multiloculata*

Abstract We describe three new and one poorly-known species of psamminid xenophyophores (giant foraminifera), all of which were found attached to polymetallic nodules in the Russian claim area of the Clarion-Clipperton Fracture Zone (CCFZ); abyssal eastern equatorial Pacific, 4,716–4,936 m water depth). *Semipsammina licheniformis* sp. nov. is the second species of the genus to be formally described. The test encrusts the surface of the host nodule forming a flat structure with a rounded outline and rather irregular concentric zonation. The wall comprises a single layer, composed mainly of radiolarian skeletons, covering granellare branches and
stercomata strings that lie directly adjacent to the nodule surface. *Psammina multiloculata* sp. nov. has an approximately semi-circular, upright test with a weak concentric zonation that is attached to the nodule by a short stalk. The outer test layer comprises radiolarian fragments, sponge spicules, and mineral grains; the interior is divided into small compartments
containing the stercomare and granellare. *Psammina limbata* sp. nov. has a plate-like, sometimes curved, semi-circular test attached to the nodule surface by basal root-like structures. The composition of the test is similar to that of *P. multiloculata*, but the interior is not compartmentalised. The most distinctive feature is the lighter colour of the curved outer margin compared to other parts of test. With the addition of these and other species described during recent decades, *Psammina* has become a rather unwieldy taxon that requires revision. *Spiculammina delicata* Kamenskaya 2005, previously known from a single specimen, is the most abundant species in our collection. The test exhibits considerable morphological
variation, particularly in terms of the degree of branching. The new specimens confirm the placement of this species in the family Psamminidae rather than the Syringamminidae, which it superficially resembles, as well as its sessile mode of life. Two additional species in our material,
Stannophyllum radiolarium Haeckel, 1889 and *Stannophyllum* sp., belong to the order Stannomida. Like the psamminid species, both were found attached to nodules. Xenophyophores are a dominant megafaunal taxon within the CCFZ. Although limited, our new material suggests that this region hosts many novel taxa.

Keywords Protista . Xenophyophores . Megabenthos .
Polymetallic nodules . Eastern equatorial Pacific . Abyssal