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

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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, 4716 - 4936 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		

	CCFZ. Although limited, our new material suggests that this region hosts many novel taxa.		
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	21	nodules in the Russian claim area of the Clarion-Clipperton Fracture Zone (CCFZ; abyssal			
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45 46	26	covering granellare branches and stercomata strings that lie directly adjacent to the nodule			
47 48	27	surface. Psammina multiloculata sp. nov. has an approximately semi-circular, upright test			
49 50	28	with a weak concentric zonation that is attached to the nodule by a short stalk. The outer test			
51 52	29	layer comprises radiolarian fragments, sponge spicules and mineral grains; the interior is			
53	30	divided into small compartments containing the stercomare and granellare. Psammina			
54 55	31	limbata sp.nov. has a plate-like, sometimes curved, semi-circular test attached to the nodule			
56 57	32	surface by basal root-like structures. The composition of the test is similar to that of <i>P</i> .			
58 59 60 61	33	multiloculata but the interior is not compartmentalised. The most distinctive feature is the			
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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.

Key words. Protista, xenophyophores, megabenthos. polymetallic nodules, eastern equatorial Pacific, abyssal

51 Introduction

Xenophyophores are giant marine, agglutinated deep-sea protists (Tendal, 1972) 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 protistan group (Tendal, 1972). However, recent molecular analyses place at least some species within the radiation of basal monothalamous foraminifera ('monothalamids') (Pawlowski et al., 2003, 2013; 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 Lewis 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 1600 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, 2001). Therefore, in the areas where these giant protists dominate, they probably play an important role in the 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 the xenophyophore fauna attached to nodules from the 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 cm²) from different parts of the Russian claim area of the Clarion-Clipperton nodule field (13-14°N, 130-135°W) 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 energydispersive X-ray spectrographic analyzer (EDS) connected to a scanning electron microscope
(CamScan and Zeiss EV050). The holotypes are deposited in the collection of the Zoological
Museum of the Moscow State University.

109 Systematics

Recent molecular analyses place several xenophyophore species within the radiation of
'basal'' 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.

Psamminid group of species:

Semipsammina licheniformis sp. nov. Kamenskaya. Gooday, Tendal Fig. 1 a-f Semipsammina sp. Kamenskaya, Melnik, Gooday 2013: 391-392, Fig. 6d Material examined. The holotype was from St. 60-1 of R/V Yuzhmorgeologia cruise 4-06, 13.26° N, 134.41° W; depth 4777 m. The holotype is deposited under registration number F16

⁴⁷ 128 **Diagnosis.** Encrusting test covering part of nodule surface. Outline more or less rounded with
⁴⁹ 129 irregular margin that includes occasional elongate extensions. Test surface with concentric
⁵¹ 130 pattern of linear, step-like features. Maximum test dimension up to ~ 6 cm; thickness
⁵² 131 decreasing from ~3 mm in central part to ~1 mm near margin. Agglutinated test wall
⁵⁴ 132 composed of radiolarian skeletons with occasional diatom frustules and sponge spicule
⁵⁶ fragments; test wall covers interior space that contains strings of granellare and stercomare
⁵⁸ 134 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. 1 a). The thickness in the central part is about 3 mm, decreasing to 1 mm near the margins. The surface of the test 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 lobate features. 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 forms an upper layer that covers the granellare and stercomare. The xenophyae (agglutinated particles) comprise a jumble of complete and fragmentary radiolarian skeletons, with scattered micronodules and occasional diatom frustules and small fragments of sponge spicules, creating a fairly rough surface texture (Figs. 1 b, 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. 1 d). The granellare are light in colour and form strands, 50 to 100 µm in diameter, which branch but do not anastomose (Fig.1 d). The strands contain numerous granellae, $3-4 \mu m$ in length with the ovate shape typical of xenophyophore barite crystals (Fig.1 e). The stercomare masses form branching structures, ranging from less than 50 µm to more than 100 μ m in diameter, containing stercomata with a diameter <10 μ m (Fig. 1).

Etymology. From Latin and English "lichen"

Distribution. Currently know 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 Tendal511641975, is known from two specimens and some fragments attached to turtle grass rhizomes52165from the Puerto Rico Trench (depth 6000-5890 m). The plate-like body of S. fixa is54166irregularly rounded in outline, up to 5.5 mm in diameter and ~ 0.5 mm in thickness. The56167xenophyae comprise sponge spicules and mineral particles. Our new species differs from S.58168fixa mainly in the much larger size of the test and the nature of the xenophyae. There also60169appear 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; 4500 m depth) and the central North Pacific (30°N, 157°W; 5800 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 cemented xenophyae forming hard, upper and lower plates, 3) internal xenophyae forming pillar-like structures between the two plates, and 4) granellare branches and stercomare strings strongly developed between the pillars. Gooday and Tendal (1988) added three further species, P. delicata, P. fusca, and P. sabulosa, These conform 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) redescribed 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 of R/V *Yuzhmorgeologia* cruise 4-06, 13.28^o N, 134.41^oW; depth 4843 m. The holotype is 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 strings of granellare and stercomare.

Description. Holotype (Fig. 2 a-c): The test is flat, plate-like, and was attached to a nodule by its longest side without the development of a stalk. The dimension of the intact specimen is 24x18 mm but the test was broken into several fragments during preparation. One of these 18 214 fragments includes the base of a side plate (Fig. 2 c). The surface of the test is noticeably granular at the base and shows concentric zones, which are most clearly visible near the 20 215 outer margin (Fig. 2 a, 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 internal xenophyae; along the abraided margin the compartments appear as open spaces filled with dark stercomata (Fig. 2 c). 29 220 Specimen from St. 204 (Figs 2 d, 3 a-g): The specimen broke into fragments during 31 221 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 42 227 inner space of the test is divided into numerous small compartments, each measuring about 600 x 400 µm (Fig. 3 c). These spaces are occupied by granellare and stercomare. The

granellare branches are up to 50-100 µm wide and extend through several compartments (Fig.

3 c, f). They contain numerous barite crystals (granellae), no more than 2 µm in length. (Fig. 3 g, h). The stercomare masses may be oval in shape and occupy one chamber (Fig.3-d), or 51 232 arranged in strings and extend between several compartments The oval masses are typically 53 233 400-500 µm long and ~200 µm wide (Figs.3 c-d). They consist of stercomata with maximum 55 234 dimensions of ~10-15 µm.

Other material (Fig 2 e-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 $\sim 90^{\circ}$ to $\sim 170^{\circ}$ (Fig. 2 f). 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. 2 g). 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 close to the margin (Fig. 2 g, h)..

Etymology: From Latin "loculata"-divided into small volumes.

Distribution: Currently know from four sites in the Russian license area of the Clarion-Clipperton Fracture Zone, Eastern Pacific, depth 4841-4936 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, and 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 and J. zealandica Hayward and Gordon, 1984, 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, Jullienella foetida and J. *zealandica* are not xenophyophores. lacking the typical granellare and stercomare systems, and are confined to sublittoral to upper bathyal depths.

Psammina limbata sp.nov. Kamenskaya, Gooday, Tendal

(Fig.4 a-i)

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

Etymology. From Latin "limbata"- 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 sponge spicule fragments with weakly developed concentric zonation. Curved outer margin distinctly lighter than other parts of test. Interior friable with strings of granellare and masses of stercomare interwoven with looselyagglutinated spicule fragments; stercomare absent from outer margin. Weakly-developed 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 stalk and several long, branched, root-like structures (Fig.4 a, b). It is ~ 40 mm wide, ~31 mm high and ~1 mm thick. The external xenophyae that form the outer test layer comprise firmly cemented fragments of radiolarian skeletons, small mineral grains and small fragments of sponge spicules (Fig. 4 c). A weakly-developed concentric zonation on the surface of the test presumably reflects episodic growth (Fig. 4 b). A narrow zone around the outer margin comprises 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. 4 g), but they do not partition the interior space into compartments. (Fig. 4 h). The interior of the test has a friable consistency and contains larger, loosely organized spicule fragments between which are situated granellare branches, 50-100 µm diameter and masses of stercomare, up to 300 x 600 µm in size (Fig. 4 d). The absence of the dark stercomare from the marginal zone of the test is responsible for its lighter colour (Fig. 4 i). Stercomata range in size from 7 to 20 µm (Fig. 4 e) and the granellae crystals are typically 3 µm long (Fig. 4 f).

Etymology. From Latin "limbata"- bordered.

Distribution. Currently know from one site in the Russian license area of the Clarion-Clipperton Fracture Zone, Eastern Pacific, depth 4724 m (Table 1).

Remarks. *Psammina limbata* sp. nov. resembles *P. multiloculata* in the general shape and composition of the test but is not divided into compartments 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 more 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 (11.52⁰ N, 136.06⁰ 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. 5 d) 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 (Figs 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, this species was found at 19 sites in the Russian license area of the Clarion-Clipperton Fracture Zone, Eastern Pacific, depth range 4716-4824 m (Table 1). It was previously known from a single specimen obtained at 11. 52^oN, 136. 06^oW, 5400 m depth (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
- 357 Stannophyllum radiolarium Schulze 1907a: 36, 41, 42, 49, 50, 52, 53, 54
- 358 Stannophyllum radiolarium Schulze 1907b: 160, 162
- 359 Stannophyllum radiolarium Laubenfels 1948: 185
- 360 Stannophyllum radiolarium Tendal 1972: 13, 15, 44, 45, 54-55, 57, 61, 62, 69, 70, 74, 76, 77,
 - 61 81, 85, 90, pl. 10F;
- 362 Stannophyllum radiolarium Tendal 1973: 26, 28-29
- 363 Stannophyllum radiolarium Tendal 1994: 91
- 364 Stannophyllum radiolarium Kamenskaya, Melnik, Gooday 2013:392, Fig.6a

Material examined. R/V *Yuzhmorgeologia* cruise 4-08, St.8639, depth 4750 m (specimen 1);
R/V *Yuzhmorgeologia* cruise 4-06, St. 31, depth 4785 m (specimen 2).

Remarks. Both specimens were originally attached to nodules. Specimen 1 from St. 8639
370 (Fig. 7 a) has a fan-like test, measuring 22 x 15 mm, with long and thin tubular processes
371 developed at the base. Specimen 2 from St. 31 (Fig.7 b) 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. 7 c). The linellae have a diameter of 1-2 μ m and do not anastomose (Fig. 7 d, e). The granellare branches are up to 40 μ m in diameter and the granellae crystals 1-3 μ m long. The stercomare are sparsely developed but are sometimes visible as oval masses up to 200 μ m in length (Fig. 7 d).

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 3570-5515 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 4750-4785 m (Table 1).

Stannophyllum sp. Fig. 8 **Material examined:** Single specimen from R/V *Yuzhmorgeologia* cruise 18-01, St. 197, depth 4845 m.

397 Description. The single specimen, originally attached to a nodule, was approximately
398 semicircular in shape, resembling bracket fungus and measured approximately 6 by 3 cm
399 (Fig. 8 a). The width was about 1 mm near the outer margin, increasing towards the base.
400 Unfortunately, the test was damaged during collection and lost much of its original
401 morphology when placed in a Petri dish (Fig. 8 b). The colour is brownish and the
402 consistency is flexible. The xenophyae consists largely of complete and fragmentary
403 radiolarian skeletons (Fig. 8 c). The test interior is penetrated by numerous dichotomously
404 branching granellare strands (Fig. 8 d, e), about 20µm in diameter and full of granellae

crystals about 2 µm in length (Fig. 8 f, g). Stercomata are quite small (about 5 µm) and organized in oval masses of stercomare covered with organic sheath (Fig. 8 h). Linellae are simple, not anastomosed, 2 µm in diameter and form a distinct layer. **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 10 410 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 4845 m (Table 1).

Concluding remarks

Our relatively small collection of xenophyophores, obtained at depths between 4716 and 4936 m in the central part of the CCFZ (13-14°N, 130-135°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 44 428 sessile on hard substrates, including rocks and plant material (Pearcey, 1914; Tendal 1975; 46 429 Levin and Thomas 1988), as well as on and in soft sediments. Mullineaux (1987) reported the genera Semipsammina, Stannoma, Stannophyllum and Syringammina living on nodules from the central (30°N, 157°W) and equatorial (5°N, 125°W) North Pacific. Similarly, Veillette et al. (2007) found two xenophyophore-like organisms, one a fan-shaped morphotype and the other lacking agglutinated particles, on nodules from the western (9°N, 55 434 150°W) and more central (14°N, 130°W) parts of the CCFZ. Our new material confirms that where nodules are present, they represent an important habitat for these large testate protists,

which constitute a major element of the megafauna in the CCFZ. We anticipate thatadditional undescribed species will be discovered in this part of the Pacific Ocean.

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References

Brady HB (1883) *Syringammina*, a new type of arenaceous Rhizopoda, Proc. R. Soc. Lond. 35: 155–161

Buchanan JB (1960) On *Jullienella* and *Schizammina*, two genera of arenaceous foraminifera
from the tropical Atlantic, with a description of a new species. J. Linn. Soc. London. Zool.
44: 270-277

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

Gooday AJ, Tendal OS (1988) New xenophyophores (Protista) from the bathyal and abyssal
 north-east Atlantic Ocean. J. Nat. Hist. 22: 413-434

Haeckel E (1889) Report on the deep-sea Keratosa collected by H.M.S. Challenger during the
years 1873-76. Report of the Scientific Results of the Voyage of H.M.S. Challenger during
the years 1873-76, Zoology 82:2

467 Hayward BW, Gordon DP (1984) A new species of the agglutinating foraminifer *Julienella*468 (Schizamminidae) from New Zealand. J. Foram, Res. 14: 111-114

Hughes JA, Gooday AJ (2001) Association between living benthic foraminifera and dead tests of Syringammina fragilissima (Xenophyophorea) in the Darvin Mounds region (NE Atlantic). Deep-Sea Res I 51:1741-1758 Kamenskaya OE (2005) Spiculammina delicata gen. et sp. n., a new xenophyophore from the eastern Pacific (Psamminidae). Invertebr. Zool. 2, 1: 23-27 Kamenskaya, OE, Saidova KhM (1998) Redescription of Psammina planata (Saidova, 1970), a hadal xenophyophore from the Kurile-Kamchatka Trench. In: A.P. Kuznetsov and O.N. Zezina (eds.) Benthos of the High Latitude Regions. Moscow.:137 Kamenskaya OE, Melnik VF, Gooday AJ (2013) Giant protists (xenophyophores and komokiaceans) from the Clarion-Clipperton ferromanganese nodule field (Eastern Pacific). Biology Bulletin Reviews 3, 5: 388-398 Laubenfels MV (1948) The order Keratosa of the phylum Porifera - a monographic study. - Occ. Pap. Allan Hancock Fdn. 3: 1-217. Lecroq B, Gooday AJ, Tsuchiya M, Pawlowski J (2009) A new genus of xenophyophores (Foraminifera) from the Japan Trench: morphological description, molecular phylogeny and elemental analysis. J. Linn. Soc. London. Zool. 156: 455-464. Levin LA (1994) Paleoecology and ecology of xenophyophores. Palaios. 5: 32-41. Levin LA, Thomas CL (1988) The ecology of the xenophyophores (Protista) on eastern Pacific seamounts. Deep-Sea Res 35, 12: 2003–2027. Levin LA, DeMaster DJ, McCann LD, Thomas CL (1986) Effects of giant protozoans (class: Xenophyophorea) on deep seamount benthos, Mar. Ecol. Prog. Ser. 29: 99-104 Mullineaux LS (1987) Organisms living on manganese nodules and crusts: Distribution and abundance at three North Pacific sites. Deep-Sea Res 34: 165-184

502

201, Pls I - IX

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504 505 Pawlowski J, Holzmann M, Fahrni J, Richardson SL (2003) Small subunit ribosomal DNA 506 suggest that xenophyophorean Syringammina corbicula is a foraminiferan. J. Eukaryotic 9 507 Microbiol. 50: 483-487 11 508 13 509 Pawlowski J, Holzmann M, Tyszka J (2013) New supraordinal classification of 510 Foraminifera: Molecules meet morphology. Marine Micropaleontology 100: 1-10 511 18 512 Pearcey FG (1914) Foraminifera of the Scottish Antarctic Expedition. . Transactions of the Royal Society of Edinburgh 49: 991 - 1044. 20 513 22 514 $\frac{10}{24}$ 515 Saidova KhM (1970) Benthic foraminifers in the Kurile-Kamhatka Region based on the data of the 39th cruise of the R/V Vityaz. Trudy Instituta Okeanologii 86: 134-161 516 ²⁷ 517 29 518 Schlumberger C (1890) Note sur un foraminifere nouveau de la côte occidentale d'Afrique. 31 519 Mémoires de la Société zoologique de la France 3: 211-213 33 520 521 Schulze FE (1907a) Die Xenophyophoren, eine besondere Gruppe der Rhizopoden. -Wiss. 522 Ergebn. dt. Tiefsee-Exped. Valdivia 11: 1- 55 523 40 524 Schulze FE (1907b) Die Xenophyophoren. Bull. Mus. comp. Zool. Harv. 51: 143-162 42 525 44 526 Tendal OS (1972) A monograph of the Xenophyophoria (Rhizopoda, Protozoa). Galathea 46 527 Report 12: 7-99. 528 ⁴⁹ 529 Tendal OS (1975) A new xenophyophore, living on solid substratum, and its significance. 51 530 Deep-Sea Res 22: 45-48. 53 531 55 532 Tendal OS (1973) Xenophyophoria (Protozoa, Rhizopoda) from the collections of the R/V "Vitiaz". Zoologichesky Zhurnal 52: 25-30 533 534

Tendal OS (1994) Protozoa Xenophyophorea Granuloreticulosa: Psammina zonaria sp.nov. from the Wester Pacific and some aspects of the growth of xenophyophores. In: A. Crosnier (ed.). Resultats des Campagnes MUSORSTOM. Vol. 12. Mém. Mus. Nat. Hist. 161: 49-54 Tendal OS (1996) Synoptic checklist and bibliography of the Xenophyophorea (Protista), with a zoogeographical survey of the group. Galathea Report 17: 79-101 Tendal OS, Lewis KB (1978) New Zealand xenophyophores: upper bathyal distribution, photographs of growth position, and a new species. N.Z. J. Mar. Freshw. Res. 12: 197-203 Veillette J, Sarrazin J, Gooday AJ, Galéron J, Caprais J-C, Vangriesheim A, Juniper SK (2007). Ferromanganese nodule fauna in the equatorial north Pacific ocean: species richness, faunal cover and spatial distribution. Deep-Sea Research I 54: 1912-1935.

569	Figure captions
$^{1}_{2}$ 570	
$^{3}_{4}$ 571	Fig. 1. Semipsammina licheniformis sp. nov., Stn.60-1, cruise 4-06, holotype, registration
${}^{5}_{6}$ 572	number F-16; a, b, d, light micrographs; c, e, f, scanning electron micrographs.
7 573 8	a- Intact specimen on the surface of the host nodule
9 574	b- Fragment of the surface of the test
10 11 575	c- Surface of test showing xenophyae (mainly radiolarian skeletons)
$^{12}_{13}$ 576	d- Underside of outer test layer showing granellare branches and dark masses of
$^{14}_{15}$ 577	stercomare
$\begin{smallmatrix}16\\17\end{smallmatrix}$ 578	e- Granella (barite crystal) on the surface of a granellare branch
¹⁸ 579	f- Strings of stercomare composed of stercomes
19 20 580	Scale bars: a- 1 cm; b- 1 mm; c- 100 μm, d- 1 mm; e- 10 μm; f- 30 μm
21 22 5 81	
$^{23}_{24}$ 582	
$^{25}_{26}$ 583	Fig. 2. Psammina multiloculata sp.nov.; light micrographs.
${}^{27}_{28}$ 584	a – Holotype from Stn. 28, cruise 4-06, registration number F-17
29 585 30	b – Fragment of holotype
31 586	c – Fragment of holotype with base of secondary plate
32 33 5 87	d – Fragments of specimen from Stn. 204, cruise 18-01
$^{34}_{35}$ 588	e - Specimen from Stn. 8655, cruise 4-09, side view
$\frac{36}{37}$ 589	f - Specimen from Stn. 8655, cruise 4-09, top view
³⁸ 590 39	g – Specimen from Stn.t.8726, cruise 4-09, side view
40 591 41	h – Specimen from Stn. 8726, cruise 4-09, margin of the test showing internal
42 592	compartments.
43 44 593	Scale bars: a, e, g – 10 mm, b – 5 mm, c-1,5 mm
$^{45}_{46}$ 594	
$\frac{47}{48}$ 595	
49 596 50	Fig. 3. Psammina multiloculata sp.nov., specimen from Stn.204, cruise 18-01; scanning
51 597 52	electron micrographs.
53 598	a – Surface of the test
54 55 599	b - Detail of surface showing xenophyae (fragments of sponge spicules and radiolarians)
56 57 600	c – Test interior showing compartments
⁵⁸ 601	d – Oval stercomare mass within compartment
60 61 602	e – Stercomare strings (left) and granellare branch (right)
62 63	
64 65	

	603	f - Granellare branch
1 2	604	g – Detail of granellare branch containing numerous granellae (barite crystals)
3 4	605	h – Single granella
5 6	606	Scale bars: a, c - 1000 μ m, b, d, f - 100 μ m, e - 30 μ m, g - 10 μ m, h - 3 μ m
7 8	607	
9 10	608	Fig. 4. Psammina limbata sp.nov., Stn. 25, cruise 4-06, 4724 m, holotype, registration
11	609	number F-18.
12 13	610	, a - Intact test attached to host nodule.
14 15	611	b - Test detatched from nodule showing concentric zonation.
16 17	612	c - Surface of the test showing xenophyae.
18 19	613	d - Outer layer of test underlain by internal xenophyae (mainly sponge spicules),
20	614	stercomare and granellare
	615	e - Stercomare mass
23 24	616	f - Single granella (barite crystal)
25 26	617	g - Small ridge on underside of outer test layer
27 28	618	h - Weakly-developed zonation on underside of outer test layer inside test
	619	i - Margin of test consisting of sponge spicules
31	620	Scale bar: a, b - 1 cm, g - 1 mm, d, i -200µm, c, h - 100µm, e- 20µm, f - 3 µm
32 33	621	
34 35	622	Fig. 5. Spiculammina delicata, variation in test morphology of specimens attached to nodules
36 37	623	(cruise 4-06).
38 39	624	a - Stn. 118
40 41	625	b - Stn. 166
42	626	c – Stn. 159
43 44	627	d – Stn. 43
45 46	628	e – Stn. 119
47 48	629	f – Stn. 164
49 50	630	
	631	
53	632	Fig. 6. Test structure of Spiculammina delicata, from Stn. 25, cruise 4-06; scanning electron
54 55	633	micrographs.
56 57	634	a - Surface of the test
58 59	635	b - Detail of test wall showing xenophyae (sponge spicules)
60 61	636	c - Test interior containing stercomare, granellare and xenophyae
62		
63 64		
65		

	637	d – Strings of stercomare between inner xenophyae				
1 2	638	Scale bar: a – 200 μm; b, – 100 μm; d – 20 μm; c-10 μm				
3 4	639					
5 6 7 8 9 10 11 12 13	640					
	641	Fig. 7. Stannophyllum radiolarium; a,b, light micrographs; c - f, scanning electron				
	642	micrographs.				
	643	a- Specimen from Stn. 8639; dimensions 22x15 mm				
	644	b- Specimen from Stn.31 attached to host nodule; dimensions 32x25 mm				
	645	c- Surface of the test showing xenophyae (radiolarians).				
16 17	646	d- Linellae and stercomare mass				
18	647	e- Detail of linellae				
	648	f- Granellare branch with granellae				
21 22	649	Scale bar: c,d-100 μm; e, f, 10 μm				
23 24	650					
25 26	651	Fig. 8. Stannophyllum sp. from Stn 197, cruise 18-01; a,b, light micrographs; c - i, scanning				
27 28	652	electron micrographs.				
29 30	653	a- Specimen as originally found in box core, attached to a nodule				
31	654	b- Damaged fragment in Petri dish				
32 33	655	c- Test surface showing xenophyae (radiolarians)				
34 35	656	d, e- Test interior with granellare branches and internal xenophyae				
36 37	657	f- Single granella (barite crystal)e				
38 39	658	g- Mass of granellae within granellare branch				
40	659	h- Stercomare				
41 42	660	i- layer of linellae				
43 44	661	Scale bar: b- 1 cm; d- 300 μm; c, e- 100 μm; i- 30 μm; h- 10 μm; f, g- 3 μm				
45 46	662					
47 48	663					
49 50	664					
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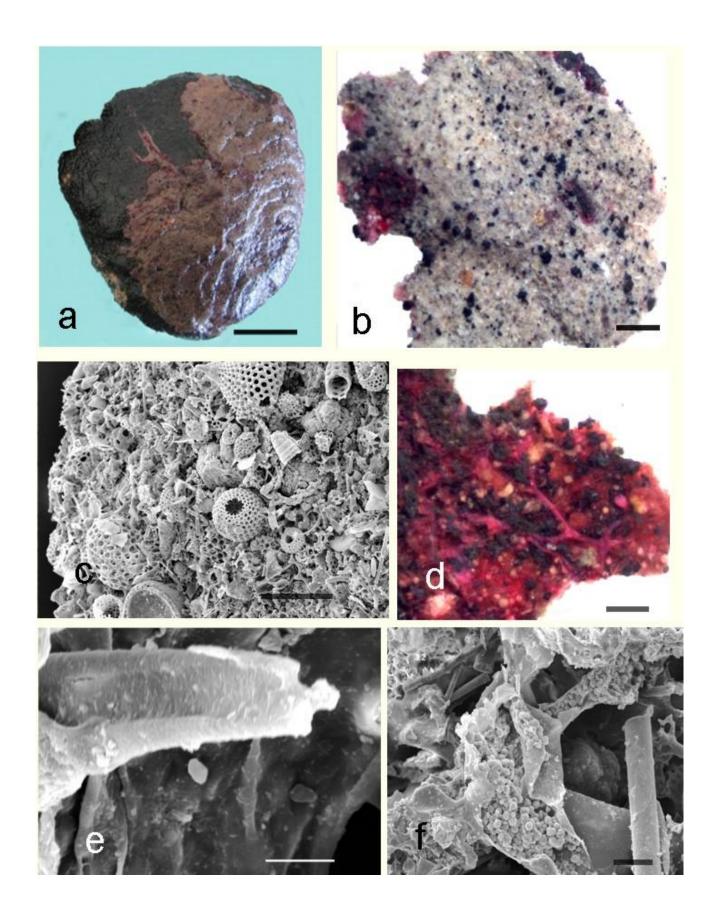
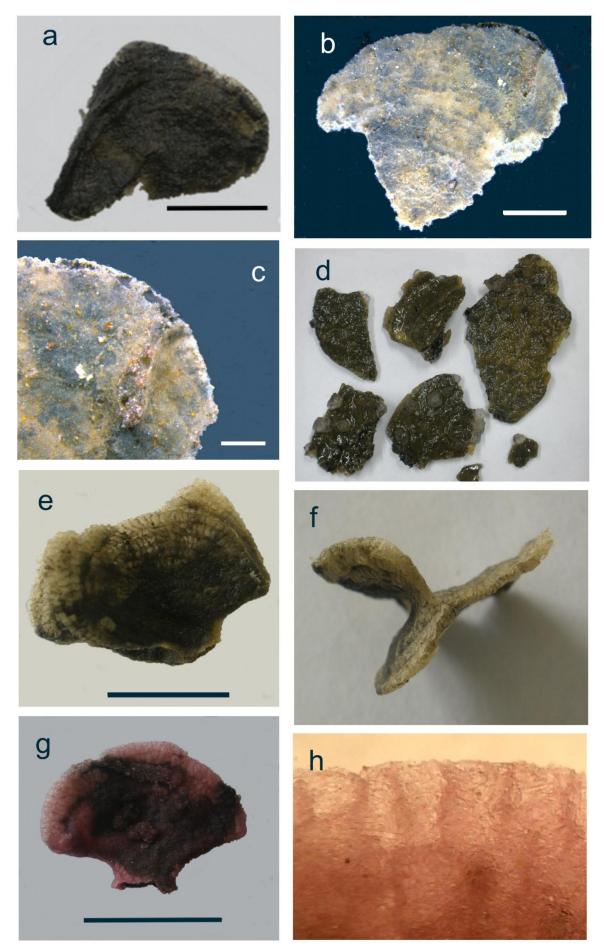
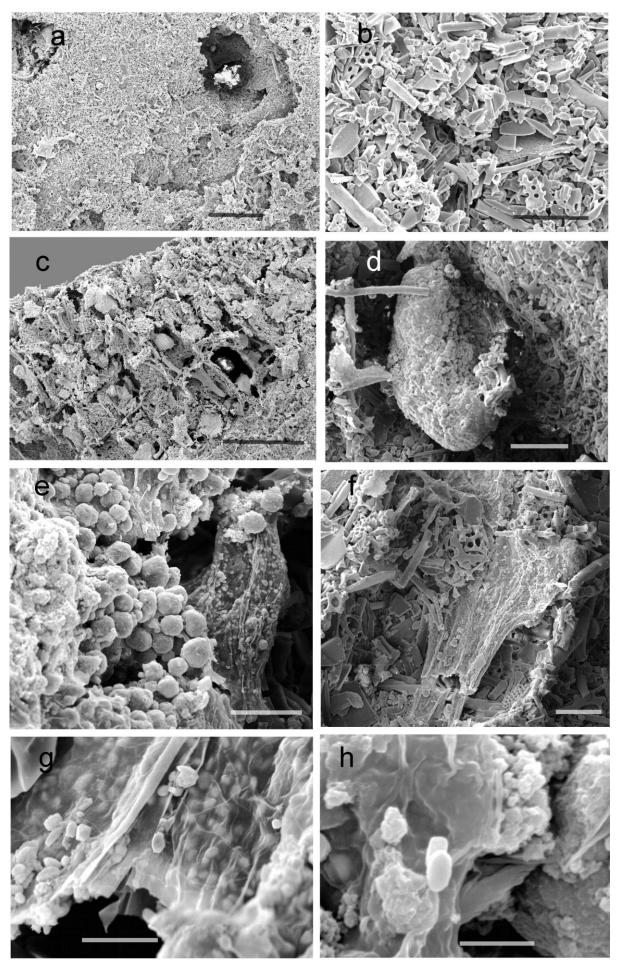


Fig.1







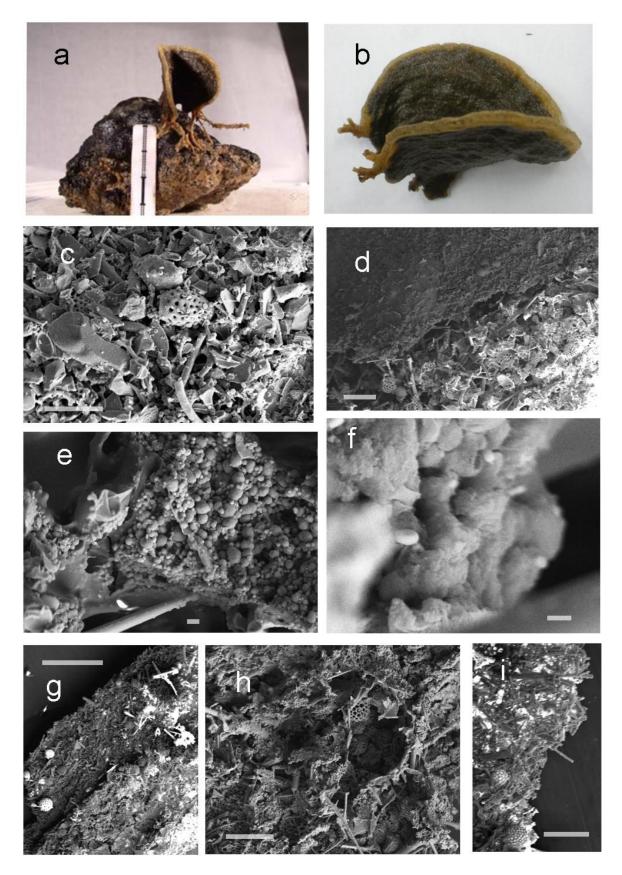
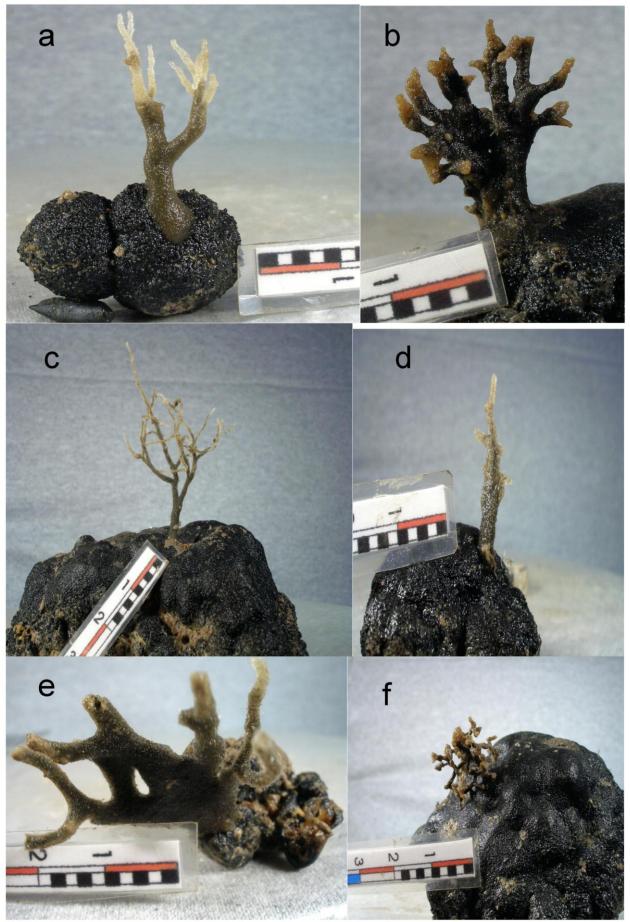


Fig.4



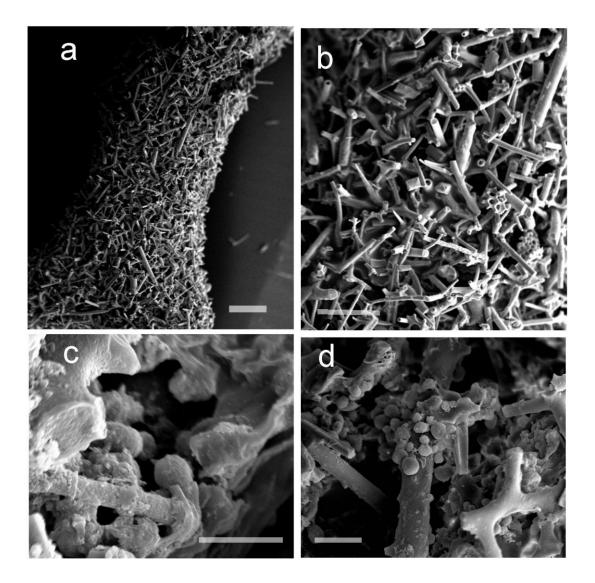
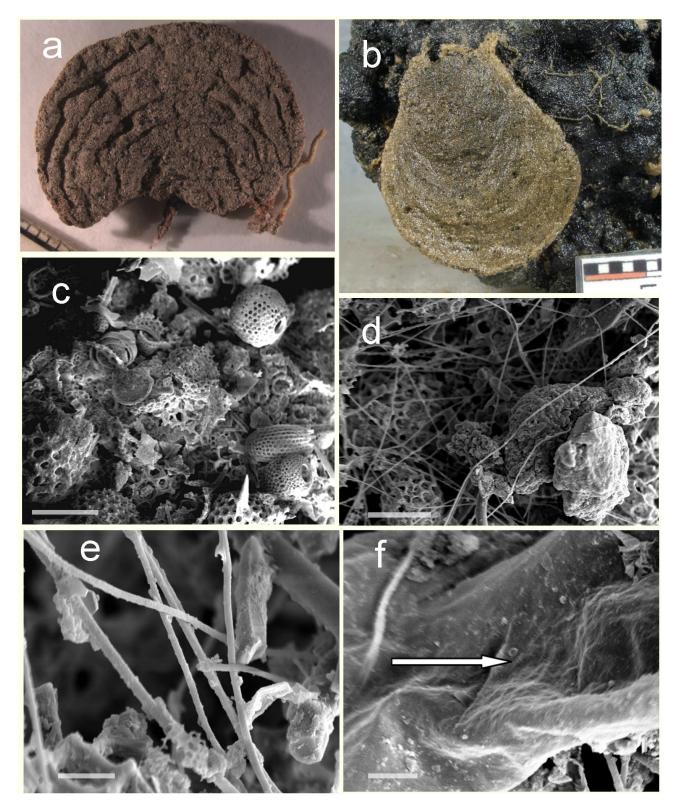
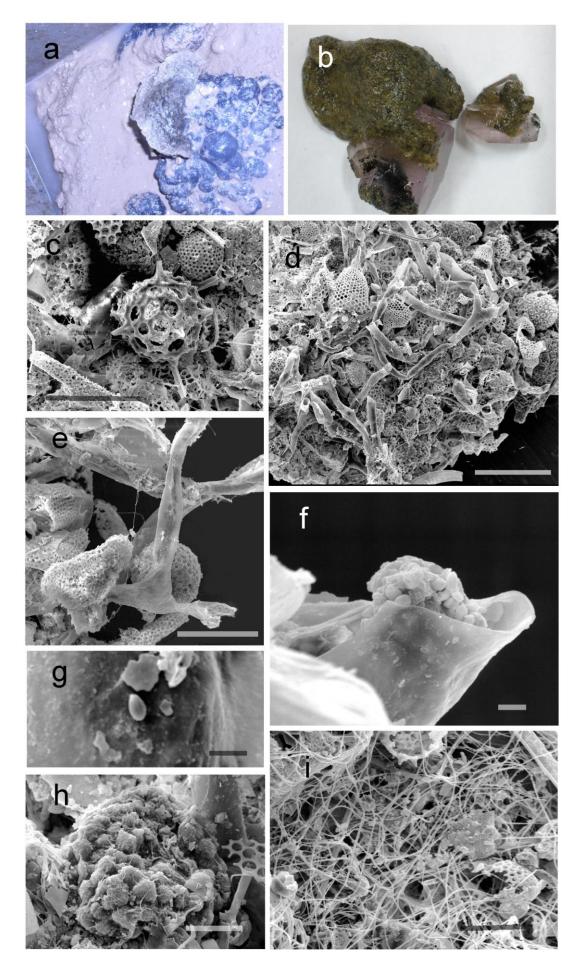


Fig.6







Station	Cruise	Year	Coordinates	Depth	Species
Ν			N, W	m	1
25	4-06	2006	13.28° 134.45°	4724	Psammina limbata,
					Spiculammina delicata
28	4-06	2006	13.29° 13.41°	4843	Psamina multiloculata
31	4-06	2006	13.31° 134.41°	4785	Stannophyllum radiolarium
34	4-06	2006	13.31° 134.32°	4742	Spiculammina delicata
39	4-06	2006	13.26° 134.47 [°]	4716	Spiculammina delicata
43	4-06	2006	13.28° 134.42°	4753	Spiculammina delicata
49	4-06	2006	13.29° 134.34°	4755	Spiculammina delicata
52	4-06	2006	13.24° 134.53°	4787	Spiculammina delicata
60-1	4-06	2006	13.26° 134.42°	4777	Semipsammina licheniformis
85	4-06	2006	13.27° 134.32°	4820	Spiculammina delicata
94	4-06	2006	13.23° 134.44°	4772	Spiculammina delicata
95	4-06	2006	13.23° 134.43°	4786	Spiculammina delicata
118	4-06	2006	13.24° 134.34°	4778	Spiculammina delicata
119	4-06	2006	13.24° 134.33°	4825	Spiculammina delicata
122	4-06	2006	13.19° 134.51°	4820	Spiculammina delicata
133	4-06	2006	13.22° 134.37°	4788	Spiculammina delicata
150	4-06	2006	13.27° 134.43°	4778	Spiculammina delicata
151	4-06	2006	13.27° 134.43°	4776	Spiculammina delicata
159	4-06	2006	13.26° 134.45°	4755	Spiculammina delicata
164	4-06	2006	13.26° 134.43°	4769	Spiculammina delicata
166	4-06	2006	13.26° 134.42°	4777	Spiculammina delicata
167	4-06	2006	13.26° 134.42 [°]	4789	Spiculammina delicata
197	18-01	2003	13.55° 129.02 [°]	4845	Stannophyllim sp.
204	18-01	2003	13.90° 129.14 [°]	4896	Psammina multiloculata
8639	4-08	2009	12.77° 133.41°	4750	Stannophyllum radiolarium
8655	4-09	2010	12.72° 133.59°	4841	Psammina multiloculata
8726	4-09	2010	13.54° 133.42°	4936	Psammina multiloculata

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