A new infaunal xenophyophore (Xenophyophorea, Protozoa) with notes on its ecology and possible trace fossil analogues

Infaunal xénophyophore
Xénophyophore ecology
Trace fossil analogues
Trench fauna
W. Pacific

Endofaune de xénophyophores
Écologie des xénophyophores
Traces fossiles analogues
Faune abyssale
Pacifique Ouest

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ABSTRACT

Xenophyophores are a group of large, benthic deep-sea rhizopods. Photographic investigations have shown species from several genera to live on the sediment surface. Here, an infaunal xenophyophore, *Occultammina profunda* n. gen., n. sp., taken in a box core at 8 260 m in the Ogasawara Trench (Western Pacific), is described. The species, which has been met with only in heavily fragmented form, lives in the 1-6 cm sediment layer and is a dominating macrofauna element in the samples. A patchy distribution on the scale of 10 cm is indicated. On the basis of a detailed analysis of the nature of the sediment facies at the sample site, X-ray radiographs of sediment slices, and direct observation of *Occultammina* tubes *in situ*, it is concluded that the trace fossil analogues of this species resemble *Megagrapton* or *Protopaleodictyon*. A further aspect of the discovery of *Occultammina* is that other infaunal xenophyophores may exist that have regular polygonal networks of tubes, and that these may be the makers of *Paleodictyon*.

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RÉSUMÉ

Une nouvelle espèce endofaune de xénophyophores (Xenophyophorea, Protozoa). Remarques sur son écologie et sur d'éventuelles traces fossiles analogues.

Les Xenophyophorea constituent un groupe de grands rhizopodes benthiques de mers profondes. Les investigations photographiques ont montré que des espèces appartenant à plusieurs genres vivent sur la surface du sédiment. On décrit ici un xénophyophore endobenthique, *Occultammina profunda* n. gen., n. sp. recueilli dans une carotte à 8 260 m dans la fosse d'Ogasawara (Pacifique occidental). L'espèce, qui a été trouvée seulement sous forme de fragments, vit dans la couche supérieure du sédiment (1 à 6 cm) où elle est un élément dominant de la macrofaune dans les échantillons. La distribution en est inégale (à une échelle de 10 cm environ). D'après l'analyse détaillée de la nature du sédiment au site de prélèvement, les radiographies des lames et l'observation *in situ* des tubes d'*Occultammina*, on conclut que les traces fossiles analogues à celles de cette espèce ressemblent à *Megagrapton* ou *Protopaleodictyon*. Enfin la découverte d'*Occultammina* suggère qu'il peut exister une autre endofaune de xénophyophores constituant un réseau polygonal régulier de tubes, et que ces formes pourraient être à l'origine de *Paleodictyon*.

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INTRODUCTION

Xenophyophores are a group of benthic, deep-sea rhizopods, within which many species reach several centimeters in test diameter (Levine *et al.*, 1980; Tendal, 1972). The results of a number of photographic investigations suggest that the growth position for species of seven of the eleven genera is on the sediment surface (Lemche *et al.*, 1976; Tendal, Lewis, 1978; Tendal, Gooday, 1981; Nichols, Tendal, in prep.).

Here, a new, infaunal xenophyophore is described as *Occultammina profunda* n. gen., n. sp. The discovery of this species shows that the xenophyophore ground plan also allows for a life under the sediment surface. The ecology of *Occultammina profunda* and the possible trace fossil analogues of its tubes are described and discussed.

Xenophyophore terminology is in essence the same as in other protozoan groups, especially the Foraminifera. A few terms, however, need definition:

Granellae are barite crystals in the plasma;

Granellare is the plasma and the surrounding organic tube system;

Stercomare are strings or masses of stercomes;

Stercomes are spherical or ellipsoidal masses of what are thought to be waste and excretion products;

Xenophyae are foreign bodies used in the construction of the test.

METHODS

The material treated here was found in samples taken with a Scripps-type box corer (Hessler, Jumars, 1974).

Subsamples for meiofauna investigations were taken immediately after collection of the box corer on board ship. Samples were taken at intervals of 0-1, 1-2, 2-3, 3-6, 6-9, 9-12, 12-15, 15-20, 20-25, and 25-30 cm from cores of 10 cm^2 cross sectional area. They were fixed in 5% formalin containing rose bengal a few hours after collection. Within 2 months, they were transferred to 70% alcohol.

Subcores for macrofauna investigations were stored in a freezer (−20°C) for about 9 months. The cores, of 100 cm^2 cross section, were sliced after defrosting using the same sampling intervals as for meiofauna.

Subcores for geological analysis were packed in plastic wrap and kept at 4°C without prior fixation. Vertical and horizontal slices of these cores, 1 to 2.5 cm thick, were X-rayed using the techniques described by Bouma (1969). Fine grained film was used (Fuji Softex film). Organisms, visible in the radiograph, were extracted by gently washing the sediment slices with a water bottle, and were stored in tap water at room temperature. Material from these samples was usable for gross morphology investigations only.

RESULTS AND DISCUSSION

Systematics

Superclass Rhizopoda von Siebold, 1845.

Class Xenophyophorea Schulze, 1904.

Order Psamminida Poche, 1913.

Family Syringamminidae Tendal, 1972

The new species is assigned to this family because the test is constructed of well-defined tubes. Xenophyae are restricted to the tube walls and only the granellare and stercomare strings are found in the tube space.

Genus *Occultammina n. g.*

Diagnosis

Test of single, sometimes bifurcated tubes. The tube wall consists of two distinct layers of xenophyae. The test is buried in the sediment.

Remarks

Occultammina differs from the only other genus of the family, *Syringammina* Brady, 1883, in all characters given in the diagnosis. The test in *Syringammina* is a tightly coherent organized system of tubes with uniformly constructed walls. The species live on the seabed.

Occultammina profunda n. sp.

Material

Numerous fragments. Ogasawara Trench near the Bonin Islands, W. Pacific (28°28.3′N, 143°19.6′E), 8 260 m, March 3, 1980, box corer. Type specimen and additional material deposited in the Zoological Museum, Copenhagen.

Description

Most specimens were found in the 1-6 cm layers of box core subsamples. They can be very faintly detected in X-ray radiographs of the undisturbed samples. The position *in situ* is subhorizontal, but in some cases near vertical.

The generally single, but sometimes bifurcating, straight, cylindrical, light grey tubes reach a length of at least 25 mm and measure 0.5-1 mm in diameter (Fig. 1). They are extremely fragile and break into fragments on removal from the sediment block.

The tube wall is 75-120 µm thick and is composed of poorly cemented xenophyae arranged in two distinct layers. The smooth outer layer is 15-30 µm thick and consists of fine clay particles with a few scattered silt particles. The inner layer is 50-90 µm thick and is composed of silt-sized mineral grains and fragments of what seem to be radiolarian tests. The inner surface is uneven due to the protruding parts of these particles.

On the inside of the tube wall, there are 1-4 longitudinally running ridges (Fig. 2). Morphologically they are thickenings of the inner wall layer. All degrees of their development are found, from some barely seen to others forming complete partitions by fusion of two opposite ridges. Often originating at points of stercomare

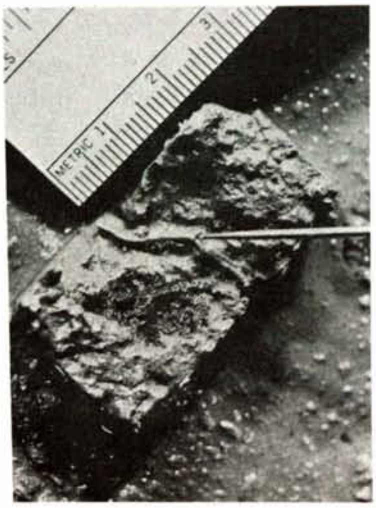

Figure 1

Plan view of a horizontal tube of Occultammina profunda *exposed by washing a slice of sediment with a jet of water. The pointer indicates a branching point — the branch was washed away. The tube was located in a radiograph prior to washing.*

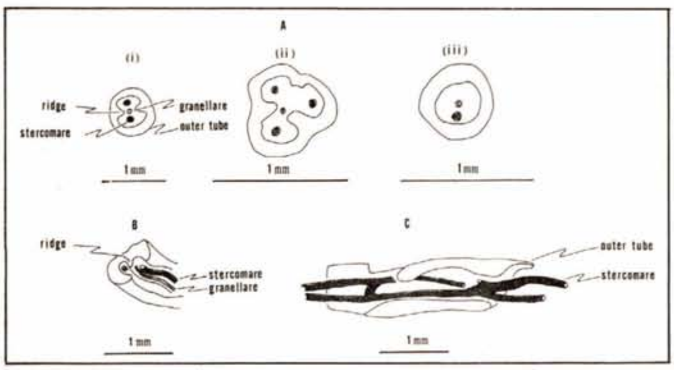

Figure 2

Morphology of Occultammina profunda *(traced from dried specimens viewed under a binocular microscope) A. Cross-sections of tubes: (i) two stercomare strings (most common); (ii) three stercomare strings (quite common); (iii) one stercomare string (rare). B. Oblique view showing ridge which separates stercomare. C. Longitudinal view of tube which has been split open to reveal anastomosing stercomare.*

bifurcations, they tend to separate the stercomare strings from each other. The number and size of the ridges have no bearing upon the diameter of the tube.

Internally, the tubes contain one central granellare string and 1-3 peripheral stercomare strings that virtually fill the space (Fig. 2 B and C).

Granellare generally run as single, sometimes bifurcating strings. They are circular in cross-section and measure 40-130 µm in diameter. Near bifurcations they are often flattened, up to about 260 µm wide and about 65 µm thick. The covering is a thin, < 0.5 µm thick, membrane. The plasma contains large numbers of spherical nuclei, 3-4 µm in diameter. Granellae are not seen.

Stercomare are well-defined, dichotomously divided, sometimes anastomosing, dark strings (Fig. 2 C). Approximately circular in cross-section, they measure 125-160 µm in diameter. They are covered by a thin, < 0.5 m thick, transparent membrane. The stercomes are more or less ellipsoidal and measure 15-25 µm, generally about 20 µm, in diameter. Most stercomes are one mass of unidentifiable small particles (type 1, Tendal, 1972, p. 73), but some are seen that consist of a large number of small spherical bodies each of which is composed of fine granular matter (type 2, Tendal, *op. cit.*).

Remarks

The characters used above as generic distinctions clearly differentiate *Occultammina profunda* from each of the three known species of *Syringammina*. Other separating morphological features that can be seen even in small fragments, are the presence of inner longitudinal ridges and the very fine-grained xenophyae of the outer test layer in *O. profunda* as opposed to the lack of ridges and the coarser xenophyae in the tubes of the *Syringammina* species.

Ecology of Occultammina profunda

From the four subcores (100 cm² each) for macrobenthos studies, 142 fragments of *Occultammina profunda* were collected in sieves of 0.5 and 1 mm mesh (only fragments containing granellare were counted). This corresponds to a density of $3.6 \times 10^3 \pm 3.1 \times 10^3$ fragments per square meter. With the exception of one echiurid worm, *O. profunda* was the only macrofaunal species found at this box core station.

O. profunda was concentrated below the surface of the sediment (Fig. 3). The high density layers were from 1 to 6 cm depth and only 3 fragments were found in the 0-1 cm layer of the sediment. This vertical distribution indicates that *O. profunda* is living buried within the sediment.

The spatial distribution of *O. profunda* was patchy. Statistically, the null hypothesis that *O. profunda* is distributed randomly was rejected because the variance to mean ratio (20.4) of the number of fragments of this species is significantly ($p < 0.001$) larger than 1 (Chi-square test, Pielou, 1969).

Two adjacent subcores contained a high density of fragments, while the other two had a low density. This suggests patchiness on a scale of about 10 cm. One possible interpretation is that each patch consists of one or two individuals made up of a network of interconnected tubes which were broken into fragments on sampling. Another possibility is that each patch consists of a large number of small individuals. X-ray radiographs indicate that individuals are at least ~2.5 cm in size (see next section). Therefore the former possibility seems more likely.

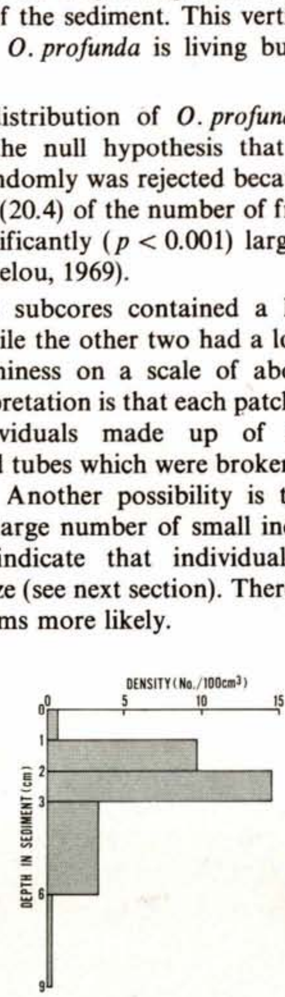

Figure 3

Density distribution of Occultammina profunda *fragments with respect to depth in the core. Only fragments with protoplasm stained by rose bengal were counted.*

Possible trace fossil analogues

To determine the possible trace fossil analogue of the tube system of *Occultammina profunda*, it is first necessary to establish the nature of the sedimentary facies at the sample site, as some trace fossils are facies specific.

Sedimentary facies

Occultammina profunda occurs within a distal turbidite facies (Fig. 4). The stratigraphic succession in the box core is interpreted as consisting of four turbidite beds ranging between about 4 to 7 cm in thickness, and showing varying degrees of disturbance due to bioturbation. The oldest (i. e. deepest) turbidite (4 in Fig. 4) is the least disturbed by bioturbation and has an almost complete Bouma (1962) sequence. Thin, basal lenses of volcanic sand (? Bouma division A) are overlain by finely laminated silts and sand (Bouma division B), which in turn are overlain by contorted silt/clay laminations with some micro-cross laminations (Bouma division C). These in turn are overlain by parallel silt/clay laminations (Bouma division D), and the sequence is capped by bioturbated pelagic mud (Bouma division E). The overlying turbidites (1 to 3 in Fig. 4) are much more disturbed by bioturbation, but when all four geological subcores are examined, sufficient evidence exists in beds 2 and 3 (Fig. 4) to indicate their turbidity current origin (i. e. undisturbed patches of parallel and micro-cross laminations). In the case of bed 1 (Fig. 4), which extends to the present-day surface, bioturbation has been so thorough that only patches of the basal sand remain and no laminations are visible, but it is reasonable to assume a turbidity current origin for the lower part of this bed as well.

Figure 4
Positive of an X-ray radiograph of a 2.5 cm thick vertical slice of sediment from the box core. Dark laminae are sand. There are four turbidite beds (labeled 1 to 4). Turbidite 4 has been subdivided A to E following the sequence for turbidites proposed by Bouma (1962). Vertical bar is 5 cm long (exposure: 38 kV, 4 mA, 3 minutes).

Morphology of tubes.

Outlines of the sediment tubes occupied by *Occultammina profunda* are very faintly visible in X-ray radiographs. Figure 5 illustrates a branching tube network traced from a radiographic negative viewed under a binocular microscope. This network is horizontally orientated, but other radiographs reveal some vertically orientated sections. It is unknown whether the vertical shafts connect to the surface, but one of us (Y.S.) did find unoccupied tubes of simple cross-section (*cf.* Fig. 2 A (iii)) in the upper 0-1 cm layer of sediment, which may be parts of an *Occultammina profunda* network and may represent connections to the surface.

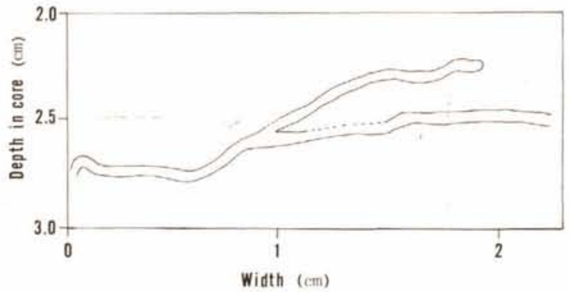

Figure 5
Side view of the morphology of Occultammina profunda *tubes, as traced from a radiograph. The upper branch trends into the plane of the page. The lower branch is sub-parallel to the page.*

Mode of preservation of the tubes

As *Occultammina profunda* tubes occur just below the sediment-water interface in a turbidite facies, the most likely mode of preservation would be that proposed for graphoglyptid burrows by Seilacher (1977, Fig. 1, p. 292), i. e. the infaunal network of horizontal tunnels is first exposed by erosion during the deposition of the next turbidite. Figure 1 illustrates such a situation where an unbroken tube of *Occultammina profunda* has been exposed by washing with a jet of water. The exposed network is then cast by deposition of sand that forms the base of the overlying turbidite. The cast might be internal, if the tube system is broken open, o, more likely, external if the tube network is lifted from the substrate by suction.

This leads to the intriguing question: what is the trace fossil equivalent, if any, of *Occultammina profunda* tubes? Unfortunately, we do not have a complete enough picture of the tube network to give a clear answer to this question, but, if a trace fossil analogue exists, and this seems likely considering the abundance of *Occultammina profunda* tubes in this box core, it should occur in deep-sea turbidites. The most likely candidates therefore, seem to lie amongst the more irregular graphoglyptids. An external cast of the tubes in Figures 1 and 5 could form part of an irregular *Megagraphton* or *Protopaleodictyon* net (see Seilacher, 1977, for descriptions of these traces). On the other hand, an internal cast of the tubes, would have distinctive runnels paralleling the length of the tube casts. No such trace fossil has been described.

However, the most interesting aspect of this infaunal xenophyophore probably does not lie in the possible trace fossil analogues of *Occultammina profunda* tubes. Rather, it lies in the fact that the discovery of an infaunal xenophyophore opens up the possibility that infaunal xenophyophores with very regular polygonal networks of sediment tubes may exist (*cf.* epifaunal *Syringammina*), and these could be the makers of the well-known trace fossil *Paleodictyon* (such an infaunal xenophyophore has since been found in a box core collected from the Japan Trench [Swinbanks, in prep.]). *Paleodictyon* traces have been reported in the tops of box cores collected from the Atlantic (Ekdale, 1980), and hexagonally-arranged black dots, which may be the burrow openings of an infaunal *Paleodictyon* network, have been described from bottom photographs of the Mid-Atlantic Ridge (Rona, Merrill, 1978; Rona, 1980). Such hexagonally-arranged burrow openings (?) were also found in bottom photographs of the Ogasawara Trench close to the area where the present xenophyophore was collected but at a shallower depth ($\sim$2 900 m, S. Ohta, pers. comm.). The organisms responsible for the above-mentioned structures are unknown, but the results of this and another study (Swinbanks, in prep.) suggest that they may be infaunal xenophyophores.

CONCLUSIONS

The main results of the present investigation are that:

1) the discovery of *Occultammina profunda* n. gen., n. sp. establishes the existence of infaunal xenophyophore species;

2) in the known morphological details this species is within the general xenophyophore ground plan;

3) the species, which is a dominating macrofauna element of the sample, lives well below the surface of the sediment, in the 1-6 cm layer, shows patchy distribution, and

4) possibly has trace fossil equivalents much resembling *Megagrapton* or *Protopaleodictyon.*

Acknowledgements

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