Reports

Paleodictyon: The Traces of Infaunal Xenophyophores?

Abstract. *A xenophyophore found just below the surface of a box core of modern deep-sea sediment from the Japan Trench has a threadlike plasma body that extends through horizontal, anastomosing networks of organically bound sediment tubes (the organism's test). The tubes resemble some of the polygonal networks of the trace fossil* Paleodictyon. *Such xenophyophores may be the makers of* Paleodictyon, *and the complex, regular geometry of* Paleodictyon *may be determined by the xenophyophore's anastomosing body shape.*

The horizontal, netlike trace fossil *Paleodictyon*, interpreted as a cast of the tunnel system of an infaunal deep-sea organism, is one of the most distinctive ichnogenera of ancient deep-sea flysch deposits and is found all over the world (*1*). *Paleodictyon* includes many ichnospecies, ranging from irregular nets without regular vertical outlets to regular nets of hexagonal mesh with regular vertical outlets (*1*). These trace fossils are important in paleoecological and paleoenvironmental investigations as indicators of deepwater sedimentary environments. Crimes and Crossley have suggested that orientated *Paleodictyon* nets with elongate mesh may indicate the direction of ancient geostrophic contour currents (*2*). Despite extensive study, the maker of *Paleodictyon* is not known. Ekdale reported the occurrence of *Paleodictyon* in the tops of box cores of modern deep-sea sediment from the Atlantic, and Rona has identified possible outlets of *Paleodictyon* networks in photographs of Mid-Atlantic Ridge sediments, but the organisms responsible for producing the traces were not found (*3*).

Xenophyophores are a little-known group of deep-sea, giant protozoans ranging in size from a few millimeters to 25 cm (*4*). Several species are known to live on the seabed (*5*). Recently, a syringamminid xenophyophore living in tubes of sediment was found at depths of up to 9 cm in a box core from the bottom of the Ogasawara Trench (sample depth 8260 m) (*6*). Although the tubes of this species appear to have a fairly simple, branching geometry, discovery of this xenophyophore opened up the possibility that infaunal xenophyophores with complex, polygonal networks of anastomosing tubes of sediment might exist (like figure 3 in (*4*)], and these could be the makers of *Paleodictyon* (*6*). Fragments of such a xenophyophore have now been found in the top few centimeters of a box core collected in July 1981 from the Pacific side of the Japan Trench (38°32.2′N; 144°19.9′E; depth, 6440 m) during a cruise of the R.V. *Hakuhō Maru* of the Ocean Research Institute, University of Tokyo. Most fragments have characteristics of the family Syringamminidae, but some (~ 15 percent), which may be the same species, resemble the family Psamminidae. The geometry and nature of the organism's sediment tubes and their possible affinity to certain ichnospecies of *Paleodictyon* are reported.

Only fragments of the organism could be obtained from the box core because the tube systems are difficult to detect (they were not visible in x-ray radiographs of 2-cm-thick horizontal slabs of sediment) and are extremely fragile once uncovered. Most fragments, revealed by spray washing of horizontal slabs, occurred a few millimeters below the surface of the sediment, but some containing plasma were found down to a depth of 4 cm. Several complete, horizontally orientated polygons with broken side branches were found along with one specimen with two interconnected polygons (Fig. 1), suggesting that the complete organism consists of a net of interconnected polygons. The polygons range from four- to eight-sided, some are hexagonal, and they are 1 to 10 mm across (Fig. 1). A few short (~ 1 mm) subvertical to vertical outlets were observed at or near branching points. Most of the 300 fragments recovered were broken tubes commonly with one or more branches bifurcating at ~ 120°, suggesting parts of polygons. The tubes range from 500 to 1000 μm (average, 785 μm; $N = 10$) in external diameter and from 320 to 650 μm (average, 480 μm; $N = 10$) in internal diameter, with an average wall thickness of 150 μm (range, 90 to 250 μm; $N = 11$). The inner and outer walls are smooth (apart from the roughness of constituent silt and fine sand grains).

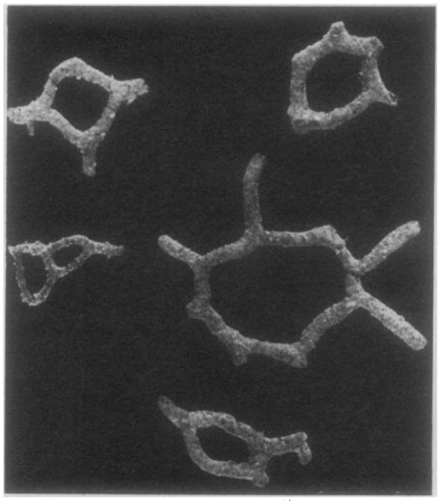

Fig. 1. Polygonal fragments of the infaunal xenophyophore with broken side branches. In the largest polygon, the tubes of sediment are about 1 mm in diameter and the polygon mesh is about 1 cm across. Note that one fragment consists of two interconnected polygons.

The sediment within which the xenophyophore was found is a poorly sorted sandy mud (median grain size, 5.0 ± 0.3 phi units; $N = 3$) (*7*) containing about 1 percent gravel. It is composed largely of terrigenous and volcanic quartz and feldspar, although the sand fraction contains about 8 percent siliceous tests of diatoms and radiolarians. X-ray radiographs reveal no distinct layering in the upper 30 cm of the sediment, which has been extensively reworked by burrowing organisms, making interpretation of the mode of deposition uncertain. The sediment making up the xenophyophore tubes resembles the surrounding substrate, but the tube sediment is better sorted, consisting almost entirely of silt and fine sand (median grain size, 4.1 ϕ) (*7*), and the sand fraction contains fewer (~ 1 percent) siliceous tests and less quartz.

Only about 10 percent of the fragments were living (that is, contained plasma stained by rose Bengal) and even some of these contained dead sections. In the living sections, the sediment tubes contain a thin, centrally placed granellare string (the plasma body encased in a thin membrane) surrounded by stercomare (clusters of stercomes encased in thin organic membranes), or in some, stercomes are loose, fragmented, and appear partially decomposed. The stercomes, which are dark spherical masses (~ 20 μm) of uncertain composition, are one of

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the most characteristic features of xenophyophores and are thought to be waste products (4). The stercomare are usually stringlike and anastomosing, but in a few (~ 1 percent of all fragments, living and dead), a single stercomare forms a tubelike inner lining to the sediment tube. The granellare string ranges from 4 to 100 μm in diameter and the stercomare strings from 40 to 150 μm in diameter. Combined, the granellare and stercomare virtually fill the sediment tube, although there are small gaps.

The dead sections usually contain only stercomes in various stages of decay. Observations suggest that the dark stercomes gradually become lighter in color and eventually break up into loose pale grey "fluff" which occupies little volume within the otherwise hollow tubes of sediment. About 25 percent of all fragments are completely hollow, including one polygonal fragment. About 15 percent of all fragments contain agglutinated silt and fine sand grains inside the sediment tubes; these fragments may belong to a different species.

A partially uncovered network of the xenophyophore's tube system (Fig. 2A), exposed by washing a horizontal slab of sediment with a spray, resembles a photograph of *Paleodictyon (Glenodictyum) imperfectum* illustrated by Seilacher (*1*, plate 3). The irregular and occasional curved polygons of unequal size (Fig. 1), generally lacking vertical outlets, also resemble this ichnospecies [compare with figure 14d in (*1*)], although the mesh size is smaller in the xenophyophore: 1 to 10 mm as opposed to 10 to 25 mm in *P. (Glenodictyum) imperfectum*. Some tubes of the xenophyophore end in blind alleys; this is more typical of the subichnogenus *Squamodictyon*, and the two interconnected polygons in Fig. 1 also resemble *Squamodictyon* [compare with figure 13b in (*1*)]. However, *Squamodictyon* can occur within more angular *Paleodictyon* nets (*2*). Thus, affinity to two subichnogenera presents no contradiction.

Seilacher interpreted *Paleodictyon* and other graphoglyptids as tunnel systems "reinforced by a stronger than usual mucus film" (*1*, p. 292). He suspected the presence of a mucus lining because outlines of the tunnel walls are sharp, and in some, compactional collapse and flattening of the tunnel system has occurred prior to preservation. Such flattening is only possible if the walls are strongly bound. Little is known about the nature of the agent binding the sediment in the walls of xenophyophore tubes except that it is organic—since it is broken down by H_2O_2 (*8*)—ferruginous (*8*), and may contain mucopolysaccharide (*4*). The lack of tubes at depth in the present box core sample suggests that the binding agent decomposes with time.

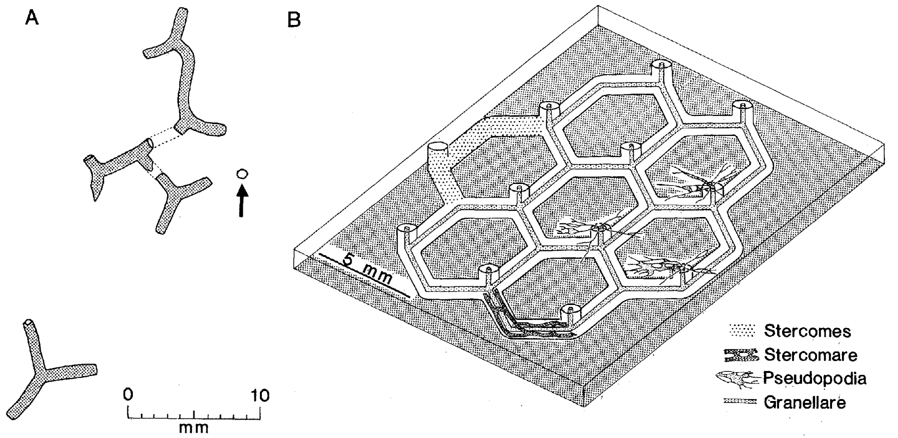

Fig. 2. (A) Tracing made from the enlargement of a color slide showing a plan view of the tube network of the xenophyophore in situ; tubes were partially exposed by washing a horizontal slab of sediment with a spray. The network lay a few millimeters below the surface of the sediment. The dashed lines indicate tube sections which broke off during washing. The arrow indicates a vertical outlet (~ 1 mm long); the nature of its connection to the network on the left is uncertain as it broke off on further washing. (B) Possible form of an infaunal xenophyophore proposed to be the maker of regular *Paleodictyon* networks such as *P. (Ramidictyon) tripatens*. For clarity, stercomare have only been indicated in one section of the network, but would in fact extend throughout the living sections (that is, sections with granellare). One dead section is filled with loose stercomes. Pseudopodia, assumed to resemble those of foraminifera, extend out through the vertical outlets and form a sticky web for ensnaring meiofauna. This diagram is based on observations of the infaunal xenophyophore described in this report and on descriptions of the epifaunal xenophyophore *Syringammina tasmanensis* which forms regular polygonal networks of tubes (*4, 8*), and on Seilacher's *Paleodictyon* "farming-net" [figure 15 in (*1*)].

Seilacher has outlined various modes of preservation for *Paleodictyon* [figure 1 in (*1*)]. They involve erosion of the substrate by a turbidity current and subsequent breaking open of the tunnel system and deposition of sand within the exposed network of tunnels. Such a scheme might be applicable to xenophyophore sediment tubes in which the binding agent in the walls has undergone some decomposition. However, observations of substrate erosion with a spray suggest that in the case of fresh xenophyophore tubes a trace fossil may be formed by (i) erosion of the substrate until the tube system is exposed in half relief, (ii) uplift of the tube system by suction during erosion, and (iii) casting of the imprint of the tube network left on the substrate by sand deposition (that is, an external cast). Alternatively, the unexposed tube system could be filled with sand through the vertical outlets (that is, an internal cast); this would correspond to the rare cases of full relief preservation in *Paleodictyon* (*2*). Both internal and external casts of the present xenophyophore's tube network would yield network dimensions (that is, tunnel diameter and polygon mesh size) within the ranges reported for *Paleodictyon* (*1*).

Seilacher suggests that *Paleodictyon* are well-ventilated "search nets" used for trapping or farming meiobenthos or microorganisms, rather than being feeding structures of sediment eaters or dwelling structures of suspension feeders (*1*). This interpretation is compatible with the *Paleodictyon* organism being a xenophyophore. The internal walls of the xenophyophore sediment tubes are stained red by rose Bengal, indicating the possible presence of bacteria on which the protozoan may feed, and, when extended, the pseudopodia of the xenophyophore may well have a sticky weblike form (such as pseudopodia of foraminifera) to ensnare meiofauna [Fig. 2B; see also plate 16D in (*4*)]. I propose a major departure from Seilacher's interpretation of *Paleodictyon* to explain how the complex polygonal networks of tunnels are made. Seilacher interprets them as being the result of a complex behavioral program where, in the hexagonal *Paleodictyon* nets, a wormlike organism makes turns of precisely 120° at rigidly set distances (*1*). In my interpretation, the regular geometry directly reflects the morphology and growth of the xenophyophore's plasma body (that is, granellare) (Fig. 2B). Direct evidence that the granellare of the present xenophyophore anastomose was not found; the polygonal fragments were either dead (filled with stercomes or hollow) or the granellare was only present on one side of the polygon. However, other epifaunal syringamminid xenophyophores with polygonal anastomosing networks of tubes do have anastomosing granellare [for example, *Syringammina tasmanensis* (*4*)], and it is reasonable to suppose that in complete, living specimens the granellare of the present xenophyophore anastomose.

How or why the *Paleodictyon* organism maintains multiple vertical outlets has not been completely satisfactorily explained, but this can be understood in terms of a xenophyophore model: they could be outlets for the pseudopodia to gather food at the surface (Fig. 2B), and outlet separation may be determined by the "operation area" of the pseudopodia (that is, avoidance of overlap). The outlets may also act as "vents," providing the various branches of the organism's body with access to oxygenated sea water.

The abundance of dead sections suggests that the xenophyophore has to abandon sections of its network which have become filled with stercomare almost as fast as it can form them. Thus the gigantic and uniform size of some *Paleodictyon* nets (up to 1 m^2) (*9*) might be the result of a small threadlike organism (body width, ~ 100 μm or less) striving to maximize its areal coverage through netlike growth, while having to cope with a chronic waste disposal problem.

If *Paleodictyon* is a cast of a xenophyophore tube network, a question arises as to whether *Paleodictyon* is a trace fossil or a body fossil. Although the xenophyophore sediment tube is an order of magnitude larger in diameter than the unattached plasma body it encloses, it is nevertheless considered to be part of the organism, and its external shape is often characteristic at the species level (*4*). Thus, a cast of the tube system would seem to be a body fossil. However, the occurrence of the living organism at several centimeters depth in quite coherent sediment suggests that it may actively burrow, in which case the tube system could be regarded as a trace fossil. Alternatively, the organism may penetrate into the sediment like a root, rather than burrow.

In light of the proposed interpretation of *Paleodictyon*, the *Paleodictyon* grooves found on the tops of box cores by Ekdale (3) might be explained as either (i) the imprints of a xenophyophore tube system which had been lifted from the substrate and then fragmented by swilling sea water during or before drainage of the box core (as happened in this study), or (ii) part of the actual tunnel system of a dead xenophyophore in which the binding agent in the walls had decomposed (or was originally weak).

If *Paleodictyon* are traces of infaunal xenophyophores, the implications are quite far reaching. First, it would establish beyond doubt that *Paleodictyon* are reliable indicators of deep-sea sediments, since xenophyophores are almost exclusively restricted to the deep sea (*4*). Second, it would establish a history for xenophyophores extending back to Ordovician times; until now these primitive organisms have only been found in modern environments. Third, *Paleodictyon* would reflect an organism's growth, not its behavior. Lastly, the more than 30 ichnospecies of *Paleodictyon* (*9*) suggest the possible existence of many more species of infaunal xenophyophores, but care would have to be taken in their classification, as the presence of *Squamodictyon* within more angular *Paleodictyon* nets (*2*) indicates that morphological variation within a single species may be quite considerable.

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Crystal Site Location of Iron and Trace Elements in a Magnesium-Iron Olivine by a New Crystallographic Technique

Abstract. *A new crystallographic technique has been developed, which has been applied to the problem of locating the cations in a natural olivine crystal with the composition* $(Mg_{0.90}Fe_{0.10}Ni_{0.004}Mn_{0.002})_2SiO_4$. *The method uses the variation of characteristic x-ray emission with the direction of an exciting electron beam in an analytical transmission electron microscope. It may be applied to nanometer-sized areas and to concentrations as low as 0.1 atomic percent, is capable of distinguishing neighbors in the periodic table, and does not require external standards. The iron atoms in this crystal are evenly distributed between the two available crystal sites M1 and M2 (49.6 ± 1 percent on M1), whereas the trace elements nickel and manganese occupy the M1 and M2 positions, respectively (97 ± 5 percent nickel on M1 and 1 ± 5 percent manganese on M1).*

In many real crystals of interest to scientists, the three-dimensional periodic lattice of atomic sites is well defined. However, the assignment of particular species to these sites may be irregular, with resultant substitutional disorder. This determination of the distribution of atoms over available sites in crystals is of considerable interest in crystal chemistry, semiconductor physics, solid-state physics, and mineralogy; we deal here with a mineralogical problem. The degree of atomic order in a mineral serves as a geothermometer and geobarometer, giving petrologists information about the geologic and thermal history of rocks, such as the rate of cooling at the time of formation.

The most widely used methods for determining the positions of atoms in crystals are x-ray diffraction and neutron diffraction. However, difficulties arise when these techniques are applied to natural minerals as compared to laboratory-grown crystals, since, for a precise determination of the distribution of atoms in a crystal, the composition of the crystal must be known accurately. From the wealth of information that has been gathered over the last decade on the defect structure of minerals by transmission electron microscopy (*1*), it is now known that most natural minerals contain many inclusions of other phases. Thus the use of an average composition for x-ray structure analysis may obscure the chemical analysis of the crystal phase under study. This difficulty be-