

# Biological aspects of deep-sea manganese nodule formation

Deep-sea  
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Haute mer  
Nodules de manganèse  
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## ABSTRACT

The relative contributions of biogenic and inorganic processes to manganese nodule and crust formation is still a controversial issue. Some pertinent activities of bacteria and foraminifera are reviewed and supplemented with new findings concerning foraminifera, xenophyophores and related, non-testate rhizopodean protozoa, as well as polychaete worms, from manganese nodules, crusts and sediments in the Central Pacific. The investigations by the author, using freshly collected material with preserved cytoplasm structures, highlight the special feeding biology of the rhizopodean groups abounding on manganese nodules and crusts and in the associated sediments. All these rhizopodea are characterized by the accumulation of huge volumes of faecal pellets (stercomata) containing biogenic and mineral particles. There is evidence that these pellets constitute food residua digested extra-cellularly, and thus in contact with the ambient sea-water. The theory is advanced that by browsing the environment over a wide range, the rhizopodea gather, together with bacteria and other components of their diet, widely dispersed particulate metal oxides. During digestion, the accumulated particles are presumably subject to micro-zones of lowered pH and redox conditions, i.e. factors which govern the chemistry of manganese. While iron (and probably copper) is retained by the rhizopodea, manganese is dissolved but may later be reprecipitated and accreted immediately adjacent to the sites of digestion under and around the sedentary foraminifer or related organism, thereby contributing to nodule growth. According to this model, rhizopodean protozoa (and, additionally, polychaete worms that feed on them) control the concentration, fractionated dissolution and accretion of metals in oligotrophic regions of the deep sea.

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## RÉSUMÉ

### Aspects biologiques de la formation des nodules de manganèse

Les contributions relatives des phénomènes biogéniques et inorganiques à la formation des nodules de manganèse et de la croûte, sont encore controversées. Quelques activités des bactéries et des foraminifères sont rappelées et mises à jour en ce qui concerne les foraminifères, les xénophyophores et autres rhizopodes, aussi bien que les vers polychètes des nodules de manganèse, croûtes et sédiments du Pacifique central. En utilisant un matériel très fraîchement collecté avec des structures cytoplasmiques conservées, les investigations de l'auteur éclairent les problèmes spéciaux de biologie de la nutrition des groupes de rhizopodes des nodules, croûtes de manganèse et sédiments associés. Tous ces rhizopodes sont caractérisés par l'accumulation de volumes considérables de pelletes fécales (stercomata), contenant des particules biogènes et minérales. Ces pelletes constituent des résidus de nourriture digérée en dehors de la cellule, en contact avec l'eau de mer ambiante. Une théorie est avancée, selon laquelle, en « broutant » l'environnement sur une très grande superficie, les rhizopodes rassemblent, en même temps que les bactéries et les autres composants de leur alimentation, des particules d'oxyde métallique largement dispersées.

Durant la digestion, les particules accumulées sont sans doute soumises à des microzones à faibles conditions de pH et redox, facteurs qui gouvernent la chimie du manganèse. Tandis que le fer, et probablement le cuivre, sont retenus par les rhizopodes,

le manganèse est dissous, mais peut être précipité plus tard et accumulé immédiatement à côté des sites de digestion, au voisinage des foraminifères et autres rhizopodes, contribuant ainsi à la croissance des nodules. Selon ce modèle, les rhizopodes (et de surcroît les vers polychètes qui s'en nourrissent) contrôlent la concentration, la dissolution fractionnée et l'accumulation de métaux dans les régions oligotrophes des océans profonds.

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## INTRODUCTION

Manganese deposits are frequently found in subterranean waters, lakes and the sea. In remote, oligotrophic deep-sea areas with very low sedimentation, these ores often cover the soft bottoms densely, in the form of potato-shaped nodules with a concentric layered internal structure. On hard bottoms, there are manganese crusts. Essentially composed of manganese and iron, which are found in very variable amounts, the deep-sea manganese (or ferromanganese) accretions also contain small amounts (about 1%) of copper and nickel, and—in seamount environments—similar amounts of cobalt. Because of their valuable metal content, oceanic ore deposits have attracted considerable economic interest since the 1960s, and the conditions and causes of the formation of nodules and crusts have become the subject of interdisciplinary research. Introductions to numerous aspects of manganese nodule research have been published by Mero (1965), Cronan (1976), Glasby (1977*b*), Heath (1978), Cronan (1980), Fellerer (1980), Schneider (1981) and Halbach (1981). The mechanism of formation and growth of deep-sea manganese nodules (the following also holds true for the most part for crusts) has to be inferred from circumstantial evidence. The natural growth rate has often been estimated to be in the range of only a few millimetres per million years (see e.g. Sharma, Somayajulu, 1979), while the concentration of the participating metals in the ambient water is only in the range of few micrograms per litre or less (see Murray, Brewer, 1977; Klinkhammer, Bender, 1980). Natural conditions cannot be exactly simulated in the laboratory. On the basis of mineralogical, hydrographical and biological data concerning conditions prevailing in the nodule areas, however, several partially controversial theories have been suggested to explain nodule genesis. According to one line of research, the accretion of manganese-rich ores in the deep sea takes place by purely inorganic processes, in which the metal oxides precipitate at solid surfaces (nuclei) by adsorption and catalytic oxidation of manganese (II) and iron ions (see Crerar, Barnes, 1974; Glasby, 1974; Burns, Burns, 1975; Calvert, Price, 1977).

On the other hand, biologists have demonstrated that microorganisms are capable of forming and accumulating manganese oxides, and accordingly infer an important biogenic contribution to nodule formation. Bacteria and foraminifera have often been suggested as contributors to manganese nodule growth, and Sorokin (1972), when discussing the role of biogenic factors in the formation of such nodules, speaks of a clear example

of a biogeochemical process. Modern reviews on the biogeochemistry of manganese have been published by Marshall (1979) and Ehrlich (1981).

Nodule concentration is highest where benthic biomass, organic matter concentrations and rates of metabolism are lowest (Rowe, 1981). These relationships suggest an inorganic growth of nodules. On the other hand, close examination shows that inorganic solid surfaces do not exist in natural sea and fresh water. Every solid surface adsorbs within minutes of submersion a film of polymeric organic material, which bacteria colonize after several hours. The bacteria in turn attach extracellular, microfibrillar structures to the substratum. Finally, more highly organized representatives of the microflora and microfauna colonize the surface (compare Meadows, 1964; Loeb, Neihof, 1977; Dempsey, 1981). Organic surface films also cover manganese nodules. LaRock and Ehrlich (1975) demonstrated the existence of bacteria with an extensive slime network on nodules from comparatively shallow depths by means of scanning electron microscopy. Burnett and Nealson (1981) described microorganisms and an organic surface film on deep-sea nodules. Whether this organic layer is related to the formation or growth of nodules was not clearly established by Burnett and Nealson. They stated, however, that the organic surface layer and the associated microbiota found on manganese nodules must be taken into account in any model of accretion of manganese and iron on the nodules. Ghiorse (1980) described metal oxide encrustations on certain bacteria associated with microfibrillary structures derived from secretions from bacterial cell envelopes, and accordingly suggested a microbially-based mechanism for the accumulation of metals in connection with manganese ore accretions. Negatively-charged, extracellular polymers produced by bacteria inhabiting the surfaces of the ores could serve as cation exchange agents that scavenge divalent manganese or other metal ions, causing their accumulation on surfaces where the polymer-producing bacteria grow. The oxidation of the adsorbed manganese ions is a subsequent process, in which the bacteria could participate (see Ehrlich, 1980). The important feature in Ghiorse's concept is the reference to the special surface activity of extensive microfibrillar material on the cell body of bacteria. These microfibrils which have a colloid size range with a diameter of a few nanometres, are often produced in great masses. Their ubiquitous occurrence in waters and sediments, and their biological significance, are dealt with in an extensive literature (Leppard *et al.*, 1977). Slimy microfibrillar products are formed by many

organisms only in low nutrient media (Jannasch, 1979); their presence is consequently to be expected in oligotrophic marine regions. Biogenic microfibrils enormously magnify surfaces that are involved in adsorption processes, and for this reason, a synthesis of purely physicochemical and biological theories of manganese nodule growth is possible. As well as that of bacteria, the participation of foraminifera in manganese nodule formation has often been discussed, for instance by Graham and Cooper (1959), Greenslate (1974), Wendt (1974), Dugolinsky *et al.* (1977), Harada (1978), Margolis *et al.* (1979), Dudley (1979), Nesteroff (1979); in addition to foraminifera, nodule-colonizing metazoan groups have been mentioned by Thiel (1978) and Greenslate *et al.* (1974). Foraminifera tests have been encountered on and in manganese nodules, frequently in great numbers. They represent a solid framework in which precipitated metal oxides can accumulate (Greenslate, 1974). Other investigations have revealed iron and manganese oxides, sometimes in the form of micronodules, as relevant components of the test material (Greenslate, 1974; Dugolinsky *et al.*, 1977; Thiel, 1978; Dudley, 1979). In addition, manganese containing infillings in the tests have been described, and have been related to processes beginning after the death of the protozoa (Greenslate, 1974). In conjunction with the infilling, eventual dissolution of the tests takes place (Margolis *et al.*, 1979). Nesteroff (1979) proposed a model in which the calcareous tests of planktonic foraminifera are progressively replaced by ferromanganese hydroxides.

Test components and supposedly post-mortem infillings of foraminifera have stimulated the interest of geoscientists. The understanding of other structures has been restricted by the limitations of scanning electron microscopy, which preclude the observation of density differences in the soft bodies of fresh material. In the present work, light microscopy of foraminifera and similar protozoa (and a few polychaete worms), together with an examination of the soft parts of freshly collected material, have stimulated a consideration of a new biological mechanism of the accumulation of manganese ores in the deep sea.

## MATERIAL AND METHODS

During the cruise "Midpac 81" (June-July 1981) of the German research vessel "Sonne" (SO 18, cruise leader Pr. Dr. P. Halbach, Clausthal, FRG), 73 fragments of manganese crusts (mostly measuring 4-8 cm), 12 manganese nodules and 12 sediment samples from the Central Pacific between Hawaii and an area near the Line Islands from depths between 5369 and 1150 m were investigated. The stations of main interest for the present investigation are as follows (Table).

Immediately following collection, the specimens were placed in containers with cooled sea water (+ 4°C), and examined shortly thereafter in cool water under the stereo microscope at 25 × magnification. The sediments were carefully rinsed with cooled sea water on sieves

Table

### Location data.

Station 6:	59.7°N/165°59.8'W; depth 5356 m; red-brown radiolarian ooze.
Station 14:	8°56'N/164°34'W; depth 4922 m; manganese nodules.
Station 15:	8°57'N/164°35'W; depth 4880 m; foraminiferan ooze.
Station 31:	about 9°8'N/164°46'W; depth about 2000 m; very rough manganese crust, 5 cm thick.
Station 32/33:	about 9°12'N/164°51'W; depth about 1150 m; manganese crust, 1.5 cm thick.
Station 43:	13°0'N/164°59'W; depth 3040 m; rough manganese crust.
Station 58:	13°12'N/165°28'W; depth 1508 m; limestone with thin manganese crust.
Station 76:	about 19°24'N/170°59'W; depth about 1200 m; manganese crust.
Station 109:	20°21'N/170°35'W; depth 4250 m; brown clay with radiolarians.
Station 111:	20°5'N/170°38'W; depth 1332 m; very rough manganese crust, 1.5 cm thick.

with 73 or 250 µm mesh, in order to remove the bulk of fine fractions. The samples were stored at + 4°C. Sampling was done with free-fall grab-samplers or a multichambered heavy box dredge (construction by URAG, FRG); the application of both methods yielded well-preserved nodule and crust material with a minimum of surface damage. Samples from the sediment surfaces were taken with small plastic jars attached to the free-fall grabs; the jars had a 73-µm-screen covering a hole in the bottom and a plastic cap that was closed by the action of the grab-sampler. A possible admixture of planktonic organisms had to be taken into consideration.

Foraminiferan faecal material was examined by energy dispersive X-ray fluorescence analysis in a particular array performed by the Chemist A. Prange (University of Hamburg and GKSS) on board ship.

Reference material was preserved in 4% formaline/aqua dest. A selection of biological entities was transferred onto permanent glycerine-mounted microscopy slides and deposited in the authors' collection at the Institut für Meeresforschung in Bremerhaven.

## RESULTS

### Foraminifera and similar protozoa on crusts and nodules

Hard substrata in the samples were almost exclusively colonized by foraminifera and foraminifera-like protozoa. In addition, there were very rare, small polychaetes in tests similar to those of agglutinating foraminifera and which were only apparent after dissection under the microscope. Siliceous sponges and very rare Actinaria and lepadomorph Cirripedia were also identified.

The protozoa occurred in the following shapes:

1) soft, fine, unbranched or branched tubes (1-20 mm long, about 15-85 µm diameter), either vertically positioned or lying flat and loosely attached on the substratum. Some vertical structures were setiform with the thin end attached to the nodule; 2) white, hard or elastic dome-shaped structures (1-5 mm, see Fig. 1). These comprised agglutinations of globigerinid foraminifera tests or fragments thereof, and/or coccoliths.

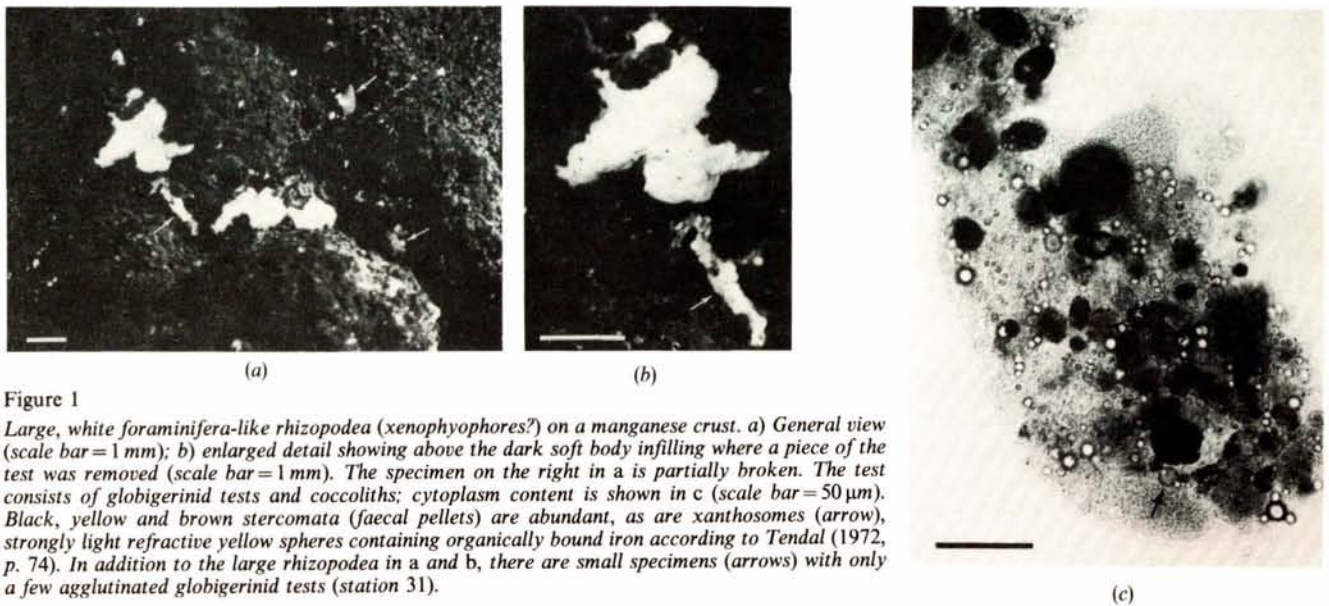


Figure 1

Large, white foraminifera-like rhizopodea (*xenophyophores?*) on a manganese crust. a) General view (scale bar = 1 mm); b) enlarged detail showing above the dark soft body infilling where a piece of the test was removed (scale bar = 1 mm). The specimen on the right in a is partially broken. The test consists of globigerinid tests and coccoliths; cytoplasm content is shown in c (scale bar = 50 µm). Black, yellow and brown stercomata (faecal pellets) are abundant, as are xanthosomes (arrow), strongly light refractive yellow spheres containing organically bound iron according to Tendal (1972, p. 74). In addition to the large rhizopodea in a and b, there are small specimens (arrows) with only a few agglutinated globigerinid tests (station 31).

Depending on the different materials, their surface was either very coarse-grained or smooth; 3) hard, branched or unbranched, white or cinnamon-coloured tubular structures of different materials very firmly attached to the substratum (1-20 mm long, compare the Figure 1 in Thiel, 1978); 4) inconspicuous, two-layered, very thin (about 50 µm), chitinous "membranes" (Fig. 3), several millimetres in size, which may have been already observed by Greenslate (1974). These perhaps bear a genetic relationship to the dome-shaped agglutinating rhizopodea already described because honeycomb-like chitinous structures like those of the membranes were observed in some agglutinations; 5) rare, soft spheres (1 mm diameter, 2 specimens at station 76), adhering directly to the surface of the crust; 6) fairly common slimy filaments and areas, mostly undetachable and therefore impossible to examine at higher magnifications.

Usually, these structures did not cover more than 1% of the crust or nodule surface. The densest colonizations were found on crust pieces from station 31, where about 5% of the surface was covered by the described structures. The remaining areas of crusts and nodules were bright and glossy.

In more than 51 specimens of all the foraminiferan types described above, accumulations of colourless opaque, yellow, brown, black (Black-speckled), round or oval pellets, generally with a diameter of 10-25 µm, occurred (compare Fig. 1-3). In some cases, the whole test of a foraminifer (or similar rhizopod) was filled by these structures. These pellets were products of the living foraminifer; they are described in the zoological literature as "stercomata", and are regarded as faecal pellets (Rhumbler, 1923, p. 75; Boltovskoy, Wright, 1976, p. 18-19; review of older literature in Tendal, 1972, p. 73). According to these references, undigestible mineral and biogenic particles are cemented together by a mucopolysaccharide substance.

A capacity for sorting different food components probably exists during the formation of the faecal pellets, because differently coloured and structured

stercomata occurred in the same individual. Large oval stercomata composed of smaller globular pellets were often visible.

The frequent presence under the foraminiferan tests, directly on manganese nodules, of large stained masses of stercomata suggests that the latter are related to ore accumulation and accretion. Certain spherical structures described by Greenslate (1974), Dugolinsky *et al.* (1977), Margolis *et al.* (1979) and Nesteroff (1979), and sometimes compared with micronodules, were probably identical with stercomata or their diagenetic products. A theory of ore accumulation based on the feeding biology of foraminifera and similar rhizopodea will be proposed in the discussion below.

A great portion of the tubiform foraminifera living on manganese crusts and nodules belong to the enigmatic, but recently described superfamily Komokiacea (Tendal, Hessler, 1977). Hessler (1974) presented these foraminifera under a Russian working term "kamochki" (today's English transliteration "komoki") in the western literature. It is noteworthy that his material also originated from a manganese nodule area (Northern Pacific; compare Hessler, Jumars, 1974). Komoki are seemingly very abundant in oligotrophic deep-sea areas (Tendal, Hessler, 1977); their fragility and inconspicuous appearance, however, prevented an earlier investigation and evaluation of their ecological significance.

The dome-shaped agglutinations of coccoliths and globigerinoid tests, as well as the "membranes" and "soft spheres", may belong to the peculiar rhizopodean group *Xenophyophorea* because typical barite crystals sometimes have been detected in their soft bodies. *Xenophyophores*, which may attain a size of several centimetres, have been almost exclusively reported from deep-sea soft sediments. Because they are closely related to the foraminifera (*see* Tendal, 1972, for review), and because their biology appears to be very similar to that of the komokiacean foraminifera (Tendal, 1979), I tentatively include all the foraminifera-like forms described above in the context of foraminifera. Characteristic of many deep-sea rhizopodea, namely



Figure 2  
Yellow, brown and black stercomata and xanthosomes of an 800- $\mu\text{m}$  large dome-shaped rhizopod (xenophyophore?), viewed from the bottom side (scale bar = 20  $\mu\text{m}$ ) (station 14).



Figure 3  
Two-layered "membrane" (xenophyophore?) from a manganese nodule. Honeycomb-like arranged chitinoid filaments (linellae?) exist between the top and bottom layers, forming chambers that contain stercomata (scale bar = 50  $\mu\text{m}$ ) (station 14).

xenophyophores, komoki and other foraminifera, are the enormous accumulations of faecal pellets (stercomata) in comparison to the small volumes occupied by protoplasm (Tendal, 1979).

Because the dark colour of the stercoma infillings in many foraminiferan tests on manganese was suggestive of heavy metal oxides, a preliminary analysis was made on board of RV "Sonne". From a large foraminifer (20 mm long, 1-2 mm broad, with constrictions like a string of beads, station 43) the faecal material was removed with a glass capillary and examined by energy dispersive X-ray fluorescence analysis. Taking the iron content as standard (i.e. iron = 100%), three analyses

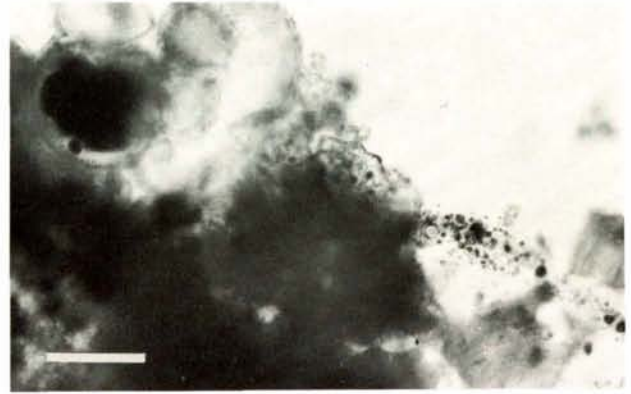


Figure 4  
Margin of a dome-shaped, 1,700- $\mu\text{m}$  large agglutination of globigerinids and coccoliths, viewed from the bottom side. Stercomata are collected in the soft body of the inhabiting sedentary rhizopod and seemingly transported into the test cavity of the globigerinid (scale bar = 50  $\mu\text{m}$ ) (stations 32/33).

yielded manganese contents of only 6-16%, whereas copper contents ranged between 16.5 and 46.6%. Benzidine tests for manganese (IV) in the protoplasmatic contents of the dome-shaped rhizopodea shown in Figure 1 gave a weak positive reaction in the large opaque stercomata under the microscope. The conspicuous brown and black stercomata, however, gave a negative reaction. Black grains in stercomata densely filling the soft, spherical form were insoluble in hydrochloric acid.

#### Rhizopodean protozoa in sediments

Apart from one nematode (*Siphonolaimus*, order Monhysterida), no metazoa were recovered during the examination of 12 sediment samples (20 ml each) aboard ship. The dominant inhabitants of the soft bottoms were foraminifera and foraminifera-like amoebae, the size of which lay in the range of 1 mm. As on the nodules, thin-walled, branched tubes filled with stercomata occurred in the sediments (komoki, about 1 specimen per ml of sediment, Fig. 5). There were also flat (about 10  $\mu\text{m}$ ), two-layered "membranes" (thickness

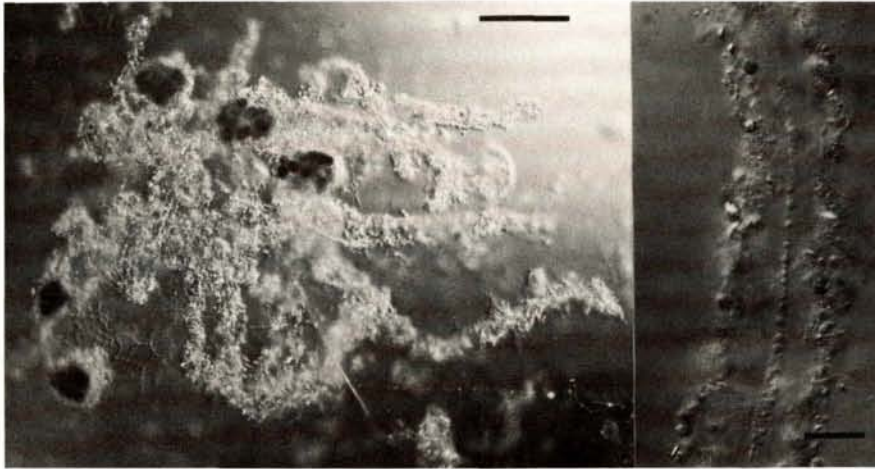


Figure 5  
Branched tubular foraminifer filled with brown and black stercomata (scale bar = 50  $\mu\text{m}$ ) (station 6).



Figure 6  
Soft, two-layered, 500- $\mu\text{m}$  large, thin "membrane" (xenophyophore?) with many stercomata in the interspace (scale bar = 50  $\mu\text{m}$ ) (station 15).

of the soft, folded walls 1  $\mu\text{m}$ ) containing large masses of black-speckled and brown oval stercomata in the interspace (Fig. 6). Of particular interest were amoeboid, apparently still unknown organisms, to which I would tentatively give the name, "slimy foraminifera". Their cytoplasm contained sediment particles at the surface without forming a sharply defined wall (Fig. 7-8). Sometimes an irregular, chitinoid wall occurred (Fig. 9). Brown and black-speckled stercomata occurred either dispersed in the cytoplasm or were concentrated in large "nests" measuring 60  $\mu\text{m}$  (Fig. 7-8). The presence of stercomata pointed to the foraminiferan relationship of these organisms. The abundance of non-testate rhizopodean protozoa cannot be assessed with accuracy. On board ship I estimated a density of 1-5 individuals of 1-mm size per 1 ml of sediment. However, I now believe this estimate to have been too low, as I presumably mistook many amorphous structures for clay



(a) (b)

Figure 7  
"Slimy foraminifer", Nomarski-photograph. a) General view, showing accumulations of stercomata (scale bar = 100  $\mu\text{m}$ ); b) detail of a branch of this specimen, optical section (scale bar = 10  $\mu\text{m}$ ) (station 6).

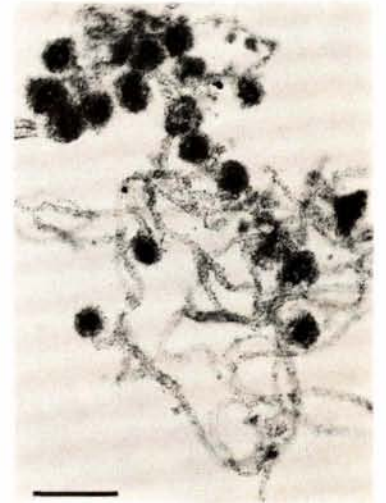


Figure 8  
"Slimy foraminifer" (scale bar = 200  $\mu\text{m}$ ) (station 6).

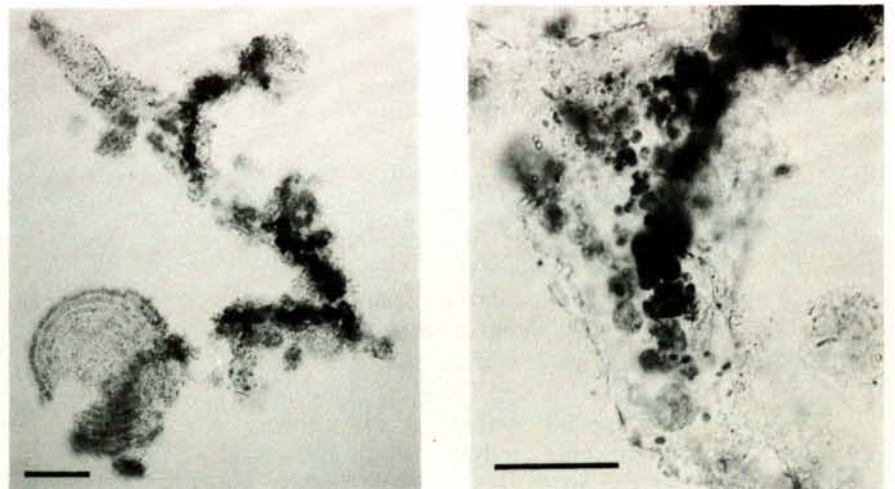


Figure 9  
"Slimy foraminifer". a) General view (scale bar = 100  $\mu\text{m}$ ); b) enlargement of central part to demonstrate delicate chitinoid wall and various stercomata (scale bar = 50  $\mu\text{m}$ ) (station 6).

flakes, and isolated and preserved only a small selection. According to a list of Tendal (1979), comparable amoebae from depths of more than 1 500 m have been seen only by Burnett (1977; see also Burnett, 1973, dealing with an abundant occurrence of small amoebae at 1 200 m depth). An illustration given by Burnett (1977) shows a 30- $\mu\text{m}$  large structure with stercomata. Thiel (1978) cited a personal communication of Burnett reporting a concentration of 20 000 non-testate amoebae/cm<sup>2</sup> of sediment from the North Pacific. Thiel (1979) reported 2 000 specimens/cm<sup>2</sup>. My assumption is that slimy foraminifera and other amorphous rhizopodea contribute to the general metabolism at oligotrophic deep-sea bottoms to a significant extent that must be of interest to the ecologist and the geochemist alike.

### Polychaetes on manganese crusts

At five stations at depths between about 1 250 and 3 000 m, 13 polychaetes in tubes were found. The tubes consisted either of a solid, homogeneous calcareous substance or of agglutinations of globigerinid tests and coccoliths, and were of lengths ranging between 3 and 15 mm. Squash preparations were made of two polychaetes. Figure 10, which concerns the gut contents of a serpulid living in a calcareous tube, shows dark faecal pellets comprising densely packed foraminiferan stercomata. A globigerinid test is also visible. In addition, dark brown spheres, presumably manganese micronodules, with diameters measuring up to 17  $\mu\text{m}$ , were observed. In another polychaete, stercomata were built into the agglutinated tube and also occurred in the gut contents. From these observations I infer that small polychaetes on manganese crusts feed on agglutinating foraminifera and concentrate the inorganic components of their prey.

### DISCUSSION

The voluminous masses of stercomata (faecal pellets) contained in the tests of foraminifera and similar organisms and situated in many forms directly on the manganese nodule surface, suggest, as mentioned above, that the feeding biology of these rhizopodean protozoa

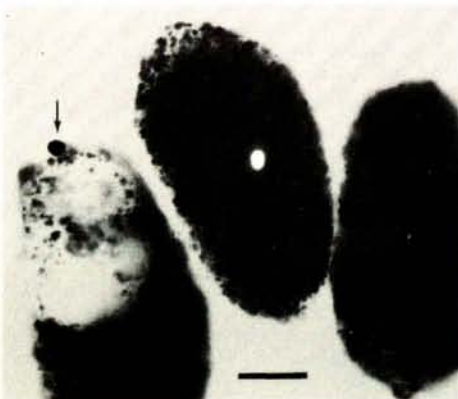


Figure 10

Faecal pellets from the gut of a sedentary polychaete containing foraminiferan stercomata, a globigerinid test (left), and brown micronodules (arrow; scale bar = 50  $\mu\text{m}$ ) (station 58).

is related to ore accumulation and accretion on nodules and crusts.

Foraminifera are omnivores, browsing their substrata with long pseudopodia that are extended from their tests in the range of several millimetres or even centimetres (reviews Boltovskoy, Wright, 1976, p. 15-19; Lee, 1980). Bacteria, detritus and the organic primary film on solid surfaces (including sediment particles) must be considered as a potential food source of deep-sea foraminifera and other rhizopodea. Bacteria have been recognized as a food component indispensable for some estuarine foraminifera (Muller, Lee, 1969). Ehrlich (1980) suggested that a complicated food web (including foraminifera and other protozoa), based on manganese oxidizing bacteria, may exist on the surface of manganese nodules. Microorganisms and other protein-containing particles are digested in the foraminifera and indigestible residua are collected in the stercomata. Thus, metal oxides concentrated e.g. by bacteria may be concentrated further by foraminifera.

According to Lengsfeld (1969), the digestive process in the foraminifer *Allogromia* takes place in its test-covered body, but in extracellular spaces (lacunes) that are incompletely enclosed by a great number of fine cytoplasmic strands that leave open connections with the ambient seawater. Nyholm and Gertz (1973) observed this with another species, and Tendal (1972, p. 78) reviewed further indications of extracellular digestion in foraminifera and xenophyophores. My own findings concur with these observations. The stercomata did not appear firmly enclosed in the cytoplasm, but were often easily washed out in the preparation for microscopic examination. Tendal (1979) suggested that the stercomata of deep-sea rhizopodea may be "fermentation chambers" operating in a symbiotic relationship between rhizopodea and bacteria, but offered no direct proof of the existence of these bacteria.

During digestion by the rhizopodea, the accumulated particles, while still in contact with the ambient seawater, are subject to a particular microenvironment presumably involving lowered pH and redox conditions, i.e. factors that govern the chemistry of manganese. Accordingly, I presume that feeding foraminifera and similar protozoa collect, over a wide range, metal oxide particles that are associated with bacteria and other food components and dissolve a part of the metal oxides, mainly manganese, during digestion. Later this fraction may be reprecipitated and accreted immediately adjacent to the sites of digestion under and around the sedentary foraminifer, thus contributing to nodule growth. Nesteroff (1979) found a higher concentration of iron relative to manganese in structures which I believe to have been stercomata, whereas the test wall of the foraminifera analyzed by Nesteroff had a composition more closely resembling that of the associated manganese nodules. These findings, together with my own observations on the relatively low manganese contents in the stercomata, are indicative of a metabolically effected separation of iron and manganese.

According to Bernstein *et al.* (1978) it seems likely that in the Pacific deep sea there is not a square centimetre

of sediment surface which is not in some way affected by the activities of benthic foraminifera. Regarding this condition, I suspect that foraminifera (and xenophophores), as centres of decomposition (see Nyholm, Gertz, 1973), are important for the mobilization of metal oxides by reductive dissolution within oligotrophic sediments. The problematic question of the mobilization of metals in this environment was discussed with regard to manganese nodule formation e.g. by Hartmann (1979), Halbach and Özkara (1979), Marchig and Gundlach (1979) and Müller and Mangini (1980).

In addition to iron, comparatively large amounts of copper (16.5-46.6% related to iron) were deposited in the faecal material of the one foraminifer investigated. Therefore, copper compounds were probably concentrated in the stercomata within the test and not, as suggested by Dudley (1979), excreted into the surrounding water. The association of copper and organic material, especially plankton organisms or detritus, has often been reported (reviews Murray, Brewer, 1977; Lewis, Cave, 1982); in the context of the composition of manganese nodules this condition is discussed e.g. by Colley *et al.* (1979), Margolis *et al.* (1979), Halbach *et al.* (1981) and Frazer and Fisk (1981).

Besides possibly contributing to the accumulation of metal oxides and their partial mobilization by changing chemical conditions in micro-environments, foraminifera and other rhizopoda may perform further particular transport functions. As a result of browsing, particles will be removed from the substratum. This removal, according to Dugolinsky *et al.* (1977), may

explain the puzzling concentration of manganese nodules at the sediment surface. In spite of slow growth, nodules are not covered by the associated sediments that are accumulating at a faster rate (for a discussion of this paradox see Glasby, 1977a; Heath, 1978; Sorem *et al.*, 1979).

It is possible that agglutinating foraminifera and similar rhizopoda enter with their soft body into the initially empty adhering tests of plankton organisms which constitute the housing of the sedentary rhizopod. In two preparations (Fig. 4) within globigerinoid tests, stercomata were found, the material of which was obviously transported in the cytoplasm of the living sedentary rhizopod. The growth of manganese oxides in cavities of planktonic microfossils (see Dugolinsky *et al.*, 1977) may be due in some instances to such material transport.

Foraminiferan stercomata have been found in the guts of small polychaetes living on manganese crusts. These worms may thus be responsible of a further concentration of metal oxides collected by their prey and their subsequent deposition on manganese crusts.

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