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In situ conditions and interactions between microbes and minerals in fine-grained marine sediments: A TEM microfabric perspective

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Abstract

Microbes, their exocellular secretions, and their impact on the mineralogy and microfabric of fine-grained continental margin sediments were investigated by transmission electron microscopy. Techniques were used that retained the in situ spatial relations of both bio-organic and mineralogical constituents. Photomicrographs were taken of characteristic mineral-microbe associations in the first meter of burial at conditions ranging from aerobic to anaerobic. Single-celled prokaryotes, prokaryotic colonies, and eukaryotic organisms were observed as were motile, sessile, and predatory species. Bacterial cells dominate the assemblage. The most commonly observed mineral-biological interaction was the surrounding, or close association, of isolated heterotrophic bacterial cells by clay minerals. Almost without exception, the external surfaces of the bacteria were covered with secreted exocellular slimes composed of cross-linked polysaccharide fibrils. These fibrils act to bind sediment grains into relatively robust microaggregates, roughly $\leq$25 μm in diameter. These exocellular polymers can significantly impact the interaction between microbes and minerals, as well as the chemical and physical transport of fluids and dissolved aqueous species through the sediment. Although pore water chemical profiles from the field sites studied have dissolved Fe and Mn, no close association was found between the microbes imaged and precipitated metal oxyhydroxides or other authigenic minerals, such as is commonly reported from laboratory cultures.

Introduction

The impact of microbes on the cycling of carbon and other dissolved biogeochemical species between fine-grained continental margin marine sediments and the overlying water column is well known, as is their influence on authigenic mineral precipitation and organic matter degradation during early diagenesis (e.g., Berner 1985; Heinrichs 1992). Less well studied are the actual microbial species present, their depth and spatial distribution, their interaction with associated clay minerals, and their impact on sediment microfabric and physical properties. Nevertheless, such information is crucial for understanding how microbes in continental margin sediments directly affect their immediate surroundings. This information also is needed to formulate mechanistically based models of microbe-mineral interaction and to interpret accurately chemical proxies that indicate microbial activity and microbe-mineral interactions in fine-grained sedimentary environments.

The influence exerted by bacteria on continental weathering rates has recently attracted significant attention. As a result, studies using transmission and scanning electron microscopy (TEM and SEM, respectively), as well as other high-resolution techniques, have been carried out recently to identify specific interactions between microbes and minerals (e.g., Thorseth et al. 1995; Bennett, P.C. et al. 1996; Barker and Banfield 1996; Barker et al. 1997; Granatham et al. 1997). Similar high-resolution studies focusing on the marine environment and, in particular, the interactions in fine-grained sediments are few (Bennett, R.H. et al. 1996; Lavoie et al. 1996a; Ransom et al. 1997).

Most studies of microbes in their sedimentary habitats have used SEM or TEM because of the small size of these organisms, commonly $\leq$1 μm, and their close association with detrital minerals. These methods are complementary, with SEM being better suited for morphological and topological studies as well as studies of coarser-grained clastic material (i.e., fine silt and sand) and TEM being better suited for finer-grained material (i.e., $<$4 μm) and investigations of interfaces, organic matter, and biodiversity. A comparison of SEM images from marine sands by

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Weise and Rheinheimer (1978) and TEM micrographs from fine-grained continental margin sediments by Ransom et al. (1997) illustrates the strengths and different scales of the two techniques.

In marine sediments, SEM emphasizes organisms (morphology only) that occur along relatively large-scale mechanical discontinuities where fracturing can occur (e.g., burrows and pore fluid channels, changes in grain size, framework grain-matrix grain boundaries, etc.) whereas TEM sections are best suited for studies of sample cross sections. Cross-sectional views permit examination of interfaces between different sediment constituents, both organic and inorganic, and textural relationships in the sediment matrix away from sediment structural or compositional discontinuities. Proper preparation and staining of TEM sections also allow preservation of the internal structures of organic matter and microbes so that they can be identified more completely. One limitation of the TEM method, however, is that common sediment framework grains, like quartz and feldspar, are difficult to ultrasection. Such minerals commonly shatter during sectioning or are plucked from the section. This severely inhibits TEM investigations of microbes associated with the surfaces of large framework grains.

SEM studies of microbes in marine sediments have focused primarily on bacteria and microbial habitats in sands and silts (Meadows and Anderson 1966; Weise and Rheinheimer 1978; DeFlaun and Mayer 1983) not those in finer-grained sediments. Despite a few early attempts (Smart and Tovey 1981: Figs. 9.4 and 9.6; Smart and Tovey 1982: Fig. 1.18; Moriarity and Hayward 1982), TEM studies of microbe-mineral relations in fine-grained sediments are a relatively recent phenomena (Lavoie et al. 1996a; Bennett, R.H. et al. 1996; Ransom et al. 1997). The present communication expands this TEM data set, focusing on what TEM studies have indicated to date about the influence of microbes on the microfabric and mineralogy of fine-grained continental margin sediments and what the mechanisms of interaction are between these microbes and their surrounding mineral milieu. This communication also compares these relations to those reported from soils, a much more extensively studied and better understood environment.

Methods

TEM microfabric analysis and observation of the in situ textural relationships between the mineral, organic, and biological constituents of aquatic sediments require careful sampling and immediate initiation of processing (within minutes). Detailed summaries of standard coring devices and the extent to which coring disturbs the sediment can be found in Richards (1962) and Bennett et al. (1977). Samples prepared for the present study were taken from recently deposited fine-grained sediments using the soda straw mini-coring method of Lavoie et al. (1996b). The soda straw method permits retrieval of undisturbed fine-grained sediment samples that are appropriately sized for TEM preparation. The thin wall of the straw (~20 μm) prevents distortion of sediment microfabric. The straw also provides a container that facilitates transport of fragile samples, as well as a receptacle into which preservation or exchange fluids can be dispensed and drained, minimizing the amount of time and liquid required for fluid exchange.

Step-by-step procedures used for the preservation, critical point-drying, embedding, and sectioning of fine-grained marine sediments are summarized in Bennett et al. (1977) and Baerwald et al. (1991). These techniques retain intact the original in situ spatial arrangement of the constituent minerals, with the sediment shown in Figure 1 being prepared in this manner. The extent of textural preservation of fine-grained sediments using these methods was investigated by Bennett (1976). He found that the void ratio data of raw sediment and that calculated from digitized TEM images of the same sediment that had been processed for TEM analysis were the same, indicating no change in the arrangement of grains during sample processing. It should be noted that the 2–3 week time period for fluid exchange with organic solvents required to critical point dry fine-grained sediments for TEM is not suitable when organic or biological constituents are to be imaged. Over these time scales, solvents leach the organic matter. Preservation of mineral-bio-organic associations (Figs. 2–4) requires modification of standard microfabric techniques and involves smaller sample sizes and rapid fluid exchanges (~10 min per step) to dehydrate the sample prior to embedding. Baerwald et al. (1991) presented a brief review of the procedures used in this study for the high-quality fixation, preservation, and embedding of samples containing microorganisms and sedimentary organic matter. A detailed description of the sampling and the preparation of water stable aggregates from which the microbes imaged in the present study were taken are given in Ransom et al. (in preparation).

Samples from which images in this communication were produced were fixed with 4% gluteraldehyde, post-fixed in osmium tetroxide, fluid exchanged as indicated above, embedded in Spurr resin, and sectioned with an ultramicrotome. Organic and biological constituents were stained with uranyl acetate and lead citrate following Hayat (1970). In some cases, ruthenium red (Luft 1971) was used to increase the visibility of polysaccharide fibrils associated with microbes in the sediment. Samples were mounted on TEM grids, carbon coated, and imaged with a Phillips 300kV TEM.

Leppard et al. (1996) examined the textural artifacts of various TEM preparations, one of which employed gluteraldehyde, Na-cacodylate buffer, osmium tetroxide, and Spurr resin in a preparation nearly identical to the one used herein to generate Figures 2–4. Results of their analysis show that, with the exception of a reduction in the volume of microbial polysaccharide fibrils, the spatial and textural preservation of the mineral and bio-organic constituents of geological samples was good to excellent. They found no noticeable volume reduction in organic

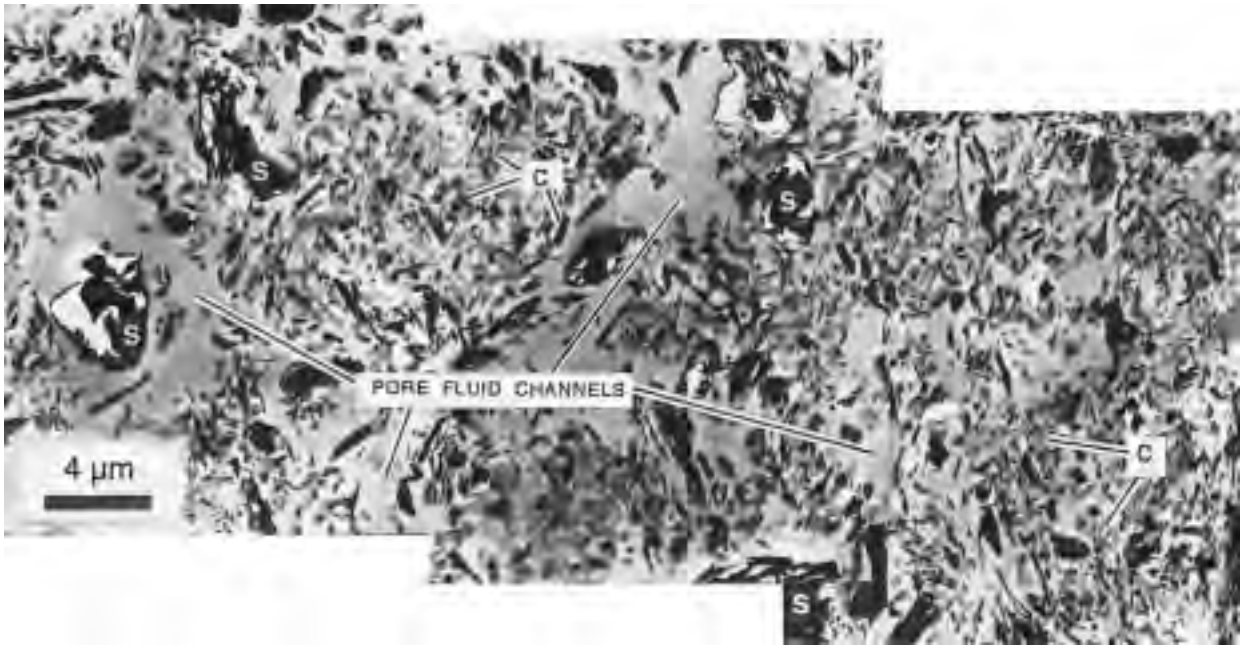

FIGURE 1. Typical in situ micro-architecture of fine-grained (~40% clay, 60% silt) continental margin sea-floor sediments in the first meter of burial. Note distinct fluid escape channels separated by domains of clay-dominated sediment matrix with aggregated structural characteristics. Micrograph is of a critical point-dried, continental slope sediment from ~2 km south of Cape Mendocino off the northern California coast that was deposited in 720 m of water and buried to 38 cm. The letter *S* denotes silt grains. Clays (c) are indicated by thin dark linear particles and medium- to light-gray equant flakes. The method used to prepare this sample did not preserve the organic matter or resident microbes.

matter when ruthenium red was used. In our samples, the absence of large voids in sections we imaged, the well-preserved external morphologies and internal details of the organisms, the similarity of the clay fabric and tactoid arrangements to those in critical point-dried samples, and the intimate intertwining of polysaccharide fibrils around and between mineral grains adjacent to microbes indicate little or no change in the textures of the sediments shown in Figures 2–4 as a result of our sample preparation.

RESULTS AND DISCUSSION

Marine sediment microfabric and the microbe-mineral environment

The architectural arrangement of grains in Figure 1 is typical of most fine-grained continental margin marine sediments in the first few meters of burial (Burkett 1992; Bennett, R.H. et al. 1996; Lavoie et al. 1996a; Ransom et al. 1997). It is within this complex arrangement of silt grains, clay minerals, bioclasts, organic matter, microchannels, and pore spaces that sediment microbes live and interact with minerals, pore water, organic substrates, and one another. Characteristic of marine sediments and evident in Figure 1 are relatively robust microaggregates generally $\leq$25 μm in diameter. These aggregates are moderately resistant to dispersal in water and are composed of minerals, organic remains, microbes, and microbial secretions (see aggregated clay-rich assemblage that occurs just above the text label in Fig. 1 and is bounded on the bottom by pore fluid channels indicated by upward-directed black lines). Similar aggregates composed of clays, organic matter, and microbes are well documented in the soil literature and thought to result from a combination of biological binding and in situ wetting and drying (Edwards and Bremner 1967; Tisdall and Oades 1982; Bennett and Hulbert 1986; Bartoli et al. 1988; Tisdall 1994). The formation of aggregates in permanently subaqueous marine environments obviously does not involve cycles of wetting and drying. However, the structural features of these sediment aggregates are similar to those of marine snow aggregates traveling laterally in the nepheloid layer just above the sea floor (Ransom et al. 1997, 1998).

Unlike organisms living at the sediment-water interface, microbes dwelling in fine-grained marine sediments must live in spaces that can comfortably contain them. As shown in Figure 1, there are various sites where such organisms can live. In soils, bacteria tend to occupy pores $<$5 μm in diameter (Foster 1988) and, outside of the rhizosphere, they occur within aggregates as opposed to outside them (Kilbertus 1980). Soil-dwelling protozoa are found in open contiguous vadose channels (Foster 1988). Similar to their occurrence in soils, bacteria in the continental margin sediments examined here are generally found as single entities inside pores in sediment aggregates (Fig. 2). On rare occasions, colonies encased in an exopolymer capsule and consisting of a single species are

also present (Fig. 3). It seems likely that these microbes will be exposed to different chemical conditions than those microbes living on sand grains or in burrows, pore fluid channels, or the sediments directly adjacent to these fluid pathways. These aggregate-dwelling microbes may be different in kind, shape, metabolic activity, and diversity from those living in areas where fluids are more readily exchangeable with the outside environment (e.g., by analogy with soils see Foster 1985; Foster and Dormaar 1991; Ladd et al. 1993). At present, no conclusions can be drawn regarding the preferred habitats of marine sediment-dwelling protozoa or other large microbial classes due to the extremely limited number of available observations.

In the centers of the continental margin sediment aggregates observed in the present study, anaerobic conditions probably prevail. This is suggested not only by the high-sediment depositional rates characteristic of continental margin deposits, but also by microelectrode studies of marine snow aggregates (Alldredge and Cohen 1987), which have found anoxic conditions prevailing in the interior of marine snow aggregates suspended in oxygenated waters. The observed prevalence of bacteria inside fine-grained marine sediment aggregates, although present in less metabolically attractive sites than those on aggregate perimeters or in fluid micro-channels, may be because these organisms are shielded from predatory microorganisms, by analogy with what is known about soil microbial ecology (e.g., Foster and Dormaar 1991). In addition, the aggregated sedimentary material would also make incorporated microbes less susceptible to attack by digestive enzymes of deposit-feeding benthic meso- and macro-fauna.

Chemical considerations affecting microbes in marine sediments

Fine-grained marine sediments are generally oligotrophic, meaning nutrients necessary for the optimal sustenance of microbial metabolic activity and rate of reproduction are not present. In such systems, short periods of relatively fast microbial growth are followed by slow growth or dormancy (Veldkamp et al. 1984). As a result, microorganisms in natural systems do not generally achieve the sizes obtained in laboratory cultures. For example, bacteria in soils (Bae et al. 1972; Lundgren 1984; Foster 1985, 1988) and marine sediments are commonly 0.2–0.5 μm in diameter, which is ¼ to ½ of their size under ideal laboratory conditions. By far the most common microbes observed in the fine-grained marine sediments examined to date appear to be sessile bacteria ~0.3–0.5 μm in diameter. These microbes are intimately linked to the surrounding minerals by web-like masses of exocellular polysaccharide fibrils (Fig. 2). The reduced size increases the surface area/volume ratio of the cell and is generally taken to indicate that organisms have minimized their energy expenditure to remain viable under oligotrophic conditions (Characklis et al. 1990).

Microbes in marine sediments in the first few meters of burial are generally (1) aerobes that get their energy by passing electrons along a series of electron acceptors to O_2; (2) anaerobes that live only in the absence of oxygen, get energy by fermentation, and produce low molecular weight organic compounds; or (3) facultative anaerobes that can operate in either mode depending on environmental conditions. In fine-grained continental margin sediments, aerobic environments generally occur only at or within a few millimeters of the sea floor or along the perimeters of irrigated burrows (Mayer 1993). In the vast bulk of the sediment, anaerobic conditions prevail; and there is a distinct hierarchy of redox reactions that result from the microbial degradation of organic matter. Different reactions dominate at different depths in the sediment column, the first being oxic respiration that is followed by denitrification and then followed progressively by manganese and iron oxyhydroxide reduction, sulfate reduction, and methanogenesis (e.g., Wang and Van Cappellen 1996). Reduced pore water species, Mn^{2+}, Fe^{2+}, NH_4^+, H_2S, and CH_4 are produced. These species are commonly used as indicators of the intensity of sediment microbial activity and a measure of how much sedimentary organic carbon is converted to CO_2 and returned to the ocean (e.g., Berner 1980; Soetaert et al. 1996). In laboratory and metal-rich natural systems, some of the redox steps appear to coincide with the precipitation or dissolution of Mn and Fe oxyhydroxides or pyrite directly adjacent to the bacteria (Nealson and Tebo 1980; Ferris et al. 1989a; Fortin et al. 1997; Tebo et al. 1997). No such associations have been observed in the TEM images of fine-grained continental margin sediments studied to date.

Microbial ecology of marine sediments

In most surface and near-surface geologic environments microbes (organisms ~1 μm in size) and other single-celled organisms (protozoa, fungi, etc.) are present in large numbers. In one gram of soil, 10^7–10^9 bacterial cells, 10^5–10^6 actinocytes, and thousands of amoebae and other large predatory eukaryotic cells are commonly present (Foster 1988). The bacterial population of marine sediments is similar (Rublee 1982; Craven et al. 1986;

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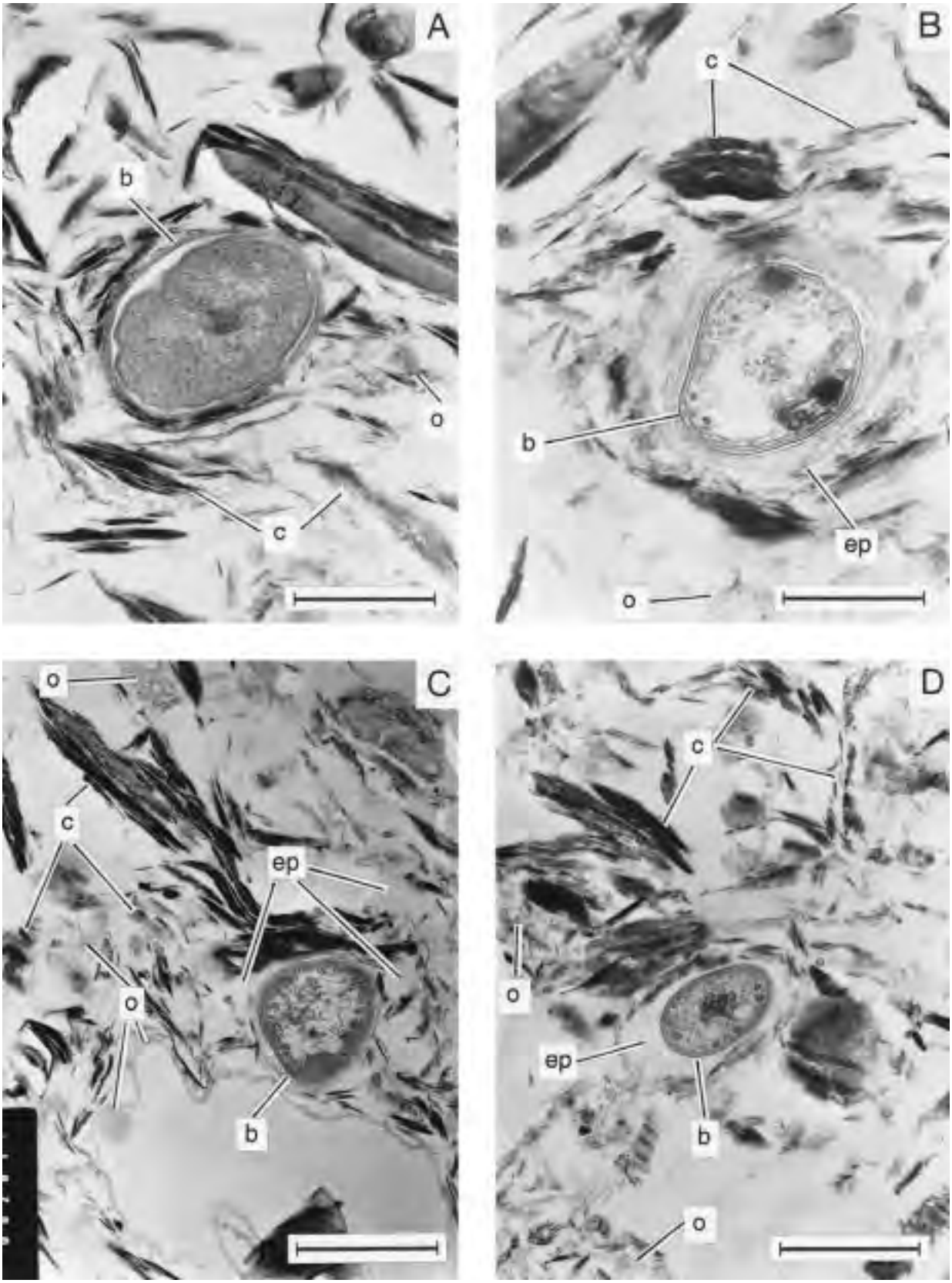
Figure 2. TEM micrographs showing the characteristic relationships in fine-grained marine sediments between bacteria (b), their exocellular polysaccharide secretions (ep), and the surrounding sediment matrix of clay (c) and organic matter (o). Samples are from surface and near-surface sediments taken from water depths of ~7 m in Eckernforde Bay, Germany. Scale bars denote 0.5 μm. Note the nearly universal presence of exocellular polysaccharide fibrils between cells and adjacent minerals, the close association of bacteria and clay minerals, and the general tangential arrangement of clay minerals around the cells and their exopolymer capsules.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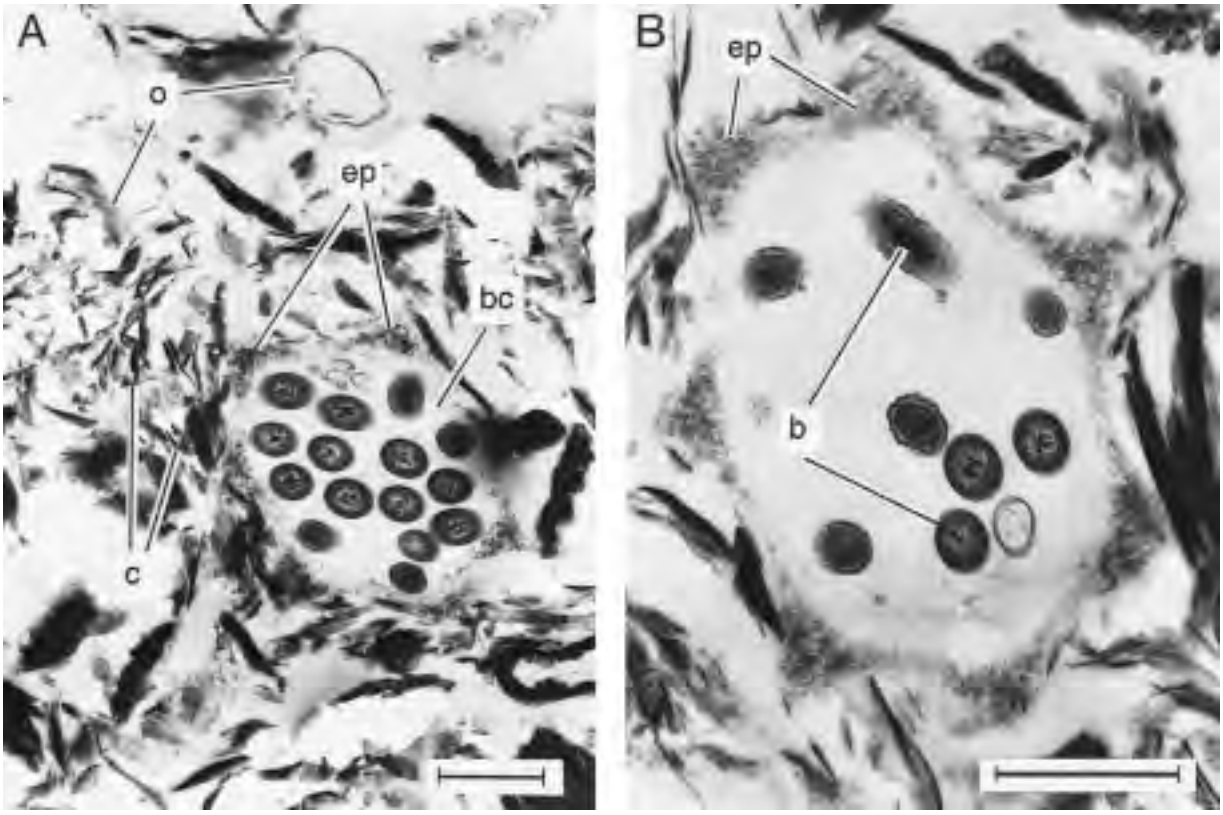

FIGURE 3. Serial sections cut through a colony of a single species of bacteria from the same location as Figure 1 on the continental slope off northern California at a burial depth of 5 cm: (**A**) TEM micrograph illustrating the relationship between the colony (bc), their exocellular polysaccharide secretions (ep), and the surrounding sediment matrix of clay (c) and organic matter (o); (**B**) Second section (slightly rotated and at higher magnification) through the colony in **A,** which more clearly shows the exocellular fibril network and its outward extrusion into gaps between surrounding clay particles. The smaller number of bacteria (b) and apparent open space inside the encasing polysaccharide network in **B** are artifacts resulting of sample preparation and staining. Scale bars represent 1 μm.

Meadows et al. 1984). Unlike in soils and freshwater aquatic systems, both of which have been studied extensively for agricultural, health, and economic reasons, standing stocks of single-celled organisms in marine sediments, other than bacteria, are poorly known, as is their change in abundance with burial depth. This is especially true for protozoa and the larger microbial species.

The vast majority of fine-grained continental margin sediments are deposited at water depths below the photic zone. As a result, the most abundant microbes inhabiting them are heterotrophs (microbes that require organic matter as a source of carbon; Figs. 2, 3, 4A, and 4B). Nevertheless, where the water is shallow and sunlight penetrates to the bottom, heterotrophs and autotrophs (microbes that produce biomass from CO_2 and sunlight; Fig. 4C) coexist. At and near the sediment-water interface

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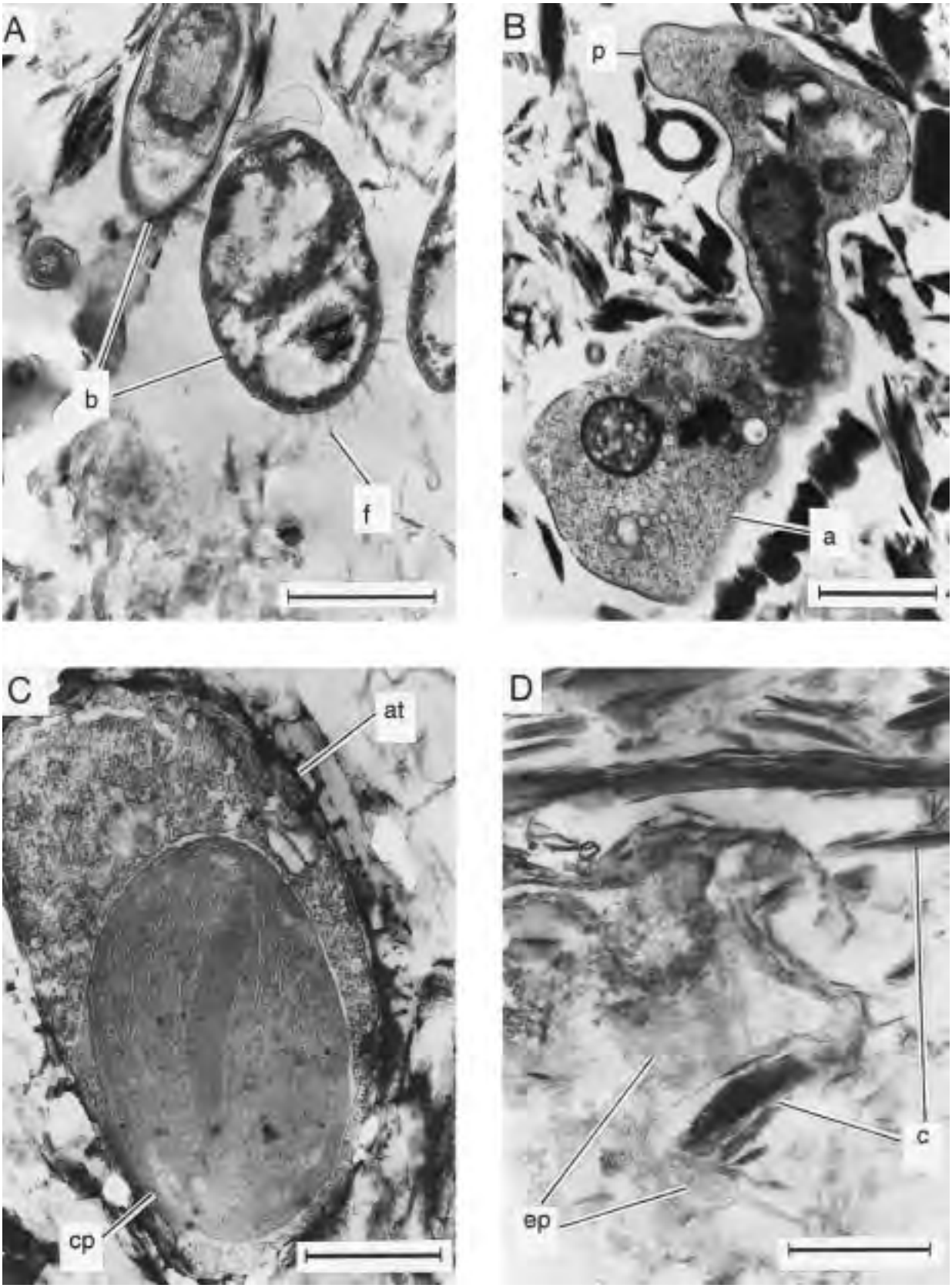
FIGURE 4. TEM micrographs indicating the diversity of the continental margin marine sediment microbial community and occurrence of bacterial exocellular polysaccharide secretions: (**A**) Motile heterotrophic bacteria (b) with cilia/flagella (f) that are used to swim through large spaces between clay and organic sedimentary detritus. Sample is from Eckernforde Bay, Germany, 1 mm below the sediment-water interface at a water depth of ~10 m at the same location as the cells in Figure 2; (**B**) Micrograph showing portion of a large amoeba using a pseudopodia (p) to make its way through pore spaces in a clay and bioclast sediment matrix. Sample is from a burial depth of 3 cm in sediments deposited in 720 m water depth on the continental slope just off Cape Mendocino in northern California and from the same box core as sediment in Figure 1; (**C**) Eukaryotic autotroph (at) containing chloroplast (cp) in the sediment 1 mm below the sediment-water interface in estuary sediments from Hopedale, Louisiana; (**D**) Large mass of bacterial exocellular polysaccharide fibrils (ep) and their characteristically intimate association with clay particles (c) from 1 mm below the sediment-water interface at the same location as (4A). All scale bars represent 1 μm, except in **D** for which the scale bar represents 0.5 μm.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where porosity is high (commonly 70 to 95%), TEM images show that some microbes are mobile. They move freely through interconnected pore spaces using flagella, cilia, and pseudopodia (Figs. 4A and 4B). To date, such motile species have been observed only in the upper few centimeters of the sediments. Physical interaction between these organisms and their mineral matrix appears to be limited. Deeper in the sediment, motile species have not been observed, possibly due to pore space reduction and a decrease in the size and the interconnectivity of voids. Although it is known that increasing pressure can drastically decrease bacterial growth rates (Characklis et al. 1990), the shrinking of habitable space with burial and the reduction in microbial mobility raises interesting questions such as the following. To what depth in fine-grained sediments do microbes, in particular bacteria, remain metabolically active? To what depth can bacterial activity significantly influence pore water chemistry and authigenic mineral precipitation? And is there a burial depth (i.e., limiting pore diameter) below which bacteria can no longer reproduce and/or remain viable as a result of insufficient space to accommodate an increase in biomass?

Microbe-mineral associations and interaction

It is obvious from Figures 2 and 3 that direct contact between bacterial cells and minerals in fine-grained continental margin sediments is non-existent or nearly so. Almost without exception, bacteria appear to be encased in extracellular slimes composed of cross-linked polysaccharide fibrils (see review in Decho 1990) with clay minerals oriented tangentially around their exopolymer cushions. This association appears to be almost universal in natural aquatic environments (Paerl 1973; Foster and Martin 1981; Foster et al. 1983; Kilbertus and Reisinger 1975; Sieburth 1975; Yokote et al. 1985). This suggests that bacteria have a specific physiological response to life in fine-grained geologic media regardless of the chemistry of the coexisting pore waters (i.e., fresh water vs. marine) and whether pore spaces are fully water-saturated or not (i.e., marine sediment vs. soil). The TEM images presented here indicate that the chemical and physical interactions between bacteria and the minerals, organic matter, and solutions that surround them is mediated by reactions and transport through this cushion of extracellular polysaccharide fibrils. Such extracellular slimes can affect sediment physical properties and permeability by binding together particles (see review in Cunningham et al. 1990) and occupying intergranular pore spaces (Fig. 4D). These secreted exopolymers also act as chemical adsorbers. The importance of these fibril networks is illustrated by the fact that the mass of microbial exopolymers in fine-grained marine sediments is estimated to be equal or greater than that of the microbial cellular biomass (Uhlinger and White 1983).

In the fine-grained continental margin sediments examined for this study, the only specific association between minerals and microbes appears to be the close association of clay minerals and sessile bacteria. The clay minerals do not show any apparent evidence of chemical attack or dissolution, merely a physical displacement. This is not to say that the clays remain unchanged chemically. Changes in the composition of the 2:1 layers of clays adjacent to microbes may occur as a result of microbially induced changes in the local redox state of the pore waters. In addition, bacteria may promote leaching of K^+ from micas, illites, or mixed layered clays, thereby increasing the number of expandable layers in the minerals. At present microbially induced changes in clay mineral composition have yet to be verified, but analytical studies of clay minerals adjacent to microbes have yet to be carried out.

As can be deduced from the soil science literature, the affinity of bacteria for clay minerals in sedimentary environments appears to be symptomatic, with the mineralogy of the clay fraction having a measurable impact on microbial metabolic activity. For example, the breakdown of glucose and aldehydes by microbes in spiked soils accelerates when expanding clays like montmorillonite are present, whereas no difference from controls is noticed when non-expandable clay minerals like kaolinite are used (Stotzky and Rem 1967; Novakova 1972a; 1972b; Filip 1973; Heijnen et al. 1990). Such clay mineral-enhanced metabolic activity has been attributed to cation exchange, where the interlayer sites of expandable minerals have acted as a sink for microbial waste products (e.g., ammonia) and/or the mineral has buffered the local pH. Close proximity to mineralogic chemical reactors is important for the viability of sessile microorganisms in fine-grained sediments because the world in which bacteria live is dominated by diffusion and viscous forces (see review in Beveridge 1988). A major challenge faced by organisms, therefore, is to enhance their access to nutrients and eliminate wastes in a relatively static environment.

The most striking textural impact of microbial habitation on fine-grained continental margin sediments is the physical displacement and engulfing of surrounding clay and silt grains by extracellular fibrils exuded by the bacteria (e.g., Figs. 2B, 2D, and 3A). These fibrils bind sediment particles together, physically displace clay grains, and occlude porosity. All have the potential to alter significantly sediment physical properties. Indeed, bacterial binding has been found to have a measurable impact on sediment rheology in coarse clastic sediments (Dade et al. 1991, 1996; Meadows et al. 1994). The impact of such binding on the physical properties of cohesive sediments, such as those depicted in this study, is still relatively unstudied.

It seems likely that chemical transport of aqueous species in continental margin sediments also will be affected by the presence of bacterial exocellular polymers. These fibrils are active adsorbers of dissolved organic compounds and metal cations (see review in Decho 1990). They react with and capture dissolved organic macromolecules in the pore waters and provide a place local to

the cell where digestive enzymes can convert large molecules into compounds capable of diffusing through the bacterial cell wall (Zobell 1943). In addition, divalent metal cations are preferentially chelated by the fibrils and induce cross-linking between polymers. This protects the organisms from exposure to potentially toxic metal concentrations and, in some cases, provides nucleation sites for the precipitation of metal oxides, hydroxides, and sulfides, such as was reported in laboratory studies (e.g., Ferris et al. 1989b; Fleming et al. 1990; Geesey and Jang 1990). One interesting aspect of the affinity for metals exhibited by these exopolymer fibrils is that the metals appear to prevent the degradation of the fibrils by inactivating enzymes that decompose unchelated polysaccharide (Lasik and Gordiyenko 1977). This process may permit the extended persistence of these polysaccharide networks to depth in the sedimentary column.

Concluding remarks

The vast majority of marine sediments are fine-grained, clay-rich siliciclastic materials whose relative abundance, compared to other sediment types, is reflected by the fact that shales and mudrocks make up almost three-quarters of the sedimentary record. To understand the direct impact of microbes on these ubiquitous and geologically important sediments, more TEM studies focusing on the role microbes play in their textural evolution and in the compositional changes in their clay and organic matter assemblages are needed. Although studies of bulk sediment properties, chemical fluxes, and proxies of microbial metabolic activity have provided us much information on the overall chemical changes that occur in marine sediments and the impact these changes have on authigenic mineral precipitation, the actual mechanisms of interaction still need clarification. It is evident from the TEM images presented here that microbes in fine-grained continental margin sediments have a significant effect on sediment microfabric evolution and physical property evolution. Indications are also that microbes and their exocellular secretions may strongly influence sediment chemical transport.

Acknowledgments

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