BIOMINERALIZATION OF IRON SULFIDES IN MAGNETOTACTIC BACTERIA FROM SULFIDIC ENVIRONMENTS

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INTRODUCTION

Magnetotactic bacteria contain intracellular iron mineral inclusions termed magnetosomes (Balkwill et al., 1980) which impart a permanent magnetic dipole moment to the cell resulting in its alignment and navigation in magnetic fields (Blakemore, 1975, 1982; Frankel, 1984). Various methods have been used to determine the mineral phase of the magnetosomes including Mössbauer spectroscopy, x-ray powder diffraction, selected area/micro-electron diffraction, and energy dispersive x-ray analysis (Frankel et al., 1979; Towe and Moench, 1981; Sparks et al., 1990). The particles in almost all magnetotactic bacteria have been shown to consist of the mineral magnetite (Fe_3O_4) (Frankel et al., 1979; Towe and Moench, 1981; Matsuda et al., 1983; Mann et al., 1987; Bazylinski et al., 1988), sometimes admixed with hydrous ferric oxide, a precursor to Fe_3O_4 precipitation (Frankel et al., 1983; Bazylinski et al., 1988).

Cells of the freshwater magnetotactic bacterium, *Aquaspirillum magnetotacticum*, have an apparent requirement for molecular oxygen to produce intracellular Fe_3O_4 (Blakemore et al., 1985). This has led to the assumption that Fe_3O_4

formation by magnetotactic bacteria is confined to surface sediments of aquatic habitats where microaerobic (i.e. microoxic, dysaerobic) conditions predominate (Lovley et al., 1987). However, various morphologically diverse forms of magnetotactic bacteria are common in reducing sediments and waters that contain high concentrations of hydrogen sulfide (H_2S) where the presence of free molecular oxygen is doubtful. Moreover, these organisms can be found in relatively high cell numbers in these environments which include salt marsh pools and semi-closed anoxic basins. Sparks et al., (1989) have even suggested that salt marsh pools are a "preferred" habitat for magnetotactic bacteria. Studies of these habitats have led to the isolation of a marine magnetotactic bacterium capable of producing intracellular single-domain Fe_3O_4 under strict anaerobic conditions (Bazylinski et al., 1988, this volume).

Several years ago we considered the possibility that magnetotactic bacteria in sulfidic environments might be producing a magnetic iron sulfide such as greigite (Fe_3S_4) or pyrrhotite (Fe_7S_8). Early elemental analyses of the magnetosomes of a complex, procaryotic, magnetotactic cell aggregate found in brackish, sulfidic salt marsh pools (Rodgers et al., 1990) showed high iron and sulfide (D. A. Bazylinski, R. B. Frankel, and R. P. Blakemore, unpublished results) but the presence of an iron sulfide was not confirmed until recently. Farina et al. (1986, 1990) studying the same or a similar organism from Brazil reported elemental analyses that also indicated that organism's magnetosomes were an iron sulfide, probably pyrrhotite, and not Fe_3O_4. In this paper, we confirm the presence of greigite (Fe_3S_4) and pyrite (FeS_2) particles in the organsim (Mann et al., 1990). In addition we report that the predominant types of magnetotactic bacteria, which include a variety of morphological forms present in these strongly sulfidic, anoxic environments, contain iron sulfides.

TYPES OF HABITAT STUDIED

Areas sampled for magnetic bacteria on both the east and west coasts of North America were of two general types . On the east coast, samples were collected from various salt marshes (Woods Hole, MA; Neponset River Marsh, Boston, MA; and Parker River Wildlife Refuge, Rowley, MA) and a stratified coastal pond (Salt Pond, Woods Hole, MA). On the west coast, samples were collected from Sweet Springs Reserve (part of Morro Bay), Baywood Park, CA.

Salt Marsh Pools. These are shallow pools usually less than 1 m deep. The water is generally brackish with salinities ranging between 12-32 ppt. The surrounding vegetation consists of marine halophytes and thus is indicative of marine input. In Massachusetts, pools were surrounded by the salt tolerant grasses *Spartina alterniflora*, *S. patens*, and *Distichlis spicata*, the rush *Juncus gerardi*, and saltwort *Salicornia* sp. The California site was dominated by *Distichlis* and *Salicornia spp.* The surface sediment appeared somewhat oxidized (greyish) but a millimeter or so below the surface the sediment was black, indicative of ferrous sulfide (FeS) production under anoxic conditions. Small mats of purple photosynthetic sulfide- oxidizing bacteria, which mainly consisted of *Amoebobacter* and *Chromatium* spp., were occasionally observed on the sediment surface. All pools emitted a strong odor of hydrogen sulfide when sediments were disturbed during sampling. Magnetotactic bacteria were collected by the method of Moench and Konetzka (1978) from jars that were filled to their capacity with sediment and overlaying water. Unlike many of the freshwater magnetotactic bacteria, organisms in these samples declined in number when kept in jars at room temperature, possibly due to the gradual loss

of H_2S from the system and were therefore collected from jars as soon as possible after sampling.

Shallow Anaerobic Basins. This type of habitat is typified by the small coastal pond, Salt Pond, Woods Hole, MA. Salt Pond is a well-characterized seasonally stratified coastal pond that is about 5.5 m in depth and has marine and freshwater input (Wakeham et al., 1984, 1987).

The anaerobic hypolimnion of Salt Pond has high concentrations of H_2S (up to 5 mM) generated from sulfate- reducing bacteria. During the summer, the anoxic (anaerobic) zone rises to within 3 m of the surface and the oxic-anoxic interface becomes quite defined (Wakeham et al., 1984), with steep oxygen and sulfide gradients. A small anoxic zone (up to 0.5 m) without detectable molecular oxygen or H_2S is also characteristic of this system (Wakeham et al., 1987; Bazylinski et al., 1990). There is a plate of anaerobic photosynthetic bacteria at the top of the hypolimnion in the anoxic zone where the H_2S concentration becomes detectable (Wakeham et al., 1987). It is in this zone and slightly below where the iron sulfide- containing magnetotactic bacteria were found and collected. Water samples from discrete depths were collected by pumping (cf. Wakeham et al., 1987).

TYPES OF MAGNETOTACTIC BACTERIA

The magnetotactic bacteria present in the sulfidic habitats were of two major types. The first is one or more complex spherical cell aggregate(s) and the second is a group of large, morphologically-distinct, rod-shaped bacteria.

Complex cell aggregate. This organism is apparently common in brackish, sulfidic habitats. It has been observed in these environments on both North American coasts (this study) and South America (Farina et al., 1983). The aggregate ranges from about 4-12 μm in diameter (Figure 1) and consists of about 10-30 individual cells each of which contains an average of about 31 irregularly-shaped magnetosomes approximately 75 nm in diameter (Figures 2 and 3) (Mann et al., 1990; Rodgers et al., 1990). Each cell is flagellated on one side (the outside) and the aggregate is motile as an entire unit but not as individual cells (Rodgers et al., 1990). Figure 4 shows an electron micrograph and an elemental x-ray map of the corresponding region of the magnetosomes of a single cell of the aggregate. The x-ray map clearly shows that the particles contain iron and sulfur but not oxygen. As a comparison, the crystals of the magnetosomes from cells of strain MV-1 which are known to produce Fe_3O_4 (Bazylinski et al., 1988, this volume; Sparks et al., 1990) were subjected to the same analysis (Figure 5). The elemental x-ray map of magnetosomes of strain MV-1 show that these crystals contain iron and oxygen but not sulfur, as expected.

When copper grids with cells of the complex cell aggregates were left stored in air for several weeks low levels of oxygen were detected at the edges of the iron sulfide particles suggesting that they are susceptible to at least surface oxidation (1 or 2 crystals in Figure 4). Furthermore, elemental X-ray mapping indicated the presence of large amounts of Cu in the cells. This was subsequently determined to be due to the interaction of the sulfide-rich water and sediment with the Cu grids. Therefore, Ni grids were used in subsequent work.

Convergent beam (micro-) electron diffraction showed that every particle in every cell examined was crystalline.

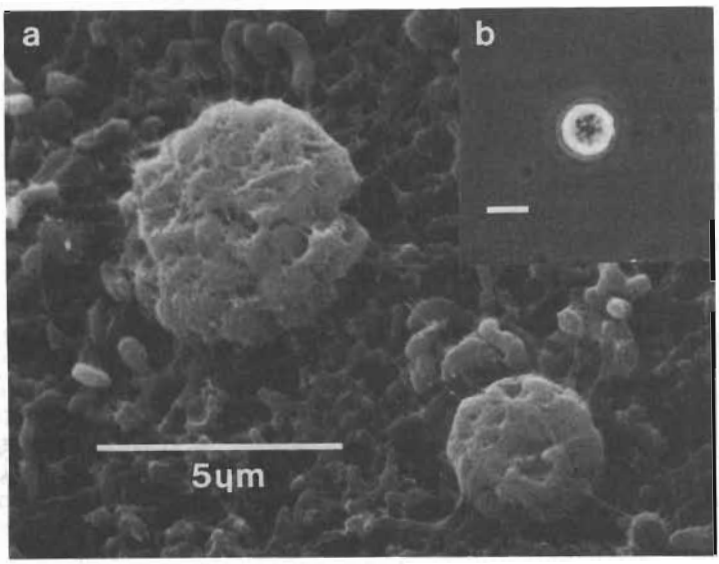

Figure 1. Scanning electron micrograph (a) of two complex cell aggregates on a tortuous membrane filter. The aggregates are slightly flattened due to the vacuum filtration procedure. Web- like material surrounding the organisms are flagella coating their outer surface. Insert (b) is a phase contrast micrograph of the organism. Bars represent 5 μm.

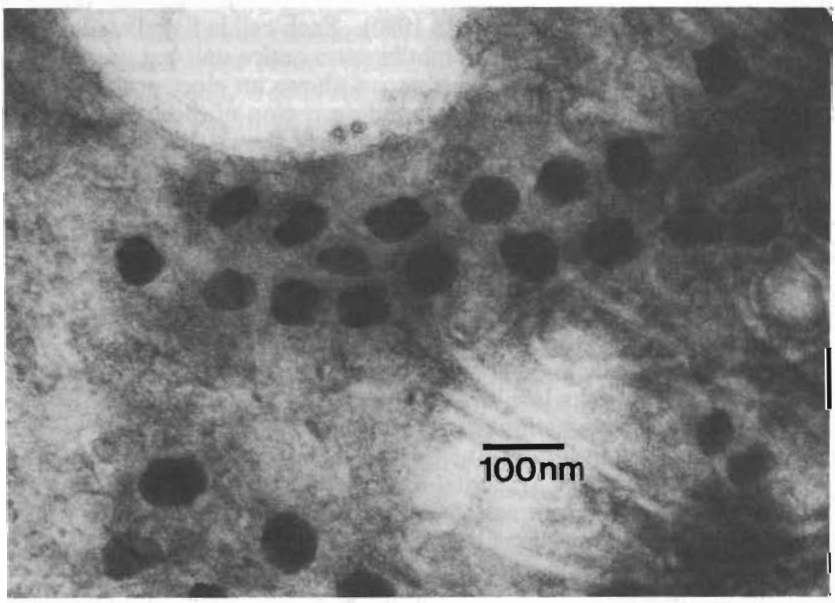

Figure 2. High magnification electron micrograph of individual iron-sulfide magnetosomes in a cell of the complex cell aggregate. Bar represents 100 nm.

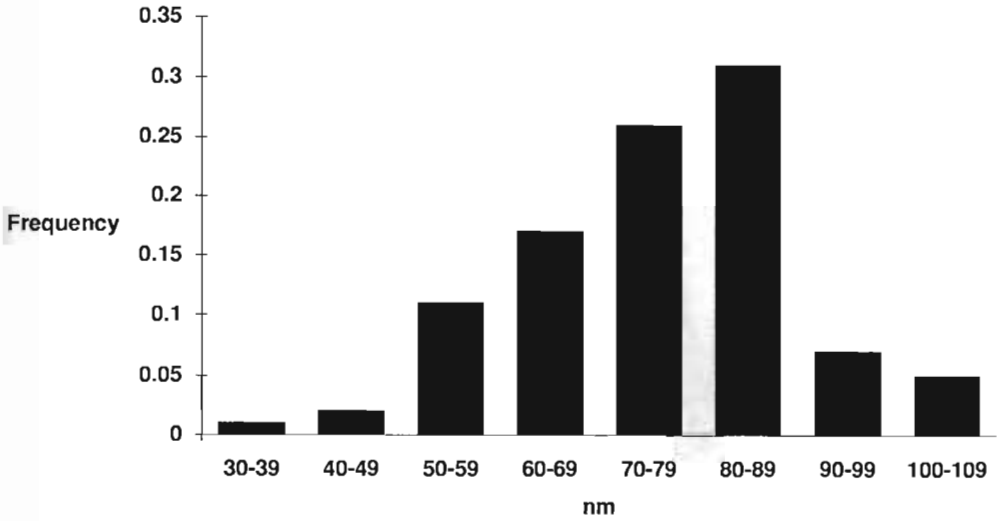

Figure 3. Particle size histogram of intracellular iron sulfide inclusions.

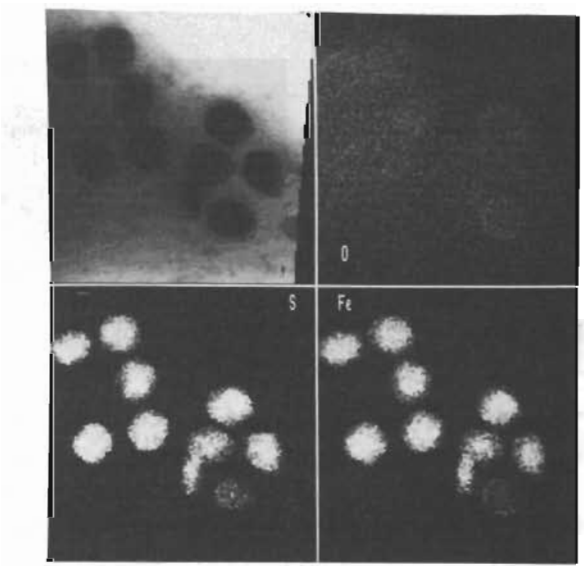

Figure 4. Fe, O, and S elemental density x-ray map of magnetosomes within a cell of the complex cell aggregate. Particles are approximately 75 nm in diameter.

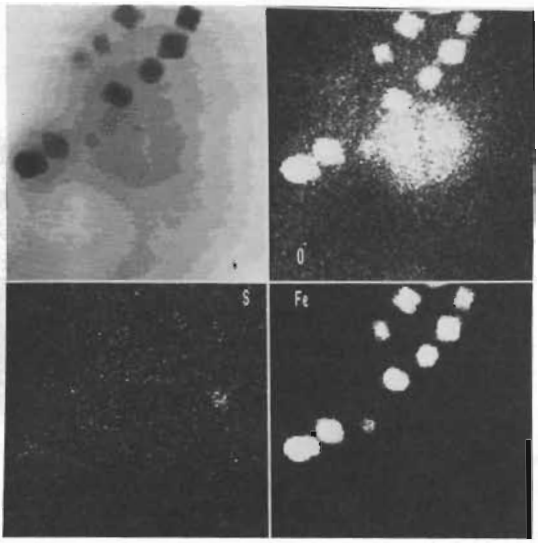

Figure 5. Fe, O, and S elemental density x-ray map of magnetosomes in a cell of strain MV-1, a Fe_3O_4-producing magnetotactic bacterium. Particles are parallelepipeds and average roughly 50 x 35 x 35 nm.

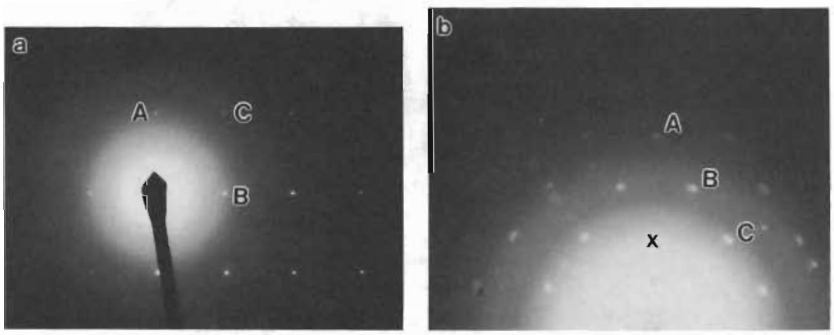

Figure 6. Single crystal diffraction patterns of intracellular iron sulfides.

a) Greigite, [$\bar{2}$ 3 $\bar{3}$] zone; reflection A, (3 1 $\bar{1}$) (2.98 Å); reflection B, (0 2 2) (3.5 Å); reflection C, (3 3 1) (2.26 Å). Angles 0 2 2 ∧ 3 1 $\bar{1}$ = 90°; 0 2 2 ∧ 3 3 1 = 49°. Crystallographic data: space group Fd3m, a = 9.876 Å. The diffraction pattern corresponding to the [1 1 $\bar{3}$] zone of greigite was previously reported by Mann et al. (1990).

b) Pyrite, [$\bar{1}$ 1 0] zone. Reflection A, (2 2 0) (1.91 Å); reflection B, (1 1 1) (3.13 Å); reflection C, (0 0 2) (2.7 Å). Angles: 2 2 0 ∧ 0 0 2 = 90°; 1 1 1 ∧ 2 2 0 = 35°. Crystallographic data: space group Pa3, a=5.417 Å.

Mann et al. (1990) have recently identified the mineral composition of the particles in the complex cell aggregate using electron diffraction as ferrimagnetic greigite (Fe_3S_4) and non-magnetic pyrite (FeS_2) (Table 1). Most of the powder patterns gave d spacings corresponding to FeS_2 suggesting that Fe_3S_4 was a minor component of the intracellular crystals. Moreover, as many of the major d spacings of Fe sulfides such as greigite, pyrrhotite, and pyrites overlap, single crystal diffraction patterns were required to provide unequivocal identification of these phases.

Table 1. Electron diffraction data for bacterial iron sulfide inclusions.

Data[a]	Source[b]		Assignment[c] greigite	pyrite
3.57		S	3.50 (220)	
3.16	R	S		3.128 (111)
3.06		S	2.98 (311)	
2.69	R			2.709 (200)
2.51	R		2.470 (400)	
2.28		S	2.26 (331)	
2.12	R			2.211 (211)
2.04		S	2.017 (422)	
1.89	R	S	1.901 (333)	1.915 (220)
1.71	R		1.746 (440)	
1.65		S	1.671 (531)	
1.60	R	S		1.633 (311)
1.55		S		1.564 (222)
1.35	R		1.383 (711)	1.354 (400)
1.26		S	1.286 (731)	
1.22	R		1.235 (800)	1.211 (420)
1.07	R	S	1.054 (664)	1.043 (333)
0.89		S		0.903 (600)

[a]Experimental d spacings in Å.
[b]R, powder ring pattern; S, single crystal pattern.
[c]Standard mineral d spacings in Å. X-ray powder diffraction file: greigite (16-713), and pyrite (6-710); (hkl), Miller indices.

Figure 6 shows single crystal electron diffraction patterns recorded from intracellular crystals in the complex cell aggregate. Two phases, Fe_3S_4 and FeS_2 were unequivocally identified on the basis of crystallographic relationships between {hkl} reflections in reciprocal space. Greigite patterns were obtained along three different zone axes ($[1\ 1\ \bar{3}]$, $[\bar{2}\ 3\ \bar{3}]$ (Figure 6a) and $[4\ \bar{5}\ \bar{13}]$). The reflections showed no evidence of streaking indicating that the particles were well-defined single crystals. Diffraction patterns of pyrite were recorded mainly along the $[\bar{1}\ 1\ 0]$ zone (Figure 6b); again the patterns were characteristic of well-ordered single crystals. Lattice imaging of the crystals was difficult due to the thickness of the particles. The few images recorded were characteristic of single crystals with irregular surfaces (Figure 7).

Interestingly, although the crystals appear to be crystallographic single domains, they have a diversity of morphologies within the same cell, rather than species- specific morphologies found in the Fe_3O_4-producing magnetotactic bacteria (Mann et al., 1987b). Individual crystals were found to be roughly

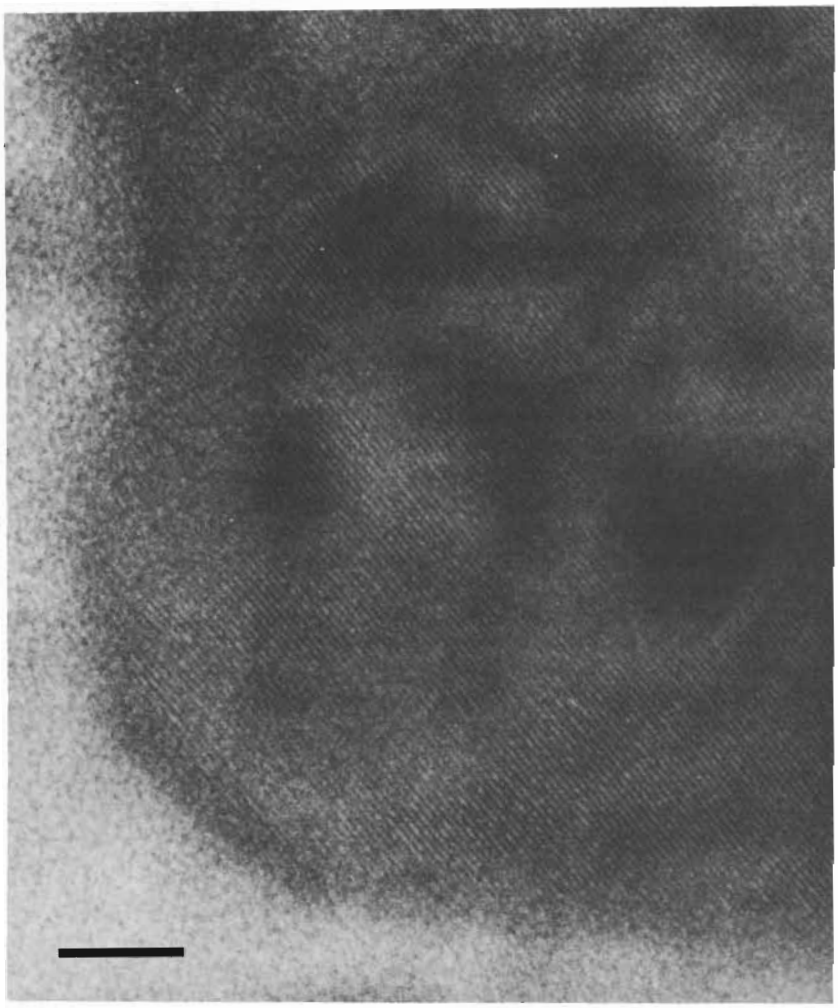

Figure 7. Lattice image showing (111) (3.13 Å) fringes of FeS_2. The fringes are coherent across the intracellular particle. Some discontinuities can be observed in the fringes but the images are coherent across these areas. These features reflect marked differences in particle thickness due to irregular crystal surfaces. Bar = 5.5 nm.

cuboidal, some roughly parallelepipedal, and even "flake"-shaped. Many appeared irregular in shape. It was not possible to distinguish greigite from pyrite particles on the basis of morphology alone.

Rod-shaped bacteria. Sulfide-rich sediments and water collected from all sites contained large numbers of magnetotactic rod-shaped bacteria. All moved slowly as compared to the complex cell aggregate or to Fe_3O_4-producing coccoid magnetotactic bacteria (e.g. Blakemore, 1975; Moench and Konetzka, 1978). Thus it took a longer period of time for the rod-shaped organisms to collect at the edge of a water droplet in a magnetic field than the other organisms.

Most cells were relatively large, ranging from about 3-5 μm long by 1-2 μm wide. One type, common to all collecting sites, had a dark filament longitudinally traversing the cell that was visible using phase contrast microscopy (1000 x). This filament was found to be a double or sometimes a triple chain of magnetosomes arranged side by side (Figure 8). Elemental x-ray analysis of the magnetosomes in this organism showed them to be iron-sulfides (Figure 9). Individual crystals had the same morphologies as described for the complex cell aggregate.

Other rods, like the complex cell aggregates, had fragmented or partial chains of magnetosomes (Figure 10; corresponding x-ray map, Figure 11) with others having an apparently random arrangement. Regardless of the arrangement of the magnetosomes, the particles in every rod- shaped cell examined were iron-sulfides and, based upon convergent beam diffraction patterns, were all truly crystalline. No cells were found that contained both iron-sulfide and iron-oxide type crystals. Moreover, iron- oxide containing magnetosomes were observed in only one cell type, a coccus, from Sweet Springs Reserve, CA. It should be noted, however, that our collecting technique in salt marsh pools does not ensure that the entire sediment and water was anaerobic or contained sulfide in situ. Generally though, the concentration of sulfide in the sediment, together with the fact that all air bubbles were eliminated before the jars were sealed, was enough to scavenge any traces of oxygen that may have been present or introduced while collecting. In fact, populations of the iron-sulfide containing magnetotactic bacteria were more stable in jars that were kept sealed and refrigerated.

Other organisms. Strain MV-1, a partially characterized Fe_3O_4 -producing magnetotactic bacterium was isolated from a salt marsh pool of the Neponset River Marsh, Boston, MA (Bazylinski et al., 1988). However, cells in the jar from which it was isolated did not enrich until several days after it was opened to the air. Before this time cells of this type were not observed. In addition, after enrichment cells were clearly confined to the sulfide-no sulfide interface where some free molecular oxygen was probably available. The types of organisms containing the iron- sulfide particles were found below this interface (if this interface was even present due to very high amounts of H_2S) in the water column and in the sediment as well. Few cells of the MV-1 type were observed below this interface in the jar of sediment and water from which it was isolated at least until sulfide was no longer detected in the water and the sediment.

DISCUSSION: BIOLOGICAL AND BIOGEOCHEMICAL SIGNIFICANCE

Particulate intracellular iron sulfides were apparently first described by Issatchenko (1912, 1929) who even reported the process of pyrite formation and pyrite granules occurring within bacterial cells. Although it is doubtful he

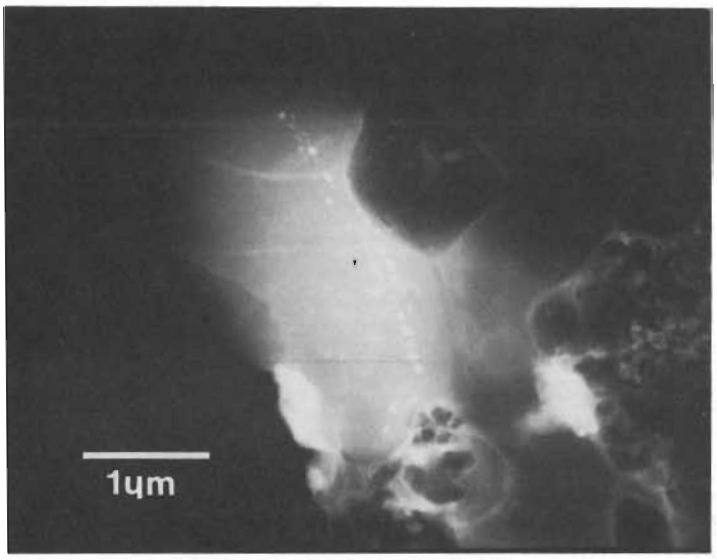

Figure 8. Scanning-transmission electron micrograph (negative- image) of a rod-shaped bacterium collected from a salt marsh pool, Woods Hole, MA. This cell contains a double chain of magnetosomes that traverse the cell longitudinally. Bar represents 1 μm.

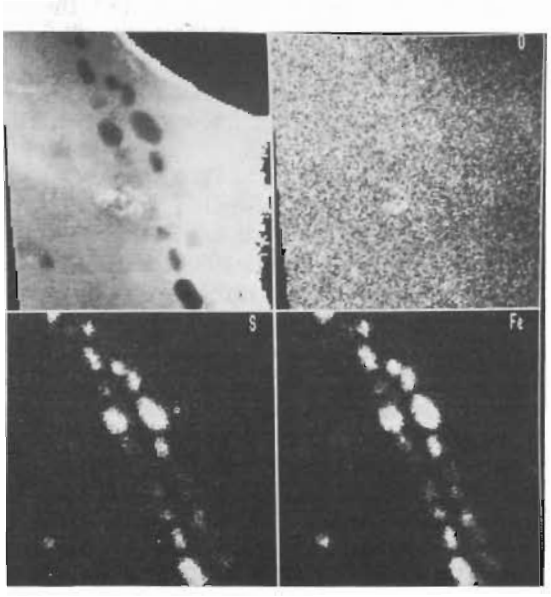

Figure 9. Fe, O, and S elemental density x-ray map of the magnetosomes from the cell shown in Figure 8.

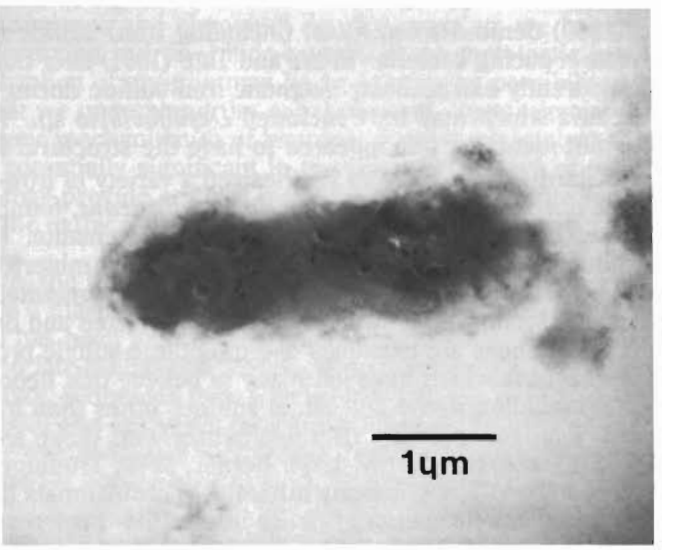

Figure 10. Scanning transmission electron micrograph (normal image) of a rod-shaped bacterium collected from a salt marsh pool, Woods Hole, MA. This cell contains several small chains of magnetosomes and some not in any specific arrangement. Bar represents 1 μm.

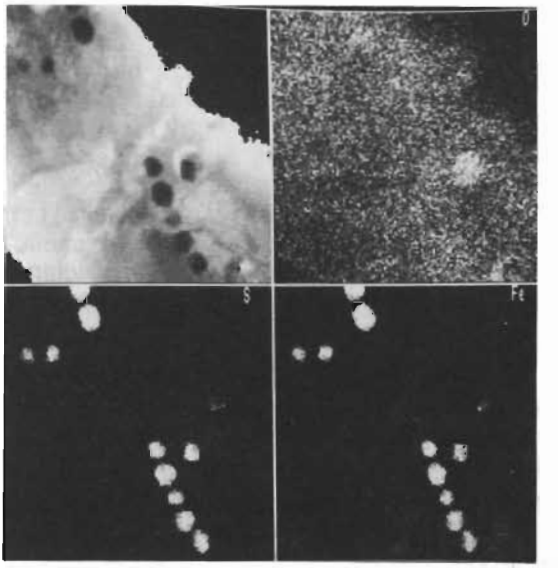

Figure 11. Fe, O, and S elemental density x-ray map of the magnetosomes from the cell shown in Figure 10.

could have known the composition of the inclusions he had observed visually, his ideas of metal inclusions within bacteria and of the potential role of bacteria in mineral formation were interesting and insightful.

Miller (1950) demonstrated metal (including iron) sulfide formation in cultures of sulfate-reducing bacteria. Freke and Tate (1961) later noted the the formation of an apparently extracellular magnetic iron sulfide during sulfate reduction by bacteria which may have included *Desulfovibrio* sp. The magnetic compound was not identified but appeared to have the structural formula $2FeS{\cdot}Fe_2S_3$. Rickard (1969a, b), who synthesized a variety of iron-sulfide minerals using a pure culture of *Desulfovibrio desulfuricans*, found the material of Freke and Tate (1961) to be a mixture of greigite and hematite. Extracellular iron-sulfide production in these cases are analogous, in biomineralization terms, to extracellular Fe_3O_4 production by the anaerobic non- magnetotactic iron-reducing bacterium, strain GS-15 (Mann et al., 1990) isolated and described by Lovley et al. (1987). These are examples of indirect iron-sulfide production by sulfate-reducing bacteria which have led many to believe that deposits of such sulfidic minerals including pyrite and metal sulfides other than iron, are "biogenic" and are at least partially microbially mediated (Love and Zimmerman, 1961; Love and Murray, 1963; Berner, 1970; Trudinger et al., 1972; Howarth, 1979; Morse et al., 1987; many others). Microbial mats have also been implicated in the indirect formation of pyrite in the mid- Proterozoic Newland Formation (Belt Supergroup, Montana, USA; Schieber, 1989).

Certain sulfate-reducing bacteria, such as some *Desulfovibrio* and *Desulfotomaculum* species, were shown to produce intracellular electron-dense particles consisting of FeS when grown in media containing relatively high concentrations of iron (Jones et al., 1976). The particles appeared to be randomly oriented and amorphous, rather than crystalline, based upon electron diffraction studies. Efforts to separate the particles from lysed cells of these bacteria by density gradient centrifugation were unsuccessful. It is noteworthy that no sulfate-reducing bacterium is presently known to be magnetotactic.

The iron-sulfide inclusions in magnetotactic bacteria described here are clearly differentiated from the examples discussed above. This and the studies by Mann et al. (1990) and Farina et al. (1990) are the first reports of intracellular biomineralization of truly crystalline iron sulfides in a bacterium. The discovery of ferrimagnetic greigite in the complex aggregate certainly explains the magnetotactic response of the organism. The presence of pyrite in the cells, however, was totally unexpected. Based on thermodynamic considerations, greigite would be converted to pyrite under highly reducing conditions at neutral pH (Berner, 1967). In addition, elemental sulfur, which may also be present in some cells or in the sediment and/or water column, catalyzes this transformation (Berner, 1970). However, even with the catalytic effect of elemental sulfur, pyrite formation from the iron monosulfides is a slow process. Howarth (1979) found rapid production of pyrite from ferric oxyhydroxide when the partial pressure of H_2S was kept low (10^{-4} atm) rather than high (1 atm) at pH 7.5. Because H_2S is known to be toxic to even those organisms that produce it, perhaps cells can keep the intracellular concentration of H_2S low with respect to the external environment thereby creating conditions that might favor pyrite production from as yet undetermined iron compounds, perhaps including greigite.

Dissolution and pyritization of Fe_3O_4 particles has been shown to occur in reducing sediments containing H_2S (Kobayashi and Nomura, 1972; Canfield

and Berner, 1987). The process is slow (the "half-life" of Fe_3O_4 ranging from 50-1000 years) and is dependent on the H_2S concentration, the Fe_3O_4 concentration, and the surface area of the Fe_3O_4 (Canfield and Berner, 1987). The product of the process is an Fe_3O_4 crystal with a suface coating of pyrite. Based upon our elemental x-ray analyses and elemental density mapping, we have no evidence that this is occurring in iron-sulfide-containing magnetotactic bacteria although external pyritization of greigite may be an interesting possibility. It is imperative that we understand the metabolism of these organisms in order to understand their mechanism(s) of biomineralization. It is clear that these organisms are potentially significant in the biogeochemistry of pyrite in sulfidic habitats and may provide a direct means of "biogenic" pyrite formation, as compared to the extracellular process mediated by sulfate-reducing bacteria.

Greigite, the thiospinel of iron that is isomorphous with Fe_3O_4 (Skinner et al., 1964), is a major component of black sedimentary iron sulfide (Morse et al., 1987) and has been found in sediments in Belgium (Jedwab, 1967), unconsolidated late-glacial and postglacial sediments in Lake Superior (Dell, 1972), and anoxic sediments from Chesapeake Bay (R. B. Biggs cited by Demitrack, 1985) and the Black Sea (Berner, 1974). Slow-moving, large, rod-shaped magnetotactic bacteria of the type described in this paper have also been observed in anoxic Black Sea sediments (depth approximately 2000 m; D. A. Bazylinski, unpublished results). The elemental composition of the magnetosomes of these organisms were not determined, however. Magnetite has also been observed in Black Sea sediments (Creer, 1974).

Demitrack (1985) made an exhaustive search for fine-grained Fe_3O_4 produced by magnetotactic bacteria in Eel Marsh, Woods Hole, MA, a habitat rich in magnetotactic bacteria. The magnetic remanence in these sulfidic sediments was found to be due not to Fe_3O_4 but to fine-grained greigite. The greigite particles were roughly cuboidal and were about 100 nm on a side, similar to the intracellular crystals described in this study. Demitrack concluded that Fe_3O_4 from magnetotactic bacteria was being dissoluted under reducing conditions in the presence of H_2S and that greigite was precipitating via an inorganic mechanism through the action of sulfate-reducing bacteria as in the experiments of Freke and Tate (1961). Based upon the results of Kobayashi and Nomura (1972) and Canfield and Berner (1987) however, one might expect to find particles of dissoluted and/or pyritized Fe_3O_4 as well. However these were not observed. Our results show that the magnetic remanance due to fine-grained greigite in Eel Marsh and perhaps other sulfidic reducing sediments may in fact be due to biomineralization of greigite by magnetotactic bacteria.

Farina et al. (1990) also report the presence of crystalline magnetic iron sulfides in cells of a complex cell aggregate found in brackish water with sulfide-rich sediment in Brazil. However, the mineral was tentatively identified as pyrrhotite (Fe_7S_8) rather than greigite or pyrite. This might indicate that the production of iron sulfides in these bacteria is not mineral specific and might be controlled by external physical and chemical parameters such as sulfide concentration or redox conditions, etc. Whether these organisms have control over the types of minerals deposited is a presently unanswered question.

IRON SULFIDES AND THE ORIGIN OF LIFE

Williams (1990) has proposed that in addition to magnetic orientation, magnetotactic bacteria might biomineralize iron sulfides for maintainence of

iron and sulfide ion homeostasis in the cell. He has also suggested that iron sulfides in these organisms might be a clue to the origin and development of metabolism in early life forms. Wächtershäuser (1988a,b) has proposed that ferrous ion and H_2S were electron (energy) sources for early autotrophic metabolism with CO_2 the electron acceptor:

$$Fe^{2+} + 2H_2S \longrightarrow FeS_2 + 4H^+ + 2e^-$$

$$FeS + H_2O\ (aq) + CO_2\ (aq) \longrightarrow FeS_2 + H_2O + HCOOH.$$

The pyrite, which is the major iron-containing product of the reactions, could in turn have provided surface binding sites for the organic products. Another intriguing idea, first suggested by Hartman (1975), is that iron sulfides could have been a direct source of energy for organisms as shown below:

$$H_2O + 2(FeS) + CO_2 \longrightarrow 2FeO + >CHOH + 2S$$

with the reaction driven by light. Perhaps the fact that large numbers of iron sulfide-containing magnetotactic bacteria are present along with the anaerobic photosynthetic, purple sulfide-oxidizing bacteria in the anoxic euphotic zone of shallow anaerobic basins such as Salt Pond is indicative of the importance of light and this type of metabolism to these organisms.

CONCLUSIONS

We conclude that magnetotactic bacteria are capable of forming magnetic iron sulfides rather than Fe_3O_4 in reducing aquatic habitats containing little or no free molecular oxygen and relatively high concentrations of H_2S. These bacteria obviously play a significant role in the biogeochemistry of iron in aquatic habitats and have also been shown to facilitate important biogeochemical transformations of nitrogenous compounds (Bazylinski and Blakemore, 1983a, b; Bazylinski et al., 1988). This study now demonstrates a great potential role in the biogeochemistry of sulfur as well, and opens a new chapter in the study of biomineralization.

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