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Biogenic Magnetite and the Magnetization of Sediments

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Biogenic magnetites are produced through the reduction of ferric iron by both biologically induced (extracellular) and biologically controlled (intracellular) processes. With few exceptions, all are ultra-fine-grained, single-domain magnetite. Biogenic magnetites formed by magnetotactic bacteria (biologically controlled) have been shown to contribute significantly to the natural remanent magnetization of carbonates and limestones, hemipelagic and deep-sea marine sediments. The input into sediments of ultra-fine-grained magnetite produced by dissimilatory iron reducing bacteria (biologically induced) has yet to be firmly established but may be even more significant. Whether either type of authigenic biomagnetite is preserved is determined by postdepositional factors including oxidation, reduction by substitution, and dissolution. Unconsolidated and lithified sediments can be screened for putative biogenic magnetite by rock magnetic techniques. It is not generally appreciated that magnetotactic bacteria and their magnetofossils can be identified by the unusual, and in some cases unique, morphologies, size range, and composition of the magnetite crystals. Magnetite produced by dissimilatory iron reducing bacteria have a distinctive morphology and size range, but it is currently controversial as to whether these can be distinguished from certain chemically precipitated magnetites. The presence of dissimilatory iron reducing bacteria, however, can be detected using microbiological techniques and sediment geochemistry. Biogenic magnetites are trace fossils and potentially useful environmental indicators and are considered to have significant input to the magnetization of most sediments, both modern and ancient.

INTRODUCTION

Ultra-fine-grained, single-domain magnetite as the primary remanence carrier in lacustrine and marine sediments has been used to study geomagnetic reversals and secular variation, to calibrate the geologic time scale, to measure rates of seafloor spreading [*Tarling*, 1983] and as an indicator of past erosional, hydrological, and atmospheric regimes [*Banerjee*, 1988]. Where and when this magnetite is formed, how it is deposited, and its eventual fate in sediments all have direct consequences on the resolution and reliability of the magnetic record.

The contribution of biogenic magnetite to the magnetization of sediments has only recently been recognized. Chitons [*Kirschvink and Lowenstam*, 1979] and later magnetotactic bacteria [*Kirschvink*, 1983] were proposed as sources of ultra-fine-grained magnetite in marine sediments [*Kirschvink and Chang*, 1984; *Chang and Kirschvink*, 1989]. The advancement of very sensitive magnetometers (e.g., SQUID) has made it possible to measure rocks and sediments with extremely weak magnetic remanence (e.g., carbonates and limestones [*Kirschvink et al.*, 1985]). Rock magnetic studies in conjunction with examination of the magnetic components by transmission electron microscopy have shown that single-domain magnetites produced by magnetotactic bacteria can be a significant source of primary remanence carrier in limestones and certain marine sediments [*Kirschvink and Change*, 1984; *Stolz et al.*, 1986, 1989*a*, *b*; *Chang and Kirschvink*, 1989; *Chang et al.*, 1987; *Petersen et al.*, 1986; *Vali et al.*, 1987; *McNeill et al.*, 1988]. These techniques have also been used to establish the presence of biogenic magnetite in ancient sediments and rocks as old as 2 b.y. [*Chang and Kirschvink*, 1989; *Chang et al.*, 1989]. As a result, magnetofossils have been proposed as trace fossils of past biomineralization processes and paleoenvironmental indicators. In all of these studies, however, magnetotactic bacteria which need molecular oxygen have been implicated as the source of biogenic magnetite. The recent discoveries of an anerobic magnetotactic bacterium [*Bazylinski et al.*, 1988] and an iron reducing bacterium (GS-15) which produces ultra-fine-grained magnetite extracellularly [*Lovley et al.*, 1987] have provided two new biological mechanisms for authigenic magnetite formation in anoxic environments. They have led to further speculation of the possible biological origin of ultra-fine-grained magnetite in suboxic sediments, banded iron formations, and hydrocarbon deposits [*Bazylinski et al.*, 1988; *Lovley et al.*, 1987; *Elmore et al.*, 1987]. In marked contrast, *Maher and Taylor* [1988] have proposed a totally abiotic mechanism for magnetite formation in soils and suggest that it is a primary source of ultra-fine-grained magnetite in lake, estuarine, and marine sediments [*Banerjee*, 1988]. In an attempt to clarify current misconceptions about biogenic magnetites we present here the mechanisms of biogenic magnetite formation (biologically induced and biologically controlled), their contribution to

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the magnetization of sediments, and the criteria for their identification in both present and ancient sediments.

BIOLOGICALLY CONTROLLED (MATRIX MEDIATED)

The biological formation of magnetite was first discovered in the teeth of chitons by *Lowenstam* [1962]. Since that time, biogenic magnetites have been found in bacteria, algae, monarch butterflies, honeybees, tuna, salmon, pigeons, and several cetaceans [*Kirschvink et al.*, 1985]. This magnetite has been used as a structural component (e.g., chiton teeth) and in orientation and navigation. Behavioral studies have provided significant evidence that from bacteria to honeybees to tuna, biologically produced single-domain magnetite is used to sense the Earth's magnetic field [*Frankel*, 1984; *Walker and Bitterman*, 1985; *Walker et al.*, 1984; *Kirschvink et al.*, 1985]. In these organisms, the mineralization is under biological control (matrix-mediated biomineralization) resulting in single-domain crystals with unique granulometry and composition [*Kirschvink*, 1983].

The biomineralization of magnetite was initially described in chitons [*Lowenstam*, 1962; *Nessen*, 1968; *Towe and Lowenstam*, 1967; *Kirschvink and Lowenstam*, 1979; *Nessen and Lowenstam*, 1985]. Chitons are invertebrates (Polyplacophora) which typically live on endolithic bacteria and algae and range in habitat from intertidal to deep sea [*Lowenstam*, 1967]. They graze the surface of limestone rocks with hard mineralized teeth, digesting the organisms and discarding the rock. The teeth are found on a grinding organ, the radula, and contain magnetite as well as other minerals (see below). The process of mineralization in the chiton teeth can be followed along the radula, and four stages have been recognized [*Kirschvink and Lowenstam*, 1979]. In the first stage, an unmineralized organic framework is laid down. In the second stage, the teeth are capped by a reddish-brown ferrihydrite ($5Fe_2O_30.9H_2O$) which has been delivered to the tooth in the form of ferritin [*Nessen*, 1968; *Kirschvink and Lowenstam*, 1979; *Nessen and Lowenstam*, 1985]. In the third stage, the ferrihydrite is reduced to magnetite as the teeth turn black. This involves iron reduction, oxygen depletion, dehydration, the conversion from hexagonal close packing to cubic, and an inverse-spinel structure [*Towe and Lowenstam*, 1967; *Kirschvink and Lowenstam*, 1979; *Nessen and Lowenstam*, 1985]. The fourth and final stage involves the thickening of the magnetite that continues to be covered by a thin coat of ferrihydrite and the addition of other mineral species which fill in parts of the tooth cap (lepidocrocite and francolite in *Chiton tuberculatus*, amorphous ferric phosphate in *Chiton stelleri*, and lepidocrocite and dahlite in *Acanthopleura echinatum* [*Kirschvink and Lowenstam*, 1979; *Lowenstam*, 1967; *Lowenstam and Weiner*, 1985; *Towe and Lowenstam*, 1967]. The magnetite in the chiton teeth consists of ultra-fine-grained, 100 × 100 × 100 nm, single-domain crystals [*Kirschvink and Lowenstam*, 1979]. The coercivity spectrum of a whole tooth (Figure 1*a*) reflects not only the single-domain nature of the magnetite, with a dipole magnetic moment of $\sim 5 \times 10^{-6}$ emu but also strong grain-grain interaction [*Kirschvink and Lowenstam*, 1979; *Cisowski*, 1981].

The discovery of magnetotactic bacteria by *Blakemore* [1975] marked the first solid example of biologically controlled biomineralization by bacteria. Not only do these bacteria take ferric iron in solution and deposit magnetite intracellularly, but they also control the composition and crystal structure as well. These bacteria have been shown to use the magnetite for orientation [*Frankel*, 1984] with north seeking bacteria in the northern hemisphere and south seeking bacteria in the southern hemisphere [*Kirschvink*, 1980; *Blakemore et al.*, 1980]. Magnetotactic bacteria come in a variety of morphologies, (rods, cocci, both unicellular and colonial, vibrio, and spirilla) and produce several morphologies of intracellular magnetite (hexagonal prisms, cuboidal, tear-drop) [*Towe and Moench*, 1981; *Matsuda et*

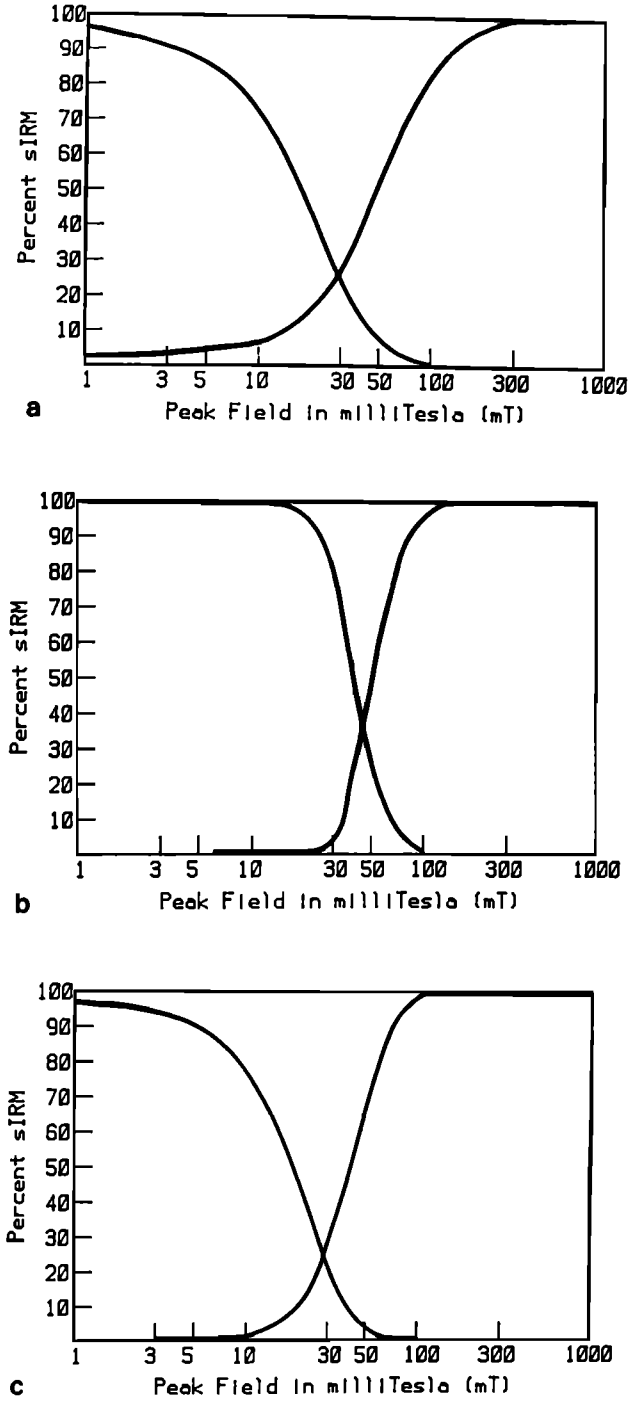

Fig. 1. Coercivity spectra of biogenic magnetites (*a*) *Cryptochiton stelleri*, (*b*) magnetococcus from Laguna Figueroa, Baja California, Mexico, (*c*) GS-15.

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al., 1983; *Mann et al.*, 1984*a*, *b*; *Frankel et al.*, 1979; *Blakemore*, 1982]. These bacterial magnetites are not only morphologically distinct but are chemically pure Fe_3O_4 [*Matsuda et al.*, 1983; *Mann et al.*, 1984*a*, *b*].

Most of the work on the physiology of magnetotactic bacteria has been done on the one organism in culture *Aquaspirillum magnetotacticum*. *A. magnetotacticum* was isolated from a freshwater pond [*Blakemore et al.*, 1979], and morphologically similar magnetotactic spirilla have been seen in other lacustrine environments [*Spormann and Wolfe*, 1984; *Vali et al*, 1987]. It is a bipolarly flagellated spirillum, grows heterotrophically on organic substrates (e.g., succinate, fumarate, tartrate), and is a strict microaerophile [*Blakemore*, 1982]. It produces a chain of 20 or so cuboidal magnetite crystals, 40–50 nm in diameter, with a calculated magnetic dipole moment of 1.3×10^{-12} emu [*Blakemore*, 1982]. Upward of 2% of the total dry weight of the cell is magnetite [*Blakemore*, 1982]. Oxygen is required for magnetite production but not above 5%, with the optimum at 1% [*Blakemore et al.*, 1985]. In *A. magnetotacticum*, the magnetite is formed in a membrane-bounded structure, the magnetosome [*Gorby et al.*, 1988]. Ferric iron is supplied to the cells in a chelated form (e.g., ferric quinate) and transported through the cell wall to the magnetosome as ferrous iron [*Frankel et al.*, 1985]. Inside the magnetosome, the ferrous iron is reoxidized to form a low-density hydrous ferric oxide which matures into a high-density hydrous ferric oxide (ferrihydrite). This high-density hydrous ferric oxide is rereduced to magnetite [*Frankel et al.*, 1985].

Unlike *A. magnetotacticum*, the recently described marine magnetotactic bacterium (MV-1) can form magnetite without molecular oxygen [*Bazylinski et al.*, 1988]. Isolated from sulfide-rich sediments in an estuarine salt marsh, it grows under anerobic conditions using nitrous oxide as the terminal electron donor. MV-1 contains on average, 1.5% per dry weight magnetite in the form of 10 parallelopiped crystals, $40 \times 40 \times 60$ nm, with a dipole moment of 2.1×10^{-13} emu [*Bazylinski et al.*, 1988]. Although little is known on how the magnetite in MV-1 is formed, the crystals are produced in magnetosomes.

To date, all magnetites produced by magnetotactic bacteria are ultra-fine-grained, single-domain [*Blakemore*, 1982; *Chang et al.*, 1987]. Direct measurements on natural enrichments and pure cultures of magnetotactic bacteria have revealed the magnetic properties of the crystals [*Chang et al.*, 1987; *Stolz et al.*, 1986, 1989*b*; *Moskowitz et al.*, 1988, 1989]. The saturation isothermal remanent magnetization (sIRM) and alternating field demagnetization (AF of sIRM) occur quite abruptly between 30 and 75 mT (Figure 1*b*). The median destructive field of the AF of sIRM is around 35 mT and gives a positive Lowrie-Fuller test [*Lowrie and Fuller*, 1971; *Johnson et al.*, 1975], for single-domain magnetite [*Stolz et al.*, 1989*b*]. *Lins de Barros and Esquivel* [1985] have calculated the magnetic moments for different types of magnetic microorganisms and depending on the size of the organism and the amount of magnetite per cell, the values range from 0.3×10^{-12} to 5.4×10^{-11} emu/cell.

The magnetite in *A. magnetotacticum* is cuboidal and conforms to the octahedral form found in abiogenic magnetite [*Mann et al.*, 1984*a*]. However, both the hexagonal prisms and tear-drop-shaped crystals do not appear to be octahedral and represent morphologies unique to biologically produced magnetite (Figures 2*a* and 2*b*). In the case of the hexagonal prisms, elongation of the axis perpendicular to the (111) face of the octahedron results in an apparent sixfold axis of symmetry [*Matsuda et al.*, 1983], as illustrated in Figure 3. Extensional growth normal to the (111), with the corresponding development of prismatic faces, is in reality a result of crystal distortion and not crystal symmetry modification. Nonetheless, this habit is of considerable interest because uniaxial growth along [111] axes corresponds to the "easy direction" of magnetization in magnetite. Crystal elongation also clearly enhances magnetic shape anisotropy and dipole-dipole interactions. It is also possible that the hexahedroid morphology is not magnetite, but a magnetoplumbite (hexagonal symmetry) structured oxide mineral of $AM_{12}O_{19}$ composition (M = Fe and Mn, and A = vacancy or Na, K, Ca) [*Haggerty et al.*, 1987]. One possible candidate is the specific crystal structure described by *Grey et al.* [1987], in which spinel layers alternate with AMO_3 layers perpendicular to the *c* axis of hexagonal magnetoplumbite. As such, the crystal would still behave as a single domain dipole magnet, with strong anisotropy. *Towe and Moench* [1981] have detected vacancies in the crystals of an unidentified magnetotococcus and *Mann et al.* [1984*a*] have seen them in crystals from *A. magnetotacticum*. No major cation substitution has been reported in any biogenic magnetite, but equally, no direct chemical analysis have been possible. The tear-drop- or bullet-shaped crystals pose another intriguing problem, but these have recently been ascribed to the cuboidal habit [*Mann et al.*, 1987*a*, *b*] and are the result of crystal growth confined by an organic matrix.

BIOLOGICALLY INDUCED MAGNETITE

The recent discovery of a type of bacterium which couples the oxidation of organic matter with the reduction of iron, manganese, or nitrate has provided the first example of biologically induced magnetite formation. Designated GS-15, this bacterium was isolated from anoxic sediments from the Potomac Estuary and is a nonmotile, nonmagnetotactic, anaerobic, gram negative rod (Figure 2*c* [*Lovley et al.*, 1987]). GS-15 grows by oxidizing simple organic compounds such as acetate, butyrate, and ethanol with the reduction of Fe (III), manganese Mn (IV), or nitrate as the terminal electron donor [*Lovley and Phillips*, 1988]. When the iron is provided in an amorphous oxide form, GS-15 reduces only a third of the Fe (III) to Fe (II). The Fe (II) reacts with the remaining Fe (III) to form magnetite [*Lovley et al.*, 1987]. In the Potomac estuary where GS-15 was isolated, this process has been shown to effect significantly the cycling of ferrous iron in the system as the magnetite is not subject to further microbial reduction [*Lovley and Phillips*, 1986]. If GS-15 is provided with a chelated form of ferric iron (e.g., ferric citrate), soluble ferrous iron is secreted into the medium [*Lovley and Phillips*, 1988]. Depending on the buffer system used (i.e., bicarbonate or potassium phosphate), this ferrous iron can react with the carbonate or phosphate to form siderite and vivianite respectively [*Lovley and Phillips*, 1988].

The crystals of magnetite produced by GS-15 are cuboidal and between 10 and 50 nm in size (Figure 2*d* [*Lovley et al.*, 1987]). Larger crystals (>50 nm) have been seen in old cultures (several months) but appear to be aggregates of smaller particles. This size range would suggest that most of the crystals are superparamagnetic [*Moscowitz et al.*, 1989].

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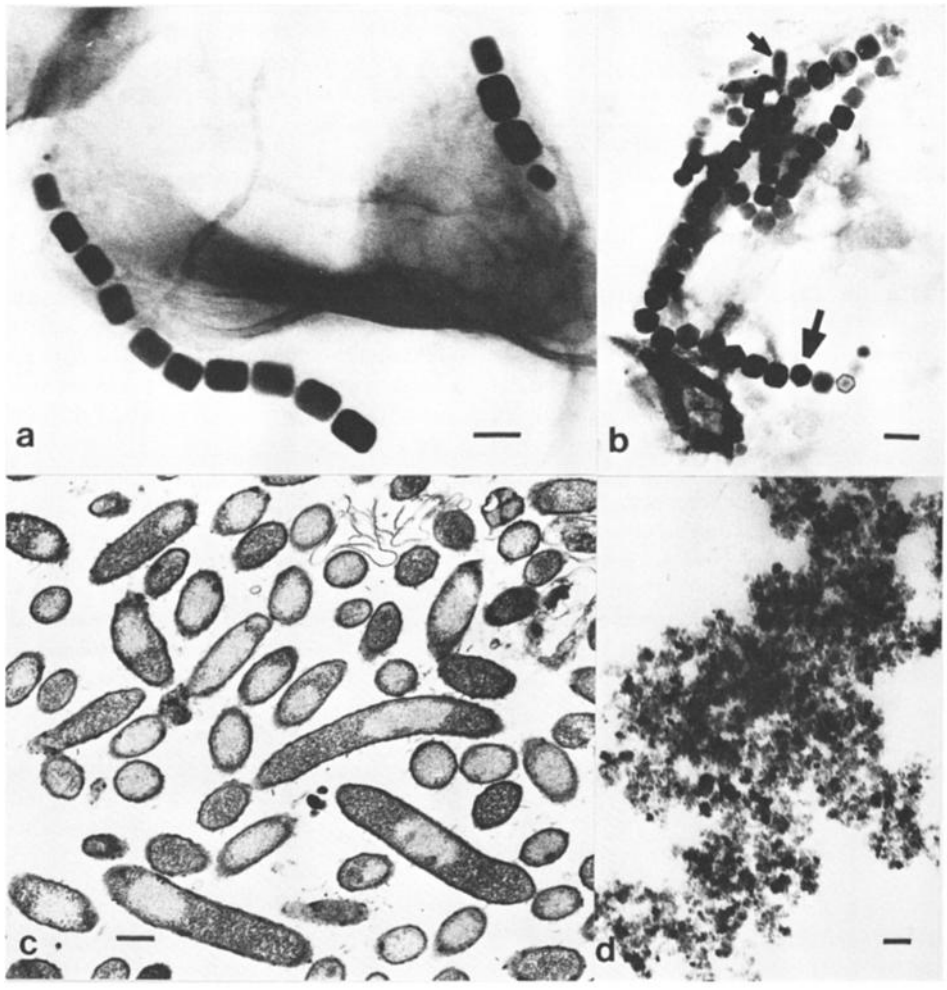

Fig. 2. Magnetite producing bacteria and their magnetite, transmission electron micrographs, all bars 100 nm, except Figure 2*c*, 500 nm. (*a*) Magnetococcus from Laguna Figueroa, Baja California, Mexico, (*b*) bacterial magnetite from the Santa Barbara Basin, note bullet-shaped (small arrow) and hexagonal (large arrow) crystals, (*c*) thin section through GS-15, (*d*) ultra-fine-grained magnetite from GS-15.

The coercivity spectrum, however, shows they behave as single-domain particles, with an abrupt sIRM and AF demagnetization between 15 and 75 mT (Figure 1*c*). The particles also give a positive Lowrie-Fuller test [*Lowrie and Fuller*, 1971; *Johnson et al.*, 1975] with the MDF of the AF of ARM greater than the AF of sIRM [*Lovley et al.*, 1987]. The cuboidal morphology and wide size distribution of the particles are in marked contrast to the distinctive shapes and size constraints found in magnetotactic bacteria. However, observations of GS-15 produced magnetite by high-resolution transmission electron microscopy has revealed no lattice defects or cation substitution (S. Mann, personal communication, 1989). Although GS-15 does not deposit the magnetite intracellular, it has been calculated that it can produce 5000-fold more magnetite per cell than magnetotactic bacteria [*Frankel*, 1987].

MAGNETIZATION OF SEDIMENT

Biogenic magnetites are a source of both detrital and authigenic ultra-fine grained magnetite. *Kirschink and Lowenstam* [1979] calculated that chitons may release up to 1.3×10^{-6} g cm^{-2} yr^{-1} of detrital magnetite through wear in intertidal and subtidal environments. More recently, magnetotactic bacteria have been shown to be a far more abundant source of detrital single domain magnetite [*Chang et al.*, 1987; *Stolz and King*, 1988; *Stolz et al.*, 1989*a*, *b*]. In stratified basins where the oxycline is in the water column, large populations ($\sim 10^5$ cells/mL) of magnetotactic bacteria can form bacterial plates (J. M. Sieburth, personal communication, 1989). Upon death and cell lysis, the ultra-fine-grained magnetite settles to the sediment where it is preserved with depth as a DRM component [*Stolz and King*, 1988].

When the oxycline is at or below the sediment water interface, magnetotactic bacteria are found in the sediment [*Stolz et al.*, 1986; 1989*a*, *b*; *Chang et al.*, 1987, 1989]. These populations can have a dramatic effect on the magnetic properties of the sediment [*Stolz et al.*, 1989*a*, *b*]. Magnetotactic bacteria are the primary remanence carrier in carbonate oozes from the Florida Keys [*Chang et al.*, 1987]. At Laguna Figueroa, Baja California, Mexico, a natural population of between 10^7 and 10^9 cells provides between 10^{-5} and 10^{-3} emu/g, values typically seen for the sediments [*Stolz et al.*, 1989*a*]. In the Santa Barbara Basin the presence

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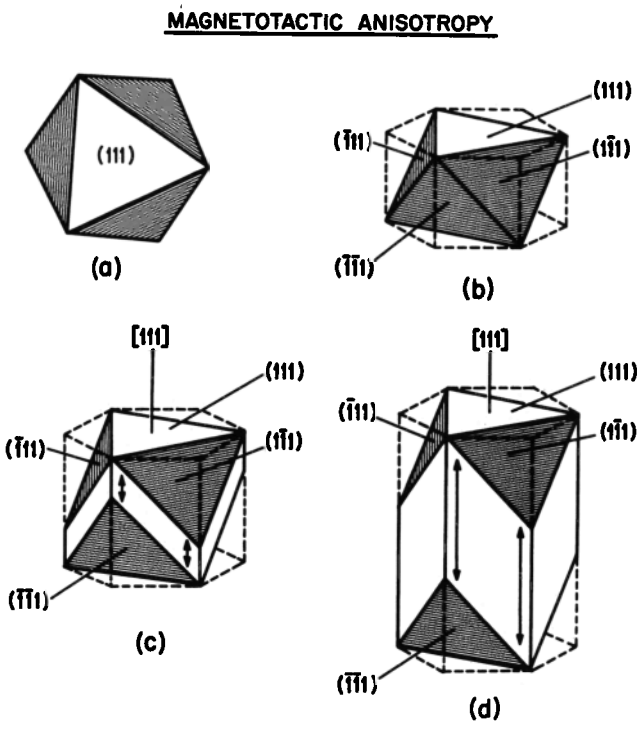

Fig. 3. Progressive crystal distortion and uniaxial growth along a zone axis [111] normal to the (111) plane (Figures 3*a* and 3*b*) of magnetite, imparting an apparent hexagonal symmetry (Figure 3*c*) but a hexahedroid morphology (Figure 3*d*), typical of magnetic particles in *Aquaspirillum magnetotacticum*.

of magnetotactic bacteria in the surface sediments accounts for a 1–2 order of magnitude increase in the natural magnetic remanence [*Stolz et al.*, 1986]. Magnetotactic bacteria also occur in great abundance ($>10^8$ cells/ml) in Lake Oneida, New York, a lacustrine eutrophic lake where manganese nodules are actively accreting (J. F. Stolz, unpublished data, 1987). Even after the cells die and lyse, the alignment of the magnetosomes in a chain is maintained because of the surrounding organic matrix [*Stolz et al.*, 1986].

Both anaerobic, N_2O using, magnetotactic bacteria (MV-1) and dissimilatory iron reducing bacteria have been proposed as primary producers of authigenic magnetite in anoxic sediments [*Lovley et al.*, 1987; *Bazylinski et al.*, 1988]. *Karlin et al.*, [1987] have reported a sharp increase in authigenic magnetite formation in suboxic marine sediments from the eastern equatorial Pacific and attribute it to magnetotactic bacteria. The increase begins just below the zone of nitrate reduction and continues into the zone of iron reduction. It is doubtful, however, that MV-1 is the source since nitrous oxide is a fleeting intermediate of nitrate reduction and nitrate was depleted at the depth of greatest magnetic remanence. *Lovley et al.* [1987] have suggested that the increase is due to biologically induced magnetite formation by dissimlatory iron reducing bacteria. An electron micrograph of the magnetic component should provide the answer.

Whether bacterial magnetites are preserved in the sediment depends on postdepositional factors. Crystals formed by magnetotactic bacteria have been found well preserved in marine sediments over 50 m.y. [*Kirschvink and Chang*, 1984; *Peterson et al.*, 1986; *Vali et al.*, 1987]. They have also been found in both modern and ancient carbonates and limestones [*Chang et al.*, 1987, 1989; *Stolz et al.*, 1989*a*, *b*]. These crystals, however, tend not to be preserved in sediments with a high content of organic carbon [*Chang et al.*, 1987]. It is interesting that both *Karlin and Levi* [1983, 1985] and *Lund et al.* [1983] explain the dissappearance of magnetite in the continental borderland as the result of reduction coupled to organic matter decay. Although this could imply dissimilatory iron reducing bacteria, GS-15 has never been shown to reduce magnetite any further, and *Lund et al.* [1983] believe that it is primarily due to pyritization. Other fates include surface oxidation to maghemite as has been shown in crystals from Deep Sea Drilling Project (DSDP) cores [*Vali et al.*, 1987; *Chang and Kirschvink*, 1989], total dissolution [*Lund et al.*, 1983; *Karlin and Levi*, 1985], or substitution by sulfur in high sulfide environments to form greigite [*Demitrack*, 1985].

Criteria for Identification

Ultra-fine-grained magnetites produced by biologically controlled (matrix mediated) biomineralization can be identified by their distinct morphology (e.g., parallelopiped, cuboidal, tear-drop), size distribution (single domain), and composition (pure Fe_3O_4). These same criteria, in addition to the environment of deposition, can be used to identify magnetofossils in unconsolidated and lithified sediments [*Chang et al.*, 1989]. Whether magnetites produced by microaerophilic magnetotactic bacteria can be distinguished from anaerobic species by morphology alone remains to be determined. The environmental niche of the bacteria (and thus their physiology), however, can be determined from the oxygen, nitrate, and nitrous oxide profiles.

Biologically induced ultra-fine-grained magnetite like that produced by GS-15 may be difficult to definatively identify in the absence of the organisms. The crystals are apparently morphologically indistinguishable from those produced by chemical means [*Taylor et al.*, 1987; *Maher and Taylor*, 1988]. However, magnetite produced by GS-15 has no lattice defects [*Mann et al.*, 1989]. Geochemical data and controlled biological experiments can also provide critical information. GS-15 was isolated from anoxic sediments where active iron reduction was occurring [*Lovley and Phillips*, 1986]. Iron reduction and magnetite formation did not occur in Potomac estuarine sediments in the absence of live organisms [*Lovley and Phillips*, 1986]. Species specific probes are required to facilitate the direct identification of dissimilatory iron reducing bacteria in natural environments.

Mineral composition and mineral structural data are inadequate, and trace element data are at best ambiguous in distinguishing between authigenic mineral phases and certain classes of biologically induced magnetic oxides. Quantitative X ray energy dispersive spectra so widely used in these studies cannot, as implied by *Banerjee* [1988], distinguish between and among magnetite, hematite, maghemite, lepidocrocite, goethite, akaganeite, or any other simple iron oxide or complex hydroxide; the method merely substantiates the presence of Fe. Biological experiments, although understandably undesirable for the paleomagnetist, are necessary to either substantiate or discount biologically induced magnetite formation. A case in point is the study by *Maher and Taylor* [1988, p. 368] in which soils were selected "that have no apparent external source of magnetite . . . ", namely, slates and limestones. On the contrary, both rock

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types may contain magnetite, but more importantly, is the lack of an unequivocal demonstration that magnetite producing bacteria (i.e., dissimilatory iron reducing bacteria) are or were absent. That the magnetic extract did not contain bacteria does not by itself support the conclusion that the observed magnetite was formed by an inorganic process.

CONCLUSIONS

The biogenic formation of magnetite is not confined to any one type of organism and has been found in prokaryotes, protoctists, and animals. It can be formed by both biologically induced and biologically controlled processes of biomineralization. Furthermore, ultra-fine-grained, single-domain magnetite can be produced in environments that range from oxic to anoxic. Chitons may contribute a small amount of magnetic remanence to sediments, but in light of the work on the bacterial input, it is negligible. Other marine animal sources (e.g., fish, cetaceans, etc.) may be disregarded as well, as the amount of magnetite compared to the size and number of organisms is very small. The bacterial sources on the other hand represent a significant source of primary remanence carrier. Microaerophilic and anaerobic magnetotactic bacteria can produce single-domain magnetite within the water column and in surface sediments depending on where the oxycline lies. In anoxic sediments, in addition to anaerobic magnetotactic bacteria, the production of magnetite can be biologically induced via dissimilatory iron reduction with substantial quantities being produced.

It is clear that rock magnetic and geochemical analyses alone are insufficient to determine the origin of the single-domain magnetite component. These studies must be augmented with granulometric (at the submicron level with transmission electron microscopy), mineral structural and composition analyses of the magnetic extracts, as well as studies of microbial activity. Determination of NRM; coercivity spectra; porewater analysis for oxygen, nitrate, nitrous oxide, and ferrous iron; morphometrics and compositions of the magnetite particles; as well as the species distribution and abundance of magnetite-producing bacteria is needed to definitively identify the biogenic source of the remanence carrier.

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