Single magnetic domains in magnetotactic bacteria

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Abstract. Magnetotactic bacteria construct an internal, permanent magnetic dipole based on single magnetic domain particles of magnetite or greigite. The organisms exert a high degree of control over the size and morphology of the particles. This may be relevant in distinguishing biogenic from nonbiogenic iron mineral particles.

1. Introduction

The theory of single-magnetic domains, published by *Kittel,* [1946] 50 years ago, has had a major impact on understanding the remanent magnetism of rocks and sediments, as well as on technological applications of magnetism, such as permanent magnet design and magnetic recording. Permanent magnet and magnetic tape manufacturers seek to produce single magnetic domains for the reasons cited by Kittel, namely, high coercive force and high remanent magnetization, but in this endeavor they have been scooped by magnetotactic bacteria which have been producing single magnetic domain particles of magnetite and greigite for perhaps billions of years. The particles are arranged within the cell to produce a permanent magnetic dipole that is a masterpiece of permanent magnet engineering.

Magnetotactic bacteria are a diverse group of motile, aquatic bacteria that orient and migrate along geomagnetic field lines *[Blakemore,* 1975; *Frankel and Blakemore,* 1980]. Each cell contains magnetosomes, which are membrane-enclosed, iron-mineral particles *[Balkwill et al.,* 1980; *Gorby et al.,* 1988; *Bazylinski,* 1995]. The magnetosomes are typically aligned in a chain, with the chain orientation close to the axis of motility of the cell *[Bazylinski et al.,* 1994]. In magnetotactic bacteria from microaerobic freshwater and marine environments the magnetosome iron mineral is magnetite, Fe_3O_4 *[Frankel, et al.,* 1979], whereas greigite, Fe_3S_4, is found in magnetotactic bacteria from sulfidic environments *[Mann et al.,* 1990]. The magnetosome membrane is presumably a structural entity that anchors the mineral particles at particular locations in the cell, as well as the locus of biological control over the mineralization process.

2. Cellular Magnetic Dipole

An electron micrograph of magnetite particles in the magnetotactic bacterium *Magnetospirillum magnetotacticum* is shown in Figure 1. The particle morphology of the particles is cubo-octahedral, with [111] axes oriented along the direction of the chain *[Mann et al.,* 1984]. A narrow particle size distribution and consistent, species-specific particle morphology and orientation are characteristic of the magnetite biomineralization processes in all magnetotactic bacteria *[Bazylinski et al.,* 1994]. Average particle dimensions for several strains is given in Table 1. Based on the calculations of *Butler and Banerjee* [1975] and others, the particle dimensions are within the permanent single-magnetic-domain range for Fe_3O_4.

When magnetosomes are arranged in a single chain, as in *Magnetospirillum magnetotacticum,* magnetostatic interactions between the single magnetic domain particles cause the particle moments to spontaneously orient parallel to each other along the chain direction *[Frankel and Blakemore,* 1980; *Frankel,* 1984]. This results in a permanent magnetic dipole with a natural remanent magnetization approaching the saturation magnetization. A cell with a chain of twenty 50 nm^3 magnetosomes would have a magnetic dipole moment = 10-12 emu, sufficient for orientation of the moment along the geomagnetic field at ambient temperature. Since the chain of particles is fixed within the cell, the entire cell will orient along the field. This results in the cell migrating along the magnetic field as it swims. Thus the bacteria have elegantly solved the problem of how to construct a magnetic dipole that will be oriented in the geomagnetic field yet fit inside a micron-sized cell. The solution is based on the ability of the bacteria to control the iron mineral type, the size and orientation of the particles, and their placement in the cell.

The permanent magnetic dipole nature of the magnetosome chain has been demonstrated by pulsed magnetic field remanence measurements on individual cells of *M. magnetotacticum [Penninga et al.,* 1995]. In these measurements, cells aligned in a weak [=10 G] field were subjected to short, magnetic-field pulses of increasing amplitude, oriented opposite to the weak alignment field. Following each pulse, the relative magnetic moment of the cell was determined using a rotating magnetic field method. The results showed that the hysteresis loops of *M. magnetotacticum* cells were square, with a coercive force = 300 G, with variation in the coercive force from cell to cell attributable to differences in length of the magnetosome chain. The results were consistent with bulk measurements on whole cells *[Penninga et al.,* 1995; *Moskowitz,* 1995].

It has recently been shown that bacteria use magnetotaxis in conjunction with aerotaxis to efficiently find the optimal location in a vertical oxygen gradient in chemically stratified freshwater and marine environments [Frankel et al., 1997]. Two types of magnetotaxis, polar and axial, have been distinguished that correspond to different aerotactic mechanisms, although both involve the passive orientation of the cellular magnetic dipole in the geomagnetic field.

3. Variations in Structure

As noted in section 2, the morphology of the iron mineral particles is species-specific. Magnetite morphologies include cubo octahedral, hexagonal prismatic, and octahedral prismatic [Mann and Frankel, 1989]. The lower symmetry forms presumably result from interactions between the magnetosome membrane and the growing crystal. Even less symmetric forms, known variously as needle-, tear-, bullet-, and arrowhead-shaped, occur in certain species [Blakemore et al., 1980; Mann et al., 1987; Vali and Kirschvink, 1991]. Two greigite forms, cubo-octahedral and rectangular prismatic are known [Heywood et al., 1990, 1991].

There are a number of variations on the magnetosome-chain motif. Some species construct chains with two or more strands of magnetosomes [Bazylinski, et al., 1994]. Others construct multiple chains per cell [Vali and Kirschvink, 1991] . In a few cases, the magnetosomes are not organized in chains but appear to be clustered in one part of the cell [Towe and Moench, 1981].

While most species make magnetosomes with only one iron mineral, there are two reported instances of bacteria that have two iron minerals. One of these (a many celled, magnetotactic prokaryote) contains particles of greigite and nonmagnetic pyrite [Mann et al., 1990]. The function of pyrite in these cells has not been ascertained. Another organism, a large magnetotactic rod, produces greigite and magnetite magnetosomes, coorganized in the same chains [Bazylinski et al., 1993, 1995]. The relative amount of each mineral in the cell is thought to depend on external chemical conditions.

Besides bacteria, several other organisms have been reported to contain magnetite, including single-celled algae [Torres de Araujo et al., 1986], salmon [Mann et al., 1988], humans [Kirschvink et al., 1992] and other eukaryotes. The algae contain many long chains of arrowhead-shaped magnetite particles that traverse the cell. The salmon particles are cubo-octahedra arranged in chains, as in the bacteria. Magnetite in human brain is bimodal, with some particles reminicent of bacterial magnetite and others generally larger than single magnetic domain size and without defined morphology. With respect to iron sulfides the presence of greigite within vacuoles in the roots of certain plants has been reported [Fassbinder et al., 1990; Stanjek et al., 1994]. The mineral may be associated with bacteria in the vacuole.

Because of their narrow size distribution, within the single magnetic domain size range for magnetite, bacterial magnetosomes can make a substantial contribution to the sedimentary paleomagnetic record [Chang et al., 1987; McNeill, 1990; Oldfield, 1994; Moskowitz, 1995]. Putative magnetite magnetosomes have been recovered from a number of freshwater and marine sediments [Petersen et al., 1986, 1989; Stoltz, et al., 1986; Vali et al., 1987; Chang and Kirschvink, 1989; Petermann and Bleil, 1993]. However, in some sediments, there is evidence for diagenetic transformation of magnetosomes [Vali and Kirschvink, 1989; Karlin, 1990; Hesse, 1994; Tarduno and Wilkinson, 1996].

4. Iron Minerals in the Martian Meteorite ALH84001

McKay et al. [1996] cited a number of features of the Martian meteorite ALH84001 as evidence for ancient life processes [1.83.0 Gal on Mars. These included ultrafine [dimensions less than 100 nm] iron oxide [magnetite] and iron sulfide [pyrrhotite and griegite] particles embedded in a finer-grained, carbonate matrix on the rim of the carbonate inclusions. In particular, the magnetite particles were cited as evidence for life primarily because of their similarity in morphology and size distribution to magnetite particles produced by magnetotactic bacteria and other terrestrial organisms and their morphological dissimilarity to magnetites in other meteorites. However, other magnetite forms in ALH84001 have been also been reported [Bradley et al., 1996]. This has raised the question of how to distinguish biogenic from non-biogenic iron minerals.

Lowenstam [1981] distinguished two modes of biomineralization, namely, biologically induced mineralization (BIM) and biologically controlled mineralization (BCM). In BIM, cellular export and diagenesis of metabolic products result in extracellular mineral formation with ions in the environment. BIM processes are not controlled by the organism and thus essentially equivalent to nonbiogrenic mineralization at ambient temperature. The absence of control can result in lack of mineral specificity and/or inclusion of impurity ions. For example, dissimilatory iron-reducing bacteria such as Geobacter metallireducens can respire Fe(III) in the form of amorphous ferric oxyhydroxide [Lovley, 1991], and export ferrous ions into the environment where they subsequently interact with excess ferric oxyhydroxide to produce magnetite as a presumably unintended byproduct. The magnetite particles have a relatively broad size distribution (Table 1) and no consistent morphology [Moskowitz et al., 1989; Sparks et al., 1990]. Some particles are only quasi-crystalline. The ferrous ions can also interact with carbonate or other anions in the medium to form siderite, $FeCO_3$, or other ferrous compounds.

In BCM, organisms exert a high degree of crystallochemical control over the nucleation and growth of the mineral particles. In general, minerals are deposited in a specific location, in or on preformed organic vesicles or matrices produced by the organism, from supersaturated solutions that are generated by biochemical processes. Thus BCM is ultimately connected to cellular metabolic and genetic control. Nucleation and growth of the mineral phase can be activated chemically or interfacially. Magnetotactic

bacteria, as noted above, form magnetite in intracellular, magnetosome membrane vesicles, from a ferric oxyhydroxide precursor and ferrous ions [Mann and Frankel, 1989]. The magnetite particles have a narrow size distribution (Table 1) and consistent, species-specific morphology, with the size constrained by the magnetosome membrane.

Because the BIM particles may be indistinguishable from nonbiogenic particles produced by inorganic reactions, it may be possible to definitively identify magnetite particles as biogenic if produced by BCM processes but not if they are produced by BIM processes. Thus narrow particle size distribution could be a marker for BCM magnetite. However, whether that size distribution is within the single magnetic domain size range depends on the functions of the magnetite in the cell. If one of the functions is related to a permanent cellular magnetic dipole, as in magnetotaxis, single magnetic domains would be expected. However, there are other possible functions associated with magnetite mineralization [Williams, 1990] including iron storage, redox homeostasis, and peroxide dismutation, that do not necessarily involve magnetism. If there is no selection for magnetic properties, the BCM process could still result in a narrow particle size distribution but not necessarily centered in the 40-100 nm size range. Interestingly, Golden et al. [1997] have recently reported that magnetite particles in the carbonate rims of ALH84001 have a narrow particle size distribution, with an average dimension of about 42 nm, comparable to terrestrial magnetotactic bacteria (Table 1). This finding raises the intriguing possibility, not just of biogenic magnetite on ancient Mars but of magnetite selected for single magnetic domain properties. This could push back the already long connection between life and single magnetic domains by one or more billion years.

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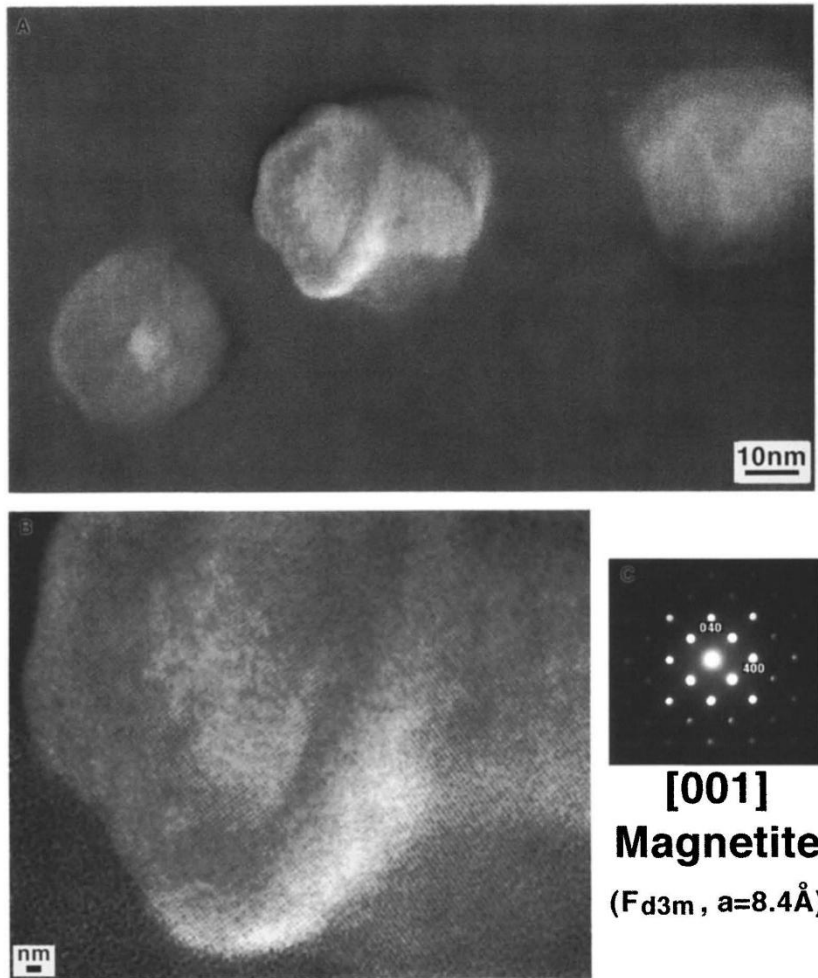
Figure 1. (a) High-resolution electron micrographs of three magnetite particles in the magnetosome chain within *Magnetospirillum magnetotacticum*, taken with a JEOL 2010 transmission electron microscope operating at 200 kV. The variation in contrast appears to be due to layered growth of the particles. (b) Lattice image of the center particle in Figure 1a, which is oriented along [001]. The lattice planes continuously cross the layers in the crystal surface, indicating coherent growth. (c) Electron diffraction pattern from the particle shown in Figure 1b. The allowed reflections of $h00$ and $0k0$ when $h,k = 4n$, $n = 1,2,3..$, such as 040 and 400, are consistent with the diamond structure (space group Fd3m) of magnetite. The lack of rotations or misfits in the pattern is consistent with the lattice image shown in Figure 1a.

Table 1. Dimensions of Magnetite Particles From Four Strains of Magnetotactic Bacteria and a Dissimilatory Iron-Reducing Bacterium

Strain	$<l>$ nm	$<w>$ nm
MV-1	53 (±11)	35 (±8)
MV-4	61 (±12)	52 (±11)
MC-1	83 (±14)	78 (±11)
MS-1[a]	42 (±6)	42 (±6)
GS-15[b]	14	11

[a]*Magnetospirillum magnetotacticum.*
[b]*Geobacter metallireducens;* range: 8-22 nm.