Review Article

Magnetosomes

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Introduction

Magnetotactic bacteria are a fascinating and diverse group of micro-organisms which share the ability to orient themselves in magnetic fields. In the northern hemisphere, these bacteria orient northward and will swim towards the south pole of a magnet. The reverse is true for those in the southern hemisphere. This behaviour, called magnetotaxis, is possible because the bacteria precipitate particles of magnetic minerals intracellularly in a membrane bounded structure, the magnetosome. Although the magnetosomes found in different species may differ in shape and composition, they all fall within a narrow size range and share the property of being a stable dipole magnet (i.e. having a permanent north and south pole). The study of these organisms has been hampered by the resistance to culture of many species. Recent success, however, has been achieved with the isolation of several new strains. In addition, ingenious methods, all involving applied magnetic fields, have been devised to obtain axenic cultures of non-culturable types (e.g. the capillary race track; Wolfe *et al.*, 1987). It has been through these efforts, in conjunction with field studies, that discoveries regarding the physiology, ecology and evolution of magnetotactic bacteria have been made. There are at least three different physiological types of magnetotactic bacteria based on their oxygen requirement and magnetic mineral formed in the magnetosome. In nature, the abundance and distribution of the different physiological types depends not on an innate need for sediment (as had been the prevailing view), but rather on the availability of iron, oxygen and sulphide. Furthermore, magnetosomes can have a profound affect on the magnetic properties of their environs and have been found preserved in ancient sediments. From an evolutionary perspective, magnetosomes are found in

two phylogenetically distinct lineages of bacteria, and thus magnetotaxis appears to have a polyphyletic origin. The purpose of this review is to highlight these recent discoveries.

Morphology and composition of magnetosomes

Magnetotactic bacteria exhibit a great diversity of cell morphologies (Fig. 1). Unicellular coccoids of varying diameters (Blakemore, 1975; Moench & Konetzka, 1978; Esquivel & Lins de Barros, 1986; Chang *et al.*, 1987), multicellular coccoids (MMP; Lins de Barros & Esquivel, 1985; Farina *et al.*, 1990; Mann *et al.*, 1990), rods of varying dimensions (Blakemore *et al.*, 1980; Bazylinski *et al.*, 1990; von Döbeneck *et al.*, 1987; Stolz, 1992), vibrios (Bazylinski *et al.*, 1988; Stolz, 1992) and spirilla (Blakemore *et al.*, 1979; Spormann & Wolfe, 1984; Matsunaga *et al.*, 1991; Schliefer *et al.*, 1991; Spring *et al.*, 1992) have been reported from numerous locations around the world. Regardless of morphology, the organisms all contain magnetosomes and are propelled by flagella. The arrangements of flagella may be polar (Bazylinski *et al.*, 1988), bipolar (Balkwill *et al.*, 1980), in tufts (Blakemore, 1975), or as is the case of the colonial coccoid, may cover only the area of cell wall that is exposed to the environment (Lins de Barros & Esquivel, 1985).

Magnetosomes are the membrane bounded magnetic intracellular inclusions found in all magnetotactic bacteria (Balkwill *et al.*, 1980; Gorby *et al.*, 1988). Their morphology, crystal structure and composition have been determined by transmission electron microscopy (TEM), high resolution TEM (HRTEM), Mössbauer spectroscopy, X-ray powder diffraction, selected area electron diffraction and energy dispersive X-ray analysis (Frankel *et al.*, 1979; Towe & Moench, 1981; Sparks *et al.*, 1990; Mann *et al.*, 1984*a, b*, 1987*a, b*). A variety of crystal morphologies have been described (Fig. 1). These

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Fig. 1. Magnetosomes. (a) Freshwater bacterium with hexagonal particles; (b) freshwater bacterium with parallelepipeds of magnetite; (c) freshwater bacterium with 'tear-drop' shaped particles of magnetite; (d) magnetotactic many-celled prokaryote (MMP) with greigite 'flakes'; (e) greigite particles at higher magnification. (a), (b) and (c) are from Lake Pymatuning, Phil., USA; bars, 1 μm . (d) and (e) are from Salton Sea, Calif., USA; bars, 500 nm and 200 nm respectively. Figures are digitally enhanced.

include truncated octahedrons (Balkwill *et al.*, 1980), parallelepipeds (Towe & Moench, 1979), hexagonal prisms (Matsuda *et al.*, 1983; Stolz *et al.*, 1990), 'tear-drop' shaped (Blakemore *et al.*, 1980) and 'flake' shaped (Bazylinski *et al.*, 1990). In rare instances even twinned crystals have been observed (von Dobeneck *et al.*, 1987).

Originally, it was thought that all these particles were made of the ferromagnetic mineral magnetite (Fe_3O_4), and were relatively pure in composition (Frankel *et al.*, 1983; Towe & Moench, 1981). Studies on organisms from sulphidic environments, however, have shown that some species have magnetosomes containing iron sulphides such as greigite, pyrrhotite and pyrite (Farina *et*

al., 1990; Mann *et al.*, 1990; Bazylinski *et al.*, 1990, 1993*a, b*). In addition, these iron sulphide containing magnetosomes may be more amenable to replacement by other cations. Copper has been found as a surface coating on greigite magnetosomes in a colonial coccoid (Bazylinski *et al.*, 1993*a*) (Fig. 2).

The magnetic properties of magnetosomes have been determined by rock magnetic methods (Stolz *et al.*, 1986, 1989*a, b*; Chang *et al.*, 1987; Moskowitz *et al.*, 1989). Irrespective of shape or composition, they all fall within the theoretical size range for single-domain magnetic particles (Butler & Banerjee, 1975). Plotting the length (in micrometres) of the particle against its axial ratio

Fig. 2. Elemental analysis of magnetite and iron sulphide inclusions. (a) magnetite from MV-1; (b) iron sulphide from colonial coccoid; (c) copper coated iron sulphide from colonial coccoid. Adapted with permission from Bazylinski *et al.* (1990, 1993b). Figures are digitally enhanced.

(width over length), all the particles cluster within a range of 0.1–0.2 (Chang *et al.*, 1987). The ‘Goldilocks principle’ can explain the strong selective pressure which

constrains the size and morphology of a functional magnetosome. If the particles are too small, they do not have enough mass to overcome the energy of thermal vibration and maintain a stable magnetic moment (i.e. they are superparamagnetic). If the particles are too big, domain walls form with randomly oriented magnetic domains resulting in a weak total magnetic moment (i.e. multi-domained). Only single-domained particles are ‘just right’ for magnetotaxis. This constraint on size and morphology, as well as the occurrence of crystal morphologies hitherto unknown in abiotically produced magnetites (e.g. hexagonal prisms and tear-drop shapes) strongly suggest that particle formation is under the strict control of the magnetosome. It also helps explain why single-domained magnetic minerals occur in phylogenetically distant organisms (see below).

Physiology of magnetosome forming bacteria

Initial studies on the first cultured magnetotactic bacterium, *Aquaspirillum* (*Magnetospirillum*) *magnetotacticum* suggested that microaerophilic conditions were necessary for magnetite formation (Blakemore *et al.*, 1984). However, with the study of iron sulphide forming magnetotactic bacteria (Mann *et al.*, 1990; Bazylinski *et al.*, 1993a) and the marine vibrios MV-1 and MV-2 (Bazylinski, 1990; Bazylinski *et al.*, 1993b), it now appears that there are at least three different physiological types. The types can be differentiated by their oxygen requirement (i.e. obligate microaerophile, facultative microaerophile and obligate anaerobe) and magnetosome composition (i.e. magnetite and/or iron sulphide). The first type produce magnetite as obligate microaerophiles. The magnetotactic bacteria *A. magnetotacticum*, *Bilophococcus magnetotacticus*, and the recently cultured marine coccoid MC-1 all fall into this category (Blakemore *et al.*, 1984; Moench, 1989; DeLong *et al.*, 1993; Meldrum *et al.*, 1993a). The second type, which include the marine vibrios MV-1, MV-2 and MV-4, are facultative microaerophiles which form magnetite either under microaerophilic conditions or, in the absence of oxygen, with nitrous oxide (Bazylinski *et al.*, 1988, 1993b; Meldrum *et al.*, 1993b). The third type can form iron sulphide particles (e.g. greigite) and appear to be strict anaerobes. Although none have been successfully cultured in defined medium, their occurrence in the sulphide rich zones of sediments and water columns strongly suggests an anaerobe physiology. The multicellular coccoid or magnetotactic many-celled prokaryote (MMP) identified from marine sediments in Rio de Janeiro, Brazil, (Farina *et al.*, 1990), Cape Cod, Mass. (Mann *et al.*, 1990), and southern California (Bazylinski *et al.*, 1993a) USA, and a large rod described from stratified marine environments (J. McN. Sieburth and

Fig. 3. Phylogenetic relationships of magnetotactic bacteria inferred from least squares distance-matrix analyses. The scale bar represents five fixed mutations per 100 nucleotide sequence positions. *Shewanella putrefaciens* is on the same branch as *Escherichia coli* with the gamma Proteobacteria (*). The dissimilatory iron reducing bacterium *Geobacter metallireducens* is on the same branch as *Desulfuromonas acetoxidans*, with the delta Proteobacteria (†). Adapted with permission from DeLong *et al.* (1993).

others, unpublished; Bazylinski, 1991; Bazylinski *et al.*, 1993a) are examples of this type. The MMP from the Salton Sea, Calif., USA, is shown in Fig. 1(d).

It should be mentioned that magnetite is also formed by bacteria capable of dissimilatory iron reduction. These bacteria do not have magnetosomes, are not

magnetotactic, and precipitate the crystals extracellularly (Lovley *et al.*, 1987, 1989). *Geobacter metallireducens* is a non-motile, strict anaerobic rode, which oxidizes acetate to CO₂ using ferric iron as a terminal electron acceptor (Lovley, 1991). When amorphous ferric oxide is the source of ferric iron, it is converted to magnetite (Lovley

Fig. 4. Magnetofossils from deep-sea sediments (southwest Pacific). (a) Oligocene; (b-d) Quaternary. All bars, 0.1 μm . Adapted with permission from von Döbeneck *et al.* (1987). Figures are digitally enhanced.

et al., 1987). Several sulphate reducing bacteria (e.g. *Desulfovibrio desulfuricans*, *D. vulgaris*), and the facultative anaerobe *Shewanella putrefaciens*, have been shown to produce magnetite by coupling iron reduction to the oxidation of hydrogen (Coleman *et al.*, 1993; Lovley *et al.*, 1989).

Many of the organisms described above have had their 16S ribosomal RNA sequence determined (Fig. 3). To date all microaerophilic magnetite forming bacteria fall within the alpha subdivision of the Proteobacteria (Schliefer *et al.*, 1991; Spring *et al.*, 1992; DeLong *et al.*, 1993). The two strains of greigite forming bacteria (MMP 1990 and MMP 1991) from Cape Cod, Mass., however, group with the sulphate reducing bacteria in the delta subdivision of the Proteobacteria (DeLong *et al.*, 1993). This suggests that magnetotaxis has had multiple origins and the apparent similarity (e.g. single-domained magnetic particles) in the two distantly related groups is due to the constraints on the size and shape of a functional magnetosome rather than to a distinct bacterial physiology or magnetosome composition. This same line of reasoning can be used to explain why such phylogenetically diverse creatures as pigeons, bees and tuna all have similarly shaped magnetosomes in their magnetic sensory organs (Stolz, 1992).

Interestingly the strict anaerobic dissimilatory iron reducing bacteria (e.g. *G. metallireducans*) also fall within the delta Proteobacteria. They cluster with the sulphate reducing bacteria (e.g. *D. desulfuricans*, *D. vulgaris*), and

are closely related to the sulphur reducer *Desulfomonas acetoxidans* (Lovley *et al.*, 1993). The facultative anaerobe *S. putrefaciens*, however, is in the gamma Proteobacteria group (DiChristina & DeLong, 1992; Semple *et al.*, 1989). This suggests that other facultative anaerobes capable of dissimilatory iron reduction may also be related to the gammas.

Ecology of magnetosome forming bacteria

A current misconception about magnetotactic bacteria is that they are found in sediments (Blakemore, 1975, 1982; Blakemore & Frankel, 1980; Frankel, 1984; Moench, 1989). Although magnetotactic bacteria have been identified in lacustrine, brackish and marine sediments (Blakemore, 1982; Moench & Konetzka, 1979; Stolz *et al.*, 1986, 1989a, b) as well as terrestrial soils (Fassbinder *et al.*, 1990), recent studies have discovered large populations in stratified waters (J. McN. Sieburth and others, unpublished; Bazylinski, 1991; Bazylinski *et al.*, 1993b). Furthermore, different species inhabit different depths in the water column often forming distinct plates. The distribution appears to be determined by the availability of soluble iron and the concentrations of oxygen and sulphide. A generalized model has been proposed, based on observations of both marine benthic and pelagic environments, that magnetotactic bacteria are restricted to the oxic/anoxic transition zone (OATZ) where iron is present in a soluble phase (J. McN.

Sieburth and others, unpublished). Data from the water column of a stratified basin in the Pettaquamscutt River (Rhode Island, USA) (Donaghay & Sieburth, 1992; Sieburth, 1989, 1991) and sediment profiles from the California Borderland (Karlin *et al.*, 1987; Reimers *et al.*, 1992) show a correlation between the profile of soluble iron (e.g. pore water iron) and the occurrence of magnetotactic bacteria (Stolz *et al.*, 1986; Stolz, 1992). The concentration of oxygen and sulphide can also be correlated with the distribution of the different physiological types. In the lower basin of the Pettaquamscutt Estuary, the microaerophilic magnetite forming bacteria (i.e. MC-1) are the first to appear. Facultative anaerobic magnetite forming bacteria (i.e. MV-4), begin to show up at a depth where oxygen becomes depleted and continue through the sulphidic zone. Anaerobic greigite forming bacteria (i.e. the MMP and large rod) are found at depths where sulphide concentrations range from micromolar to millimolar amounts (J. McN. Sieburth and others, unpublished). Although the abundance and distribution of any one physiological type can vary with changes in the physical-chemical profile (i.e. movement up or down in the water column of the OATZ), there is always a stable population ($> 10^5$ bacteria ml^{-1}). A similar scenario occurs at Salt Pond (Woods Hole, Cape Cod) although the stratification is seasonal (Bazylinski *et al.*, 1990). Furthermore, this stratification of physiological types will most likely be found in sediments when samples are collected with sufficient resolution (e.g. submillimetre scale).

Magnetotactic bacteria can have an important impact on their environs. They sequester high concentrations of iron (e.g. picograms per cell) intracellularly as magnetite or iron sulphides and thus are important components in the microbial iron cycle. For example, one large rod from the Pettaquamscutt contains on average 100 crystals of greigite per cell ($\sim 1.2 \times 10^{-13}$ g Fe per cell) and reaches a population density of 2×10^5 cells ml^{-1} . This translates to 24 μm of iron tied up as particulate iron by one cell type alone (J. McN. Sieburth and others, unpublished). When the cells die and lyse, the particles are protected from dissolution by the organic material that surrounds them and can survive burial in anoxic sediment (Stolz, 1992). Since the particles behave as dipole magnets, they contribute significantly to the magnetization of sediments (Stolz *et al.*, 1986, 1989a, b, 1990; Chang *et al.*, 1987; Peterson *et al.*, 1986, von Döbenek *et al.*, 1987; Vali *et al.*, 1987). The peak in natural remanent magnetization of several different sediment types (e.g. carbonate oozes, hemipelagic sediments) has been attributed to the occurrence of magnetotactic bacteria (Stolz *et al.*, 1986; Peterson *et al.*, 1986; Chang *et al.*, 1987; Karlin *et al.*, 1987; Vali *et al.*, 1987).

Furthermore, beautifully preserved magnetofossils

have been recovered from deep-sea sediments of Oligocene, Miocene and Quaternary ages (Fig. 4; Kirschvink & Chang, 1984; Chang & Kirschvink, 1985; Peterson *et al.*, 1986; Vali *et al.*, 1987). Even when surface oxidation has occurred, carefully extracted magnetofossils maintain their distinctive morphologies (Peterson *et al.*, 1986; Vali *et al.*, 1987). Thus the evolutionary history of magnetosomes is preserved in the rock record as magnetofossils (Chang *et al.*, 1987, 1989; Stolz *et al.*, 1989).

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