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Author	Family Name	<b>Pósfai</b>
	Particle	
	Given Name	<b>Mihály</b>
	Suffix	
	Division	Department of Earth and Environmental Sciences
	Organization	University of Pannonia
	Address	P.O. Box 158 H-8200, Veszprém, Hungary
	Email	mihaly.posfai@gmail.com

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## MAGNETOTACTIC BACTERIA

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### Definition

Magnetotactic bacteria (MTB) are a diverse group of Gram-negative, motile prokaryotes that align and migrate along the geomagnetic field. This magnetotactic behavior is based on intracellular organelles called magnetosomes, which are inorganic nanocrystals of either magnetite ( $\text{Fe}_3\text{O}_4$ ) or greigite ( $\text{Fe}_3\text{S}_4$ ), surrounded by a lipid bilayer membrane. The magnetosomes are typically arranged in one or more chains, conveying a magnetic dipole moment to the cell (Figure 1). Magnetotaxis is thought to be beneficial for the cell for finding its optimum position in vertical concentration gradients in aquatic habitats.

### History

Bacteria that responded to magnetic fields were discovered independently by Bellini (1963) and Blakemore (1975), who coined the term magnetotaxis and noted the presence of crystals in the cells. Intracellular magnetite was identified and the physics of magnetotaxis was described by Frankel et al. (1979). Iron sulfide-producing MTB were found in 1990 (Mann et al., 1990; Farina et al., 1990). The ecology of MTB and the structures and morphologies of the crystalline components of magnetosomes have been widely studied since the discovery of MTB. In the past decade, significant progress has been made in elucidating the molecular, biochemical, and genetic bases of magnetosome formation (Schüler, 2007).

### Ecophysiology

MTB are ubiquitous in both marine and freshwater aquatic habitats, where suboxic or anoxic conditions prevail, and dissolved iron is available. Because of their fastidious nature, only a few strains are available in pure culture. With one exception, all strains in pure culture have

a respiratory form of metabolism. All known MTB are microaerophiles (they require a certain amount of oxygen for growth, but exhibit a negative tactic and/or growth response to atmospheric concentrations of oxygen) or anaerobes or facultatively anaerobic microaerophiles (Bazylinski and Frankel, 2004). The physiology of MTB appears to dictate their ecology: since MTB derive energy from the proximity of oxidants and reductants, magnetite producing organisms occur in largest numbers (up to  $10^5$  cells/ml) in layers at or near the oxic–anoxic interfaces (OAI) of chemically stratified habitats. Iron sulfide-producing bacteria live below the OAI under anaerobic conditions (Simmons et al., 2004). Whereas magnetite-producing bacteria occur virtually in all types of water bodies, sulfide-producing organisms have been found in marine habitats only. Considering the large amount of iron concentrated in magnetosomes ( $10^{-15}$  to  $10^{-13}$  g Fe per cell) and the estimated population density of MTB at and below the OAI, MTB are likely to contribute significantly to the flux of reduced Fe to sediments in chemically stratified marine basins.

### Magneto-aerotaxis

Magnetotaxis means active motion guided by the magnetic field. MTB passively orient along the geomagnetic field and actively swim by means of flagella. A key element of magnetotaxis is that the cell should possess a large enough magnetic dipole moment to overcome the disorientating effects of thermal motions and be aligned parallel to the magnetic field. In the geomagnetic field, the magnetic energy of magnetotactic cells is typically ten times larger than thermal energy, which means that the cell can migrate along the field at 90% of its forward speed (Frankel et al., 1979).

“Polar” and “axial” magnetotaxis are distinguished (Frankel et al., 1997). Polar magnetotaxis is displayed by MTB that swim persistently toward one of the poles of

a bar magnet under oxic conditions. Those that swim toward the “south” pole of a magnet have North-seeking polarity, since they would swim northward in the geomagnetic field. MTB from the Northern Hemisphere are predominantly North-seekers, whereas those from the Southern Hemisphere are predominantly South-seekers (Bazylinski and Frankel, 2004).

The observation of polar magnetotaxis led to the idea that MTB are guided by the geomagnetic field to less oxygenated regions. Since the geomagnetic field is inclined downward from the horizontal in the Northern Hemisphere and upward in the Southern Hemisphere, under oxic conditions the cells with polar magnetotaxis swim downward in both hemispheres (Bazylinski and Frankel, 2004). However, if the cell is in a reducing environment, it reverses the direction of flagellar rotation and migrates upward. Since the motion of the cell is determined by both the magnetic field and the oxygen tension, the term “magneto-aerotaxis” was introduced (Frankel et al., 1997).

Axial magnetotaxis means that the axis of motion is determined by the magnetic field but its direction is not. As the cell swims, it samples the oxygen concentration and compares it with that in the recent past. Cells moving toward the optimal habitat have a decreased probability of reversing the sense of flagellar rotation, whereas those that are moving away from the optimal oxygen concentration have an increased probability of reversing the sense of flagellar rotation and thus their swimming direction (Frankel et al., 1997). The magneto-aerotactic response provides an efficient mechanism for MTB to find the OAI in their chemically stratified habitats.

### Mineralogy and magnetism

Magnetotaxis relies on intracellular grains of iron oxide or sulfide minerals. Magnetite ( $\text{Fe}_3\text{O}_4$ ) is the only iron oxide mineral that has been described to date from magnetotactic cells. The sulfide-producing cells use greigite ( $\text{Fe}_3\text{S}_4$ ) for navigation, but they also may contain nonmagnetic mackinawite ( $\text{FeS}$ ) that rapidly converts to greigite through a solid-state phase transition (Pósfai et al., 2007).

Magnetite produced by MTB is chemically pure  $\text{Fe}_3\text{O}_4$ , in contrast to grains from rocks that usually contain other transition metals besides iron. Structurally, the nanocrystals are either perfect or contain twin boundaries. The morphologies of magnetite magnetosomes are typically highly regulated, strain-specific, and in many cases, unusual for a mineral with cubic symmetry (Pósfai et al., 2007). Whereas magnetotactic spirilla contain cubooctahedral crystals, vibrio and cocci typically produce magnetite with prismatic habits (Figure 2a). Large, rod-shaped cells tend to contain arrowhead- or bullet-shaped magnetite crystals (Bazylinski and Frankel, 2004).

The sizes and shapes of magnetosomes are critical for magnetotaxis. Isolated, isometric magnetite crystals with diameters smaller than  $\sim 30$  nm are superparamagnetic, i.e., they do not have a permanent magnetic moment.

Crystals with diameters from  $\sim 30$  to  $\sim 120$  nm are magnetic single domains at room temperature, whereas grains larger than  $\sim 120$  nm contain two or more magnetic domains, reducing the net magnetic moment of the crystal. Most magnetosomes are in the single-domain range, allowing the assembly of a highly efficient internal compass that consists of a chain (or chains) of single-domain magnets. Interactions between neighboring particles in chain configurations ensure that even those magnetite particles that are small enough to be superparamagnetic or large enough to contain two or more magnetic domains if they were isolated are also constrained to be single domains (Dunin-Borkowski et al., 2001). Since elongated particles are arranged with their axis of elongation (which typically coincides with their crystallographic easy magnetization axis) parallel to the chain of magnetosomes, shape anisotropy constrains the magnetic flux lines to be parallel to the axis of motility. Thus, in most magnetite-producing cells the effects of particle size, shape and magnetocrystalline anisotropy, and magnetostatic interactions among particles in chains combine to produce the possible largest magnetic moment (Figure 2b) (Pósfai et al., 2007).

The sizes, shapes, and orientations of iron sulfide magnetosomes are less distinct than those of magnetite magnetosomes. Greigite magnetosomes typically contain planar defects, as a result of an incomplete solid-phase transformation from mackinawite to greigite. The shapes and orientations of the crystals are random, resulting in poorer confinement and greater variability in the directions of the magnetic induction lines in the cells than in magnetite-bearing bacteria. Remarkably, despite the different crystal structures, orientations, and arrangements of ferrimagnetic crystals, the magnetic moments of different cells are fairly constant (Pósfai et al., 2007), thereby satisfying the requirement for magnetotaxis.

### Cell biology and genomic analyses

Magnetic enrichments have shown great morphological and ultrastructural diversity of MTB from a wide variety of aquatic environments. Magnetite-producing morphotypes include spirilla, cocci, vibrios, and rods of various sizes, moving at speeds ranging from 40 to 1,000  $\mu\text{m/s}$ . A unique, greigite-producing magnetotactic organism, the “multicellular magnetotactic prokaryote” (MMP) consists of 15–45 cells organized around an internal acellular compartment (Keim et al., 2004). The aggregated cells of the MMP move together as one unit, with the coordinated motion of flagella on the outside of the cells.

The highly controlled, strain-specific properties of magnetite magnetosomes and their chains indicate that biomineralization is under genetic control, executed by specific proteins in the magnetosome membrane. Many details of magnetosome formation have been elucidated by studies of the biochemistry of the magnetosome membrane and genomic analyses of MTB. Workable genetic systems have been developed for two *Magnetospirillum*

strains: *M. magnetotacticum* AMB-1 and *M. gryphiswaldense* MSR-1 (Jogler and Schüler, 2007). By genetic manipulation, including the generation of mutants and the expression of magnetobacterial genes in other hosts, the major steps of magnetite biomineralization have been identified in these systems. Magnetite nucleation is preceded by the formation of vesicles, which are invaginations of the cytoplasmic membrane (Komeili et al., 2006). Dissolved ferrous or ferric iron is transported into the cell by an unknown uptake system. Magnetosome membrane proteins (MamB/MamM) are involved in the transport of ferrous iron from the cytoplasm into the magnetosome vesicle, and then magnetite formation is activated by another protein (MamA). Within the vesicle, iron is oxidized and magnetite nucleation is triggered by the Mms6 protein. The least known aspect of the biomineralization process is the control over the distinct crystal morphology. The vesicles containing fully developed magnetite crystals are anchored to a filamentous cytoskeletal structure by the MamJ protein, resulting in an ordered magnetosome chain (Scheffel et al., 2006). Genomic analyses revealed that the genes that encode the magnetosome proteins are clustered in a 130 kb region, representing a “magnetosome island.” This genomic island appears to be conserved among different *Magnetospirillum* strains and, to a lesser degree, in a magnetotactic coccus (Jogler and Schüler, 2007), raising the question of whether the “magnetosome island” is a universal feature of MTB.

### Diversity

The term “magnetotactic bacteria” does not refer to a taxonomical unit. All known MTB belong to various groups within the domain Bacteria. Most magnetotactic microorganisms that are available in pure culture are affiliated with the *Alphaproteobacteria*, including *M. magnetotacticum* and *M. gryphiswaldense*, a marine vibrio (MV-1), and a coccus (MC-1). In addition to the cultivated strains, 16S rRNA analysis of magnetic enrichments from many freshwater and marine samples revealed that a variety of magnetite-producing morphotypes are likely affiliated with the *Alphaproteobacteria* (Amann et al., 2007). Two magnetite-producing candidate species, “*Magnetobacterium bavaricum*” and “*Magnetotacticum bremense*,” are affiliated with the *Nitrospira* phylum.

Sulfide-producing MTB could not have been cultured to date, but a multicellular organism was found to be closely related to the dissimilatory sulfate-reducing bacteria within the *Deltaproteobacteria*. Another sulfide-producing MTB was assigned to *Gammaproteobacteria*. These findings may suggest that magnetotaxis based on iron oxide and sulfide nanoparticles evolved independently; however, a magnetite-producing, sulfate-reducing organism (*Desulfovibrio magneticus* strain RS-1) is also affiliated with the *Deltaproteobacteria* (Amann et al., 2007).

The diversity of MTB indicates that magnetotaxis evolved independently in several phylogenetic groups.

On the other hand, the discovery of a potentially mobil “magnetosome island” in the genome of magnetite-producing MTB could suggest that the trait of magnetotaxis was spread by lateral gene transfer among the various groups of MTB.

### Magnetofossils, paleomagnetism

After MTB die, their intracellular magnetite or greigite particles are deposited in the sediment. If diagenetic conditions are favorable, the magnetosome crystals can be preserved as magnetofossils. Magnetofossils have been identified on the basis of the special properties of magnetosome crystals, including a narrow crystal size distribution, characteristic morphologies, chemical purity and, in some cases, chain configurations. Ferrimagnetic nanocrystals presumably originating from MTB have been described from a variety of sedimentary rock types, including clays, carbonates, marls, and evaporites. The magnetofossil record extends from present-day marine and lake sediments to the Cretaceous and with lesser certainty to the late Archean (Kopp and Kirschvink, 2008).

MTB carry a primary remanent magnetization, since they are aligned with the geomagnetic field, presumably even after cell death and burial in the sediment. Because magnetofossils are single magnetic domains, they have an optimized magnetic stability and can be important carriers of paleomagnetic information. Magnetofossils can serve as environmental proxies because MTB live under specific redox conditions. They can also be markers of ancient life, albeit dubious ones, as illustrated by a lengthy debate over whether nanocrystalline magnetite particles in the Martian meteorite ALH84001 represent magnetofossils or had formed inorganically (Winklhofer and Petersen, 2007).

### Nanotechnological applications

Magnetic nanoparticles are widely used in technological applications, such as in spintronics, in magnetic inks, in high-density magnetic memory devices, and in medical applications (as contrast agents in magnetic resonance imaging and as magnetic carriers for drug targeting and delivery). Magnetite crystals produced by MTB have uniform sizes and shapes and can be separated from disrupted cells by magnetic methods with their magnetosome membrane intact. The membrane-bound bacterial nanoparticles have a large specific surface area and are well dispersed in aqueous solutions. Antibodies or proteins can be immobilized on the magnetosome membrane, producing functionalized magnetic nanoparticles (Matsunaga and Arakaki, 2007). Since bound and free analytes can be separated in a magnetic field, bacterial nanoparticles have been used for the rapid and sensitive detection of small molecules, including environmental pollutants, hormones, and toxic detergents. Immunomagnetic particles are also useful for sorting target cells from cell suspensions using a permanent magnet, and for using them in high-

performance DNA/mRNA recovery and DNA discrimination analysis (Matsunaga and Arakaki, 2007).

### Summary

MTB provide a fascinating example of microbial biomineralization and motivate interdisciplinary research at the junctions of biology, mineralogy, geology, geochemistry, and physics. The molecular and genetic bases of magnetic nanocrystal formation by MTB are now beginning to be understood. The results of research on MTB will be useful for understanding biomineralization processes and magnetic sensing mechanisms in more complex organisms, and for designing nanotechnological applications of bacterial nanocrystals.

Mihály Pósfai

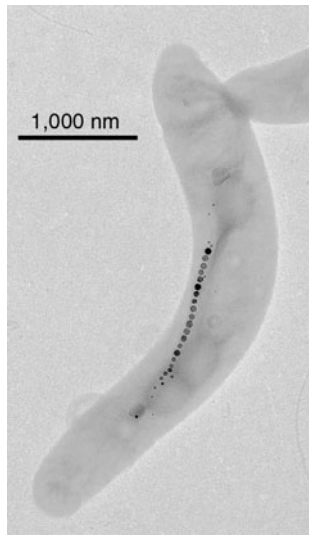
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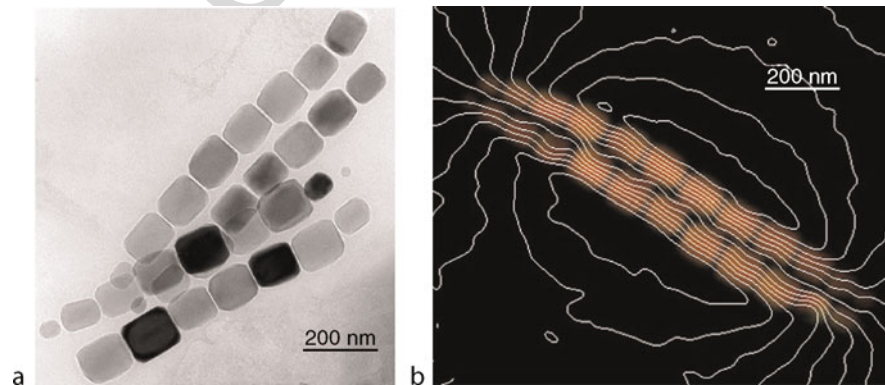
### Cross-references

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Biomineralization, General Aspects  
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Geomicrobiology  
Iron Sulfide Formation  
Microbial Biomineralization  
Molecular Geomicrobiology  
Nanocrystals, Microbially Induced





**Magnetotactic Bacteria, Figure 1** A cell of *Magnetospirillum gryphiswaldense* that contains a single chain of magnetite magnetosomes.



**Magnetotactic Bacteria, Figure 2** (a) Electron micrograph of two double chains of elongated magnetite magnetosomes from a freshwater magnetotactic coccus. (b) Magnetic induction map of a similar double chain of magnetite magnetosomes, obtained from electron holograms.