

# Magnetosomes and Magneto-Aerotaxis

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## Abstract

Magnetotactic bacteria orient and migrate along geomagnetic field lines. Magneto-aerotaxis increases the efficiency of respiring microaerophilic cells to efficiently find and maintain a position at a preferred microaerobic oxygen concentration. Magneto-aerotaxis could also facilitate access to regions of higher nutrient and electron acceptor concentration via periodic excursions above and below the preferred oxygen concentration level.

## General Features of Magnetotactic Bacteria

The magnetotactic bacteria are a morphologically and metabolically diverse group of freshwater and marine prokaryotes that align and migrate along geomagnetic field lines, a phenomenon called magnetotaxis [1]. They generally inhabit water columns or sediments with vertical chemical concentration stratification, where they occur predominantly at the oxic-anoxic interface (OAI) and the anoxic regions of the habitat or both [2]. Phylogenetically, all known magnetotactic bacteria belong to the domain Bacteria and are associated with different subgroups of the Proteobacteria and the Nitrospira phyla [2, 3].

There are relatively few axenic cultures of magnetotactic bacteria [4]. The cultured strains include *Magnetospirillum magnetotacticum* strain MS-1, *M. gryphyswaldense* strain MSR-1, *M. magneticum* strain AMB-1, a marine vibrio strain MV-1 (the name *Magnetovibrio blakemorei* will be proposed), a marine coccus strain MC-1 (the name *Magnetococcus marinus* will be proposed), *Desulfovibrio magneticus* strain RS-1, and a few uncharacterized marine strains. All the cultured organisms, except *D. magneticus*, are facultatively anaerobic or obligate microaerophiles. All are chemoorganoheterotrophic although the marine strains can also grow chemolithoautotrophically [5]. The genomes of several strains, including *M. magnetotacticum* strain MS-1, *M. magneticum* strain AMB-1 [6] and strain MC-1 have been partially or completely sequenced.

All studied magnetotactic bacteria are motile by means of flagella and have a cell wall structure characteristic of Gram-negative bacteria [4]. The arrangement of flagella varies between species/strains and can be either polarly monotrichous, bipolar, or in tufts (lophotrichous). Like other flagellated bacteria, magnetotactic bacteria propel themselves through the water by rotating their helical flagella. Reported swimming speeds vary between species/strains, from ca. 40 to 1,000  $\mu\text{m/s}$ . In general, the magnetotactic spirilla are at the slower end ( $<100 \mu\text{m/s}$ ) [7] and the magnetotactic cocci are at the faster end of the range ( $>100 \mu\text{m/s}$ ) [8].

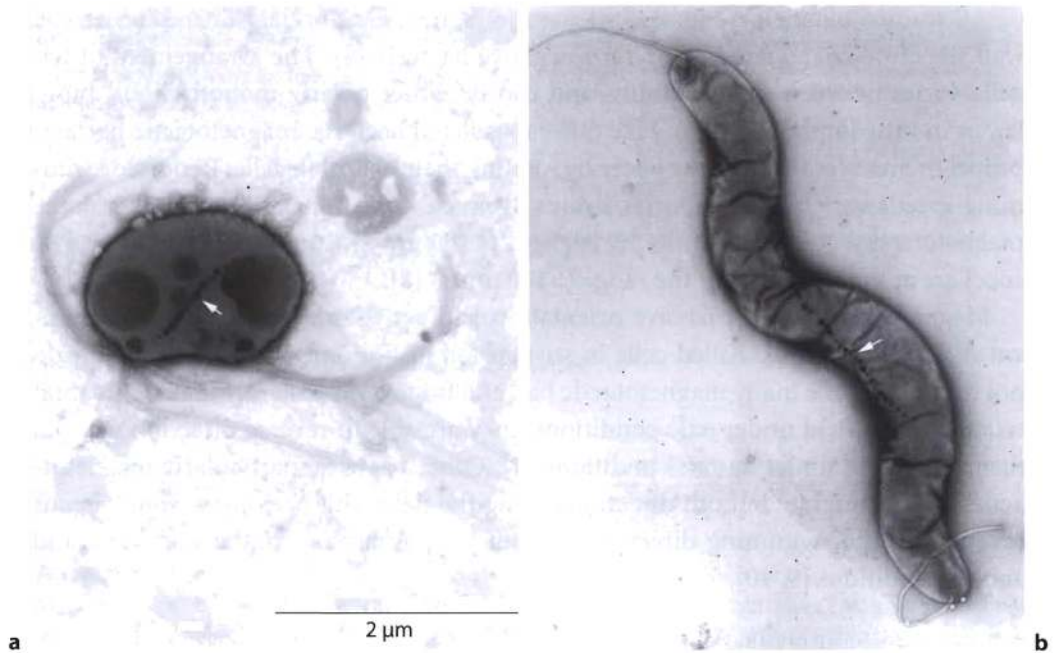
Magnetotaxis involves passive orientation and active migration along the ambient magnetic field [4]. Killed cells in suspension also orient along the field but do not migrate. While many magnetotactic bacteria migrate persistently in one direction relative to the field under oxic conditions, they are able to reverse direction without turning around under anoxic conditions [9]. Other bacteria, particularly magnetotactic spirilla, migrate in both directions along the field with occasional spontaneous reversals of the swimming direction without turning around under both oxic and anoxic conditions [9, 10].

### **Magnetosomes**

Orientation of magnetotactic bacteria in a magnetic field is due to the presence of magnetosomes, intracellular structures comprising magnetic iron mineral crystals enveloped by a phospholipid bilayer membrane [11]. The magnetosome membrane originates as an invagination of the cytoplasmic membrane and appears to control the nucleation and growth of the mineral crystal at particular locations in the cell [12, 13]. Whether the invagination pinches off to become a true membrane vesicle within the cell is under debate [13]. Regardless, magnetosomes are almost always adjacent to the cell membrane where they appeared to be anchored.

The magnetosome mineral crystals consist either of magnetite,  $\text{Fe}_3\text{O}_4$ , or greigite,  $\text{Fe}_3\text{S}_4$  [4]. These crystals are typically of order 35–120 nm in length, which is within the permanent single-magnetic-domain (SD) size range for both minerals, although magnetite crystals with lengths up to 250 nm are known [14]. In the majority of magnetotactic bacteria, the magnetosomes are organized in one or more straight chains of various lengths parallel to the axis of motility of the cell (fig. 1). Non-chain configurations of magnetosomes occur in some species, usually at the side of the cell where the flagella are inserted. Recent progress in elucidating the biomineralization process and the construction of the magnetosome chain in magnetotactic bacteria has been reviewed [12, 13].

All known freshwater magnetotactic bacteria and some marine, estuarine and salt marsh strains have magnetite magnetosomes. Other strains in the latter habitats contain greigite magnetosomes. These include an unusual multicellular bacterium and a variety of relatively large, rod-shaped bacteria [3]. The magnetosome greigite crystals



**Fig. 1.** Transmission electron micrographs: (a) the marine coccus strain MC-1 and (b) *M. magnetotacticum* strain MS-1. Both organisms have a single chain of magnetite ( $\text{Fe}_3\text{O}_4$ ) magnetosomes (white arrows). Strain MC-1 has two tufts of flagella, whereas strain MS-1 has two polar flagella. The size bar at the bottom is for both a and b.

are thought to form from non-magnetic iron-sulfide precursors [15]. Some magnetotactic bacteria, including some forms of the multicellular organism described above, contain magnetite and greigite magnetosomes, co-organized within the same magnetosome chains but with distinct morphologies for each mineral [4, 16]. Interestingly, all the magnetite magnetosomes are tooth- or bullet-shaped.

In *Magnetospirillum* species and strain MC-1, the genes for the proteins implicated in magnetite magnetosome biosynthesis are located within a genomic island. In *Magnetospirillum gryphiswaldense* the magnetosome genes are located within a hypervariable 130-kb stretch of the genome within the magnetosome island [17, 18]. The genes encoding for the proteins MamA, MamB, MamJ and MamK are located on the *mamAB* operon, while the genes for MamC and MamD are located on the *mamDC* operon. Functions for magnetosome-membrane-associated proteins have been determined for MamJ and MamK. MamJ was demonstrated to be essential for the assembly of magnetosome chains in *M. gryphiswaldense*, probably through interaction with MamK [12], and MamK is involved in the formation of a network of actin-like filaments that comprise the magnetosomal cytoskeleton and is responsible for the linear chain-like alignment of magnetosomes within the cell [13].

## Cellular Magnetic Dipole

Magnetosomes within the SD size range are uniformly magnetized with the maximum magnetic dipole moment per unit volume. Magnetite crystals larger than SD size are non-uniformly magnetized because of the formation of domain walls or other spin structures that significantly reduce the magnetic moments of the crystals. Crystals with lengths below ca. 35 nm are superparamagnetic. Although superparamagnetic particles are SD, thermally-induced reversals of their magnetic moments result in a time-averaged magnetic moment of zero. Thus by controlling particle size, magnetotactic bacteria optimize the magnetic dipole moment per magnetosome. For magnetosomes arranged in a chain, as in *M. magnetotacticum*, magnetostatic interactions between the SD crystals cause the magnetic moments to spontaneously orient parallel to each other along the chain direction [4]. This results in a permanent magnetic dipole for the entire chain with a magnetization approaching its saturation value (0.6 T). Since the chain of magnetosomes is fixed within the cell, the entire cell is oriented in the magnetic field by the torque exerted on the magnetic dipole, causing the cell to migrate along the magnetic field as it swims. The permanent magnetic structure of magnetosome chains has been demonstrated by electron holography [19].

Reported and estimated permanent magnetic moments of several organisms are ca.  $1.0\text{E}-15 \text{ Am}^2$  [19]. The corresponding magnetic energy in the geomagnetic field of  $50 \mu\text{T}$  is  $5.0\text{E}-20 \text{ J}$ . This value is greater than thermal energy at room temperature,  $4.1\text{E}-21 \text{ J}$ . The average orientation of a cell along the magnetic field as it swims is determined by the ratio of magnetic to thermal energy; for a ratio of 10, the average projection of the magnetic dipole on the magnetic field,  $\langle \cos \Theta \rangle = 0.9$ . This means the cell can migrate along the field at 90% of its forward speed. Thus a magnetotactic bacterium is, in effect, a self-propelled magnetic compass needle.

## Magnetotaxis

In the original model of magnetotaxis, all magnetotactic bacteria were assumed to have a polar preference in their swimming direction and were microaerophiles indigenous to sediments [1]. In this model, the geomagnetic field directs swimming cells downward towards the sediments along the downward-inclined field lines. Once cells reach their preferred microhabitat, they presumably stop swimming and adhere to sediment particles until conditions changed, e.g., disturbance of the sediments caused cells to be displaced into the oxic water column. This explained why magnetotactic bacteria from northern hemisphere sites appeared to predominantly migrate northward along the geomagnetic field under oxic conditions whereas as those from southern hemisphere sites migrated predominantly southward [1, 9].

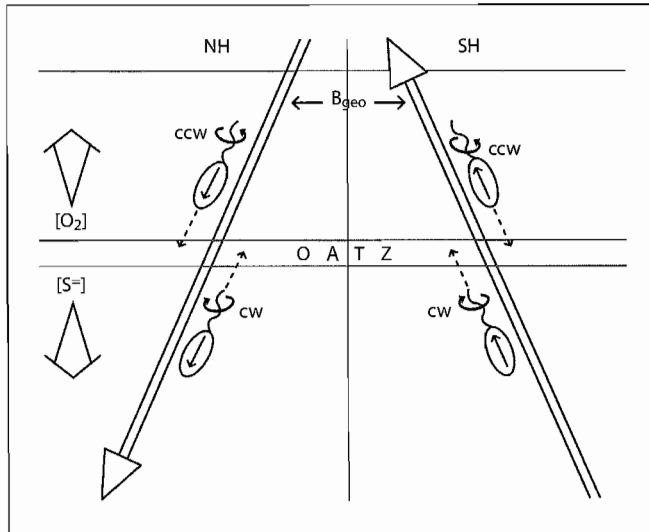
## Magneto-Aerotaxis

The discovery of large populations of magnetotactic bacteria at the OAI in the water columns of certain chemically-stratified aquatic habitats, and the isolation of obligately microaerophilic, coccoid, magnetotactic bacteria strains in pure culture, has led to a revised view of magnetotaxis [9]. The original model did not completely explain how bacteria in the anoxic zone of a water column benefit from magnetotaxis, nor did it explain how the magnetotactic cocci such as strain MC-1 form horizontal microaerophilic bands in semi-solid oxygen gradient media in shake tubes instead of accumulating and growing at the bottom of the tubes. Bands of strain MC-1 and *M. magnetotacticum* in oxygen concentration gradients in thin, flattened capillaries moved up the capillary, eventually to the meniscus, when the head space gas was switched from air to pure N<sub>2</sub>. When the N<sub>2</sub> was replaced with air, the bands moved back to their original position in the capillary. Pure O<sub>2</sub> caused the bands to move further down the capillary. This showed that magnetotactic bacteria have both aerophilic and aerophobic responses and that magnetotaxis and aerotaxis work together to guide cells to their optimal [O<sub>2</sub>] (fig. 2). The behavior observed in strain MC-1 and *M. magnetotacticum* has been denoted magneto-aerotaxis (M-A) [9]. Based on observation of individual cells in microaerobic bands, two different M-A mechanisms, polar and axial, have been proposed for strain MC-1 and *M. magnetotacticum*, respectively [9].

### Polar Magneto-Aerotaxis

Polar M-A is a two-state model in which the sense of flagellar rotation in each state is determined by the [O<sub>2</sub>] [9]. When [O<sub>2</sub>] is greater than optimal, ccw rotation causes cells to migrate along field lines through the optimal [O<sub>2</sub>] toward lower [O<sub>2</sub>], at which point the cell switches to State 2 with cw flagellar rotation, causing the cells to back up along the field lines toward higher [O<sub>2</sub>]. It is possible that the cells might detect redox potential, or internal energy level, rather than molecular oxygen [20]. In experiments with strain MC-1 in an oxygen gradient in a thin capillary, a number of cells formed an immobilized biofilm at the optimal [O<sub>2</sub>] while other cells made straight line passes through the biofilm in both directions [9]. The polar M-A model accounts for the fact that cells swam away from the biofilm following a reversal of the magnetic field. In this situation, cells in either state do not encounter the redox condition that would switch them into the other state and hence do not reverse their swimming direction. This shows that the orientation of the magnetic field is important in polar M-A.

In some polar strains, short wavelength light (<500 nm) can apparently switch the state of the cell, causing ccw rotation even under reducing conditions for which the oxygen concentration is suboptimal [9].



**Fig. 2.** Diagram of magnetoaerotaxis. Magnetotactic bacteria in the northern hemisphere (NH) are oriented in the downward inclined geomagnetic field ( $B_{geo}$ ). Counterclockwise (ccw) flagellar rotation causes the cells to migrate downward, whereas clockwise (cw) rotation causes the cells to migrate upward. Migration along the magnetic field causes cells to efficiently move between the oxidic water layer above the oxidic-anoxic transition zone (OATZ = oxidic-anoxic interface (OAI)) and the anoxic water layer below. In the southern hemisphere (SH) the geomagnetic field is inclined upward and the cellular magnetic dipole has reversed orientation in the cells.

### Axial Magneto-Aerotaxis

In axial M-A, cells migrate along magnetic field line by means of a temporal sensory mechanism that occurs in many non-magnetotactic, chemotactic bacteria [21]. Cells sample the oxygen concentration as they swim and compare the present concentration with that in the recent past. The change in oxygen concentration with time is connected to the probability of switching the sense of flagellar rotation (cw or ccw) and hence the direction of migration along the field [9]. Axial magneto-aerotactic cells moving away from the optimal oxygen concentration toward higher or lower oxygen concentration have an increased probability of reversing the sense of flagellar rotation, and hence the direction of migration, causing them to return to the band. Cells moving toward the optimum oxygen concentration have a decreased probability of reversing the sense of flagellar rotation. *M. magnetotacticum* forms microaerobic bands in which the cells are in constant motion in the band. Since the cells use the magnetic field to provide an axis but not a direction of motility, the orientation of the field is not important, as shown by the fact that while the cells rotate following a magnetic field reversal, the band remains intact.

## Redoxtaxis

The polar M-A model can be extended to a more complex redoxtaxis in habitats in which rapid chemical oxidation of reduced chemical species such as sulfur near the OAI results in separated pools of reductants and oxidants [3]. For some magnetotactic bacteria, it might be necessary to perform excursions to anoxic zones of their habitat in order to accumulate reduced sulfur compounds as a source of electrons to support growth. In this situation, polar magnetotaxis could efficiently guide bacteria, either downward to accumulate reduced sulfur species or upward to oxidize stored sulfur with oxygen. The 'oxidized state' would result from the almost complete consumption of stored sulfur or another electron donor, and the cells would swim down along the field toward the anoxic zone where they could replenish the depleted stock of electron donor using nitrate or other compounds as alternative electron acceptor. Eventually, they would reach a 'reduced state' in which the electron acceptor is depleted. In this state the cells would swim back up along the field and return to the microoxic zone where oxygen is available to them as an electron acceptor. The advantage of polar M-A is that an oxygen concentration gradient is not necessary for efficient orientation in the anoxic zone, thereby enabling a rapid return of the cell along relatively large distances to the preferred microoxic conditions. A further benefit would be that cells avoid the waste of energy by constant movement along gradients, but instead can attach to particles in preferred microniches until they reach an unfavorable internal redox state that triggers a magnetotactic response either parallel or antiparallel to the geomagnetic field lines. In any case, greater than optimal concentrations of oxygen would switch cells immediately to the 'oxidized state' provoking the typical down-seeking response of magnetotactic bacteria under oxic conditions.

Cells of strain MC-1, like other, uncultivated, magnetotactic cocci, are small (ca. 1  $\mu\text{m}$  diameter) with twin, multiflagellar bundles on one side of the cell. Magnetotactic cocci have been reported to swim at speeds in excess of 100  $\mu\text{m/s}$  (about 100 body lengths per second) [8]. In  $[\text{O}_2]$  gradients in flat, thin capillaries, cells of strain MC-1 form microaerophilic bands of cells [9]. Some cells within the band make long, straight traverses through the band whereas others stop swimming and attach to the walls of the capillary or to each other at the OAI. Cells of magnetotactic cocci thus appear to alternate between active swimming and sessile behavior.

Cells of strain MC-1 grow chemolithoautotrophically with sulfide and other reduced sulfur sources as electron donors and molecular oxygen as the terminal electron acceptor [5]. In addition, these cells also fix atmospheric dinitrogen [Bazyliński, unpubl. data]. This is presumably true for other magnetotactic cocci that inhabit the OAI in many marine and brackish habitats. However, oxidation of  $\text{S}^{2-}$  by  $\text{O}_2$  is autocatalytic, so an inverse  $[\text{O}_2]/[\text{S}^{2-}]$  double gradient (from the downward diffusion of  $\text{O}_2$  from air at the surface and the upward diffusion of  $\text{S}^{2-}$  from the anaerobic zone through the action of sulfate-reducing bacteria) will form even without the presence of bacteria. Therefore, bacteria actually have to compete with molecular  $\text{O}_2$  for  $\text{S}^{2-}$ .

Consumption of  $S^{2-}$  and  $O_2$  by bacteria at the OAI makes the gradients steeper. The coexistence or overlap region (both  $O_2$  and  $S^{2-}$  present together) is only a few hundred  $\mu\text{m}$  deep [21] and has very low ( $<1 \mu\text{M}$ ) concentrations of both  $O_2$  and  $S^{2-}$ . Thus although cells have to contend with relatively low nutrient concentrations, as well as diffusion-limited flux of  $S^{2-}$  from below and  $O_2$  from above into the overlap region, the OAI in these  $[O_2]/[S^{2-}]$  inverse gradients is on optimal positions for these organisms particularly if the habitat is nitrogen-limited and cells are fixing  $N_2$ .

Nutrient limitation is a fact of life in many marine habitats, and results in predominantly small, fast swimming cells [22, 23]. Smaller cells require lower levels of nutrients to grow and they have a higher surface-to-volume ratio ( $S/V \sim 1/R$ ), which increases their rate of nutrient uptake relative to their volume. This is especially advantageous in low nutrient conditions. However, consumption of nutrients results in a greater local depletion because of diffusion limitation. Cells can solve this problem by swimming and relying on chemotaxis to find areas of locally higher nutrient concentration. At minimum, cells have to swim fast and straight enough to outrun nutrient diffusion (about  $30 \mu\text{m/s}$  for 1 s). However, small cells lose their heading in times of the order of milliseconds from buffeting by Brownian motion. One solution is swimming faster so as to get farther before going off course, which is presumably the reason why small cells that swim fast are the rule in marine environments [23]. However, faster swimming also burns more cellular energy because the viscous drag on cells depends on their velocity.

Cells of strain MC-1 and similar marine magnetotactic cocci with bilophotrichous flagellation are fast swimmers yet have their magnetic dipole to keep their heading. As noted above, fast swimming perhaps allows them to make traverses from one side of the overlap region to the other to sequentially access higher concentrations of  $S^{2-}$  and  $O_2$ . However, small cells such as the cocci have low carrying capacity so they have to make shorter, more frequent, traversals than larger cells. In this case, the horizontal chemical stratification could guarantee a payoff that would cover the cost of fast swimming. Then why do cells of strain MC-1 sometimes stop swimming, as seen in the bands in the flat capillaries? The answer might involve nitrogen fixation, an energy-demanding process that only occurs at  $O_2$  concentrations less than about  $5 \mu\text{M}$  [24]. Since the  $O_2$  concentration in the OAI is even less, cells can fix  $N_2$  there. If a cell is fixing  $N_2$ , its energy balance might improve if it stops swimming altogether.

Cells of *M. magnetotacticum*, like all other magnetospirilla, have a single flagellum at both poles of the cell and swim at about  $40 \mu\text{m/s}$ , forwards and backwards with equal facility. Cultivated cells grow heterotrophically on certain organic acids (e.g., succinic acid) as an electron source with  $O_2$  or nitrate as the terminal electron acceptor [4]. When  $O_2$  is the only electron acceptor available in  $[O_2]$  gradients, cells form microaerophilic bands, seeking a preferred  $O_2$  concentration that presumably maximizes the proton motive force generated by transfer of electrons [20, 24]. Cells can be seen to be in constant motion making straight-line excursions above and below the band. However, because there is no autocatalytic oxidation of electron donor by



acceptor, access to nutrients is mostly limited by the diffusion of O<sub>2</sub> and electron source and consumption by the cells. In this situation, cells need only outrun diffusion in order to access increased concentrations of electron donor and acceptor below and above the preferred O<sub>2</sub> concentration, respectively. There is no need to incur the cost of faster swimming because the cellular magnetic dipole allows cells to maintain their heading, minimizing the straight run time for temporal chemotaxis.

Cells of the magnetospirilla, like those of strain MC-1, also fix N<sub>2</sub>, but since they do not expend as much energy swimming as does strain MC-1, they likely do not need to stop swimming to conserve energy for N<sub>2</sub> fixation. It should be noted that the situation for magnetospirilla in natural environments might be more complex than that for the magnetotactic cocci. The fact that cells of magnetotactic spirilla freshly collected from natural environments or newly isolated in pure culture often display polar magnetotaxis in the hanging drop assay might indicate this. Many of the magnetotactic cocci collected from natural environments contain sulfur-rich globules indicating that they are actively oxidizing S<sup>2-</sup> at the OAI. Many of the cultivated magnetospirilla possess genes encoding for CbbM, a type II ribulose-1,5-bisphosphate carboxylase/oxygenase, a key enzyme of the Calvin-Benson-Bassham cycle for autotrophy. Thus the magnetospirilla might be able to grow chemolithoautotrophically like strain MC-1 and may also use inorganic electron donors as well as organic ones.

### **Deviations from the Magneto-Aerotaxis Models**

Polar M-A has been observed in some of the freshwater spirilla [D. Schüler, pers. commun.], bacteria that are nominally axial magneto-aerotactic. Magnetic polarity was most pronounced in strains that were freshly isolated but gradually converted to axial M-A upon repeated subcultivation. Polar M-A has also been observed in cells of *M. gryphiswaldense* [D. Schüler, pers. commun.] and *M. magnetotacticum* [D.A. Bazylinski, unpubl. data] grown in semi-solid [O<sub>2</sub>]-gradient medium and placed in highly reduced medium under the microscope. However, these experiments were not entirely reproducible and thus the trigger that causes cells to switch between axial and polar M-A is not known. Since the difference between axial and M-A at the molecular level is not known, it is possible that the two models represent the endpoints of a continuum of responses.

The predominance of freshwater, southward swimming (SS), magnetotactic cocci in a pond in the northern hemisphere was reported by Cox et al. [8] without discussion. Simmons et al. [25] recently observed a population of uncultured, marine magnetotactic bacteria, collected from the anoxic zone of a coastal pond in the northern hemisphere, that were primarily SS under oxic conditions. Other, polar magnetotactic, bacteria in the sample were generally northward swimming (NS) as expected although on occasion the ratio of SS to NS cells was >0.1. Since the SS cells were not identified, it is not clear whether they are microaerophiles, leaving open the possibility that they

use the magnetic field to find a preferred position in a vertical concentration gradient of a molecule or ion other than O<sub>2</sub> or at a specific oxidation-reduction potential. If the organism turns out to be microaerophilic, then the SS response is difficult to understand on the basis of the M-A models. However, since the cells do not migrate up to the surface of the pond, something must cause them to reverse direction and swim downward in the water column. Alternatively, they may not be actively swimming but attached to suspended particulates. The solution to this intriguing mystery will require examination of the motility of the unusual cells in an oxygen concentration gradient.

### **Bacterial Hemerythrins and Magneto-Aerotaxis**

The genomes of *M. magnetotacticum*, *M. magneticum* and strain MC-1 each contain approximately 30 or more open reading frames (ORFs-possible genes) that encode for putative proteins with hemerythrin-like domains. None of these proteins have been characterized, however. Given that magnetotactic bacteria occur predominantly at the OAI and/or anoxic regions of the water column, O<sub>2</sub>-binding proteins such as hemerythrins may serve as a sensory mechanism for O<sub>2</sub>, and thus play a key role in M-A.

Hemerythrin domains contain a sequence motif that includes five histidine residues and two carboxylate ligands that coordinate two iron atoms; reversible O<sub>2</sub>-binding occurs at the di-iron site. For magnetotactic bacteria, some ORFs that encode for putative hemerythrin-like proteins are located within the magnetosome membrane protein gene islands in strain MC-1 (Mmc1DRAFT\_1515 from draft genome) and *M. gryphiswaldense* (ORF12, ORF13) [15, 17]. Other putative multi-domain proteins from other magnetotactic bacteria also include hemerythrin domains associated with signal transduction domains (e.g., histidine kinases, methyl-accepting chemotaxis proteins).

For magnetotactic bacteria migrating within and through the OAI, hemerythrins may serve to bind O<sub>2</sub> when the cell is exposed to elevated O<sub>2</sub> concentrations, and then release the O<sub>2</sub> when the cell descends into anoxic conditions. Multi-domain proteins with both signal transduction and hemerythrin domains suggests a role for these proteins in O<sub>2</sub> sensing. Even single-domain hemerythrins may serve a sensory function, if they are co-transcribed and/or acting with signal transduction proteins. Given the prevalence of hemerythrin-like ORFs in the known genomes of magnetotactic bacteria, including those within the magnetosome protein gene island [18], hemerythrins may play a role in M-A (including directing flagellar rotation).

The genomes of *M. magnetotacticum*, *M. magneticum* strain AMB-1 and strain MC-1 also show numerous ORFs that encode for putative proteins with PAS domains, providing many potential candidate genes for aero-, redox-, and (perhaps) phototaxis in these bacteria. In bacteria, PAS domains are responsible for sensing stimuli such as [O<sub>2</sub>], redox potential, and light. For example, the aerotaxis receptor (Aer) responds to oxygen concentration in the environment, and is the first step in the intracellular pathway that governs the sense of flagellar rotation in *Escherichia coli* [26]. As

mentioned above, the polar M-A coccus, strain MC-1, displays a negative phototaxis in response to short-wavelength light, but the mechanism is unknown. It is difficult to infer the precise identity of the stimulus that the PAS-containing protein is sensitive to based on amino acid sequence alone. This is also the case for numerous ORFs that encode putative methyl-accepting chemotaxis proteins in *M. magnetotacticum*, *M. magneticum*, and strain MC-1, including putative hemerythrins.

## Conclusion

Magnetotactic bacteria have solved the problem of constructing an internal, permanent, magnetic dipole that is sufficiently robust so that a cell will be oriented along the geomagnetic field as it swims, yet be no longer than the length of the cell itself (ca. 1–2  $\mu\text{m}$ ). The solution, the magnetosome chain, is very elegant and efficient in that it makes maximum use of a small amount of magnetite, assuming that cells want to maximize the ratio of magnetic moment to volume of magnetite to keep metabolic cost to a minimum. However, there are many microaerophilic organisms that form aerotactic bands without the aid of magnetism, including, for example, non-magnetic mutants of magnetotactic bacteria. Simulations of axial magnetotactic bacteria confirm the fact that M-A is more efficient than aerotaxis alone for finding the optimal  $[\text{O}_2]$ , meaning magnetotactic bacteria would find the optimal concentration before non-magnetic aerotactic bacteria with the same swimming speed, but only at high inclinations of the geomagnetic field. Many polar magnetotactic bacteria are fast swimmers, ca. 100 body lengths per second or more, so the efficiency argument may hold over a greater range of geomagnetic inclination for these organisms. Nevertheless, the question of whether aerotactic efficiency alone is sufficient to account for the persistence of magnetotaxis in bacteria over geologic time scales is still open.

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