

Chapter 8

The Magnetotactic Bacteria of the Churince Lagoon at Cuatro Ciénegas Basin



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Abstract Magnetotactic bacteria (MTB) are prokaryotes whose movements are directed by the Earth's geomagnetic field. The MTB are diverse in morphology, phylogeny, and physiology. They have unique cellular structures called magnetosomes, which are magnetic mineral crystals (iron) enveloped by a phospholipid bilayer membrane. These magnetosomes confer the ability of bacteria to have magnetotaxis. In this chapter, we will present some findings about the MTB inhabiting Churince Lagoon at Cuatro Ciénegas Basin (CCB), such as *Desulfovibrio magneticus*, *Magnetospirillum*, *Magnetospira*, *Magnetococcus*, and *Magnetovibrio*. In a phylogenetic analysis, sequences of genes that encode the magnetosomes from CCB have similarities with those found in marine sediments with volcanic activity. These observations not only conform with other studies that have shown marine ancestry in microbes from CCB but also reaffirms the magmatic influences on the deep aquifer under the Sierra San Marcos and Pinos. Thus, water overexploitation for intensive agriculture in this oasis especially endangers the processes of the iron-sulfur cycle. This biogeochemical cycle is dependent on the deep aquifer and its sediments, which likely function as a depository of ancient anaerobic microbes such as the MTB.

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Keywords Magnetotactic bacteria · Sulfur/Iron cycle · Phylogenetic analysis · Marine ancestry · Churince Lagoon

The Iron and Sulfur Cycles

Most of the bodies that comprise the solar system, including the Earth, are composed mainly of iron and silicates. Iron (Fe), because of its density, is at the center of these solar system bodies. The composition of the Earth's core, which has a radius of 3,486 km, is primarily Fe along with a little more than 10% by weight of light elements, such as nickel, copper, and sulfur. The magnetic field of the Earth or geomagnetic field is generated by the iron composition of the nucleus, the convection process that moves the fluid in the outer core, the circulation of electric currents in the atmosphere, and the rotation of the planet. All those forces together make a geo-dynamo effect that is responsible, among other things, for the Van Allen belt that protect us from harmful radiation by the solar wind (Tarbuck et al. 2005). This geomagnetic field is also a compass, a factor in biological evolution that serves as an orientation for many migratory organisms that are particularly sensitive to the magnetic signals. It also influences vital functions inside and outside of all living beings (Binhi and Prato 2017).

The oldest biological processes that have been related to iron are microbial. Consequently, this element is an important cog in Earth's biogeochemical cycles. Early life initiated in the beginning of the Archean Eon, in a warm and ferruginous (anoxic and Fe²⁺ dominated) ocean (Olson and Straub 2016), or, prior to that, in the Hadean Eon ~ 4.1 billion years ago, close to hydrothermal vents (Dodd et al. 2017). In prebiotic Earth within an ancient (Hadean) ocean, it is most likely that H₂S and reduced metal sulfides can remain in solution in anoxic seawater for lengthy periods and could have covered large areas. Thus, life may have originated at highly reduced alkaline submarine springs functioning at a distance from oceanic spreading centers (Russell and Hall 1997).

These submarine hydrothermal vents are found along the mid-ocean ridges where the seafloor spreading occurs. These vents' effluent systems provide seawater with CO₂, H₂S, dissolved H₂, and reduced transition metals, especially iron (Olson and Straub 2016). The theory of a chemoautotrophic origin of life in an iron-sulfur world suggests that primitive autocatalytic metabolism began to produce more complex organic compounds through the catalytic transition of metal centers that became autocatalytic as their organic products turned into ligands. In contrast, carbon fixation metabolism became autocatalytic by forming a metabolic cycle in the form of a primitive sulfur-dependent version of the reductive citric acid cycle (Wächtershäuser 2008). The compartmentalization that is a prior condition for the evolution of any complex system likely involved iron sulfide (FeS) deposited at a warm (< 90 °C) hydrothermal spring, these arrangements may have enabled the movement of molecules of different sizes among compartments; therefore, the last universal common ancestor (LUCA) would account for a set of multiplying,

competing, functionally diversifying, and recombining molecules sheltered by compartments (Koonin and Martin 2005). However, traces of the origin of life or even of the diversification of early life in this iron-sulfur-rich ocean are hard to detect. This is why we need analogues of early Earth in order to understand the processes of diversification and coexistence of microbial communities that are an irrefutable early signature of a living planet (Des Marais 2003).

The Extensive Diversity of Magnetotactic Bacteria (MTB)

The MTB are a morphologically, metabolically, and phylogenetically diverse bacterial group capable of incorporating environmental Fe into cell bodies called magnetosomes. The magnetosomes are formed through in vivo synthesis at the nanoscale of magnetic particles such as magnetite (iron oxide, Fe_3O_4) or greigite (iron sulfide, Fe_3S_4). The magnetosomes confer the capacity for magnetotaxis (Bazylinski 1996; Lefèvre and Bazylinski 2013). The MTB have a high potential for diverse applications such as use as biomarkers, specifically paleobiomarkers (because their magnetosomes fossilize in the direction of the poles of Earth), in the synthesis of new nanoparticles and nanomaterials, in bioremediation (i.e., wastewater treatment and heavy metal recovery) and biomedicine (i.e., magnetic resonance imaging, potential cancer treatment, functional magnetosomes for protein display, and gene delivery, magnetic cell separation, biosensor applications, and micro- and nano-manipulators) (Tanaka et al. 2010; Ginet et al. 2011; Mathuriya 2016). Another interesting example of potential use as a bioremediation tool is in the capability of MTB to absorb other toxic metals and metalloids such as tellurium. Moreover, use of these bacteria has emerged as an attractive alternative for the recapture of metals that impact the environment (Tanaka et al. 2010).

Magnetosomes within these particular bacteria are arranged in one or more strings parallel to the major axis of the cell. The lipid bilayer membrane of magnetosome consists mainly of phospholipids, 50% of which are phosphatidylethanolamine (Tanaka et al. 2006). Magnetosome vesicles are formed from the cytoplasmic membrane through an invagination process, in which vesicles are aligned along the cell through a bridge filamentous actin protein. This cellular differentiation process starts with the transport of iron and subsequent crystallization of the magnetite via processes such as nucleation, growth, and morphological regulation (Komeili et al. 2006). It is now known that more than 40 different genes encode magnetosome-associated proteins and yield magnetosome-related phenotypes in *Magnetospirillum* spp. (Uebe and Schüler 2016).

Proteomic analysis indicates that magnetosome proteins are related to the formation of the specialized magnetosome vesicle, biomineralization of iron, and magnetic detection. The genes associated with this complex are encoded into groups of genes within a genomic island, the magnetosome island (MAI). Although this genomic island is large and complex, we can find about 30 *mam* genes (magnetosome membrane) and *mms* (magnetic particle membrane specific) genes that are

organized into five polycistronic operons: the large *mamAB* operon (16–17 kb), the small *feoAB1* operon, and *mamGFDC*, *mms6*, and *mamXY* operons (Uebe and Schüler 2016). In most cases, genes coding for *MagA*, *Mms16*, and *Mms13* exhibit high levels of expression in *Magnetospirillum* (Lohße et al. 2011). For example, the *mms16* gene encodes GTPase that handles the translocation proteins across cell membranes, as well as the transport of the vesicles within the cell, specifically in the cover assembly of the vesicles. GTPase inhibition prevents synthesis of biogenic magnetic particles, suggesting that GTPase activity is required for the synthesis of this structure (Okamura et al. 2001; Arakaki et al. 2010). Moreover, the transcription of *magA* in *Magnetospirillum* is regulated by the concentration of iron in the extracellular environment. The expression of this gene in strains of *E. coli* results in vesicles exhibiting iron storage capacity. Thus, involvement of *MagA* in iron transport is also implicated in the synthesis of magnetic particles in *Magnetospirillum* (Nakamura et al. 1995; Arakaki et al. 2010). Conversely, if *mms24* is removed, there is no effect on the invagination of the membrane for the formation of the vesicle. However, the mutated MTB is not able to form crystals of iron oxide, as the accumulation of iron in magnetosome chain is altered since the molecular structure of this protein has the ability to mediate protein-protein interactions and forms multi-protein complexes that regulate the development of magnetosome (Zeytuni et al. 2011).

Although the genomic Island is large and complex, there is evidence of horizontal gene transfer (HGT) playing an important role in the development and distribution of the genes for building magnetosomes in several lineages of prokaryotes. Due to its potential mobility, the MAI is surrounded by mobile elements such as transposases and putative insertion sites near tRNA genes (Lefèvre et al. 2013; Uebe and Schüler 2016). Even if there is potential HGT related to this island, comparative phylogenetic analyses of the amino acid sequences of magnetosome proteins and the 16S rRNA gene sequences of various MTB have shown a consistent relationship between the evolution and divergence of these proteins and the 16S rRNA gene, suggesting that the source of magnetotaxis in the *Proteobacteria* phylum is monophyletic (Lefèvre et al. 2013).

What Kind of MTB Inhabit Cuatro Ciénegas?

Despite the arid climate and its very low phosphorus content, CCB harbors extensive microbial biodiversity. The diverse community includes the living stromatolites and other microbial communities that form the basis of complex food webs (Souza et al. 2012). Due to its high species endemism and its history of evolutionary radiations, CCB is classified as a globally outstanding ecosystem. Furthermore, the microbiota in Cuatro Ciénegas have a surprising marine origin (Souza et al. 2006). It is hypothesized that this unique microbiota is due to the deposition of shallow marine limestones and sulfates at the regional uplift, called the Coahuila Island, throughout the late Jurassic to early Cretaceous periods. What is more puzzling is

that many of the microbes of CCB can be traced back to a marine origin either in the Jurassic or in the late Precambrian (Moreno-Letelier et al. 2011, 2012). This is also possibly the case for the MTB.

In our study, we sampled sediment of Churince Lagoon at Cuatro Ciénegas Basin. Sediment was transported in liquid nitrogen to the laboratory, where we enriched it with synthetic marine water media and imposed a magnetic field in order to select MTB. On the other hand, we isolated environmental DNA from the same sediment and generated clone libraries of three specific genes for magnetosome synthesis, *mms16*, *mms24*, and *magA* (Arakaki et al. 2010), along with the 16S rRNA gene (Relman 1993). Additionally, the V2–V5 hypervariable regions of 16S rRNA gene were amplified and sequenced by Illumina MiSeq platform.

The 16S rRNA clone analyses from cultured lines (Fig. 8.1) revealed that we retrieved sequences similar to *Magnetospirillum magneticum* (*Alphaproteobacteria* class), originally isolated from freshwater sediment in Japan (Matsunaga et al. 1991), *Desulfovibrio magneticus* (*Deltaproteobacteria* class) (Kawaguchi et al. 1995), *Magnetococcus marinus* (*Alphaproteobacteria* class) (Bazylnski et al. 2013a), and several uncultured *Magnetococcus* clones observed in the Moskva River (Kozyaeva et al. 2017), as well as numerous uncultured bacterium clones obtained from sediment-free enrichment mediating the anaerobic oxidation of methane with sulfate

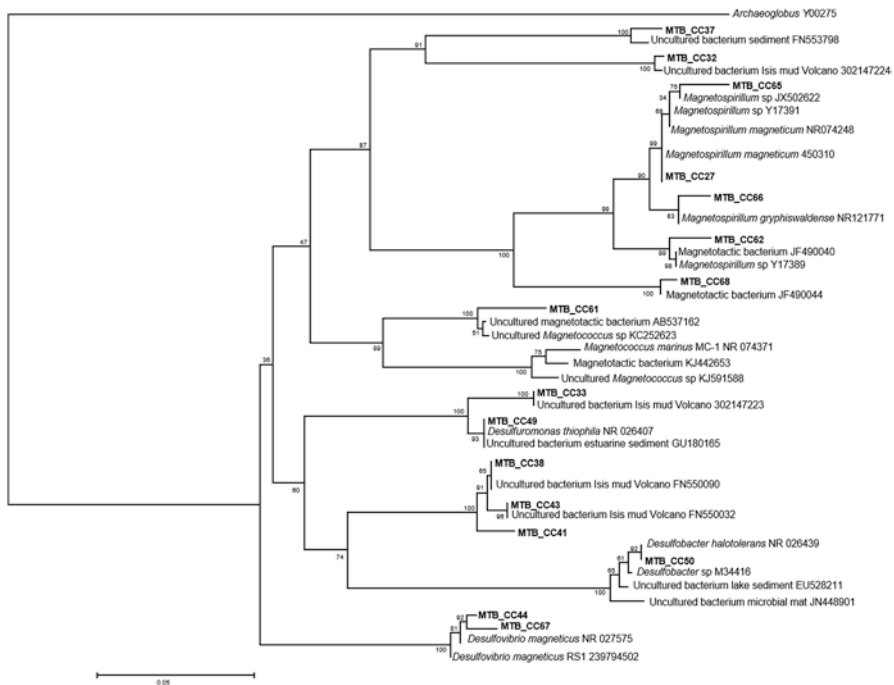


Fig. 8.1 Phylogenetic tree based on retrieved 16S rRNA gene sequence clones (in bold) of MTB from Churince Lagoon. Neighbor-joining analysis with bootstrap of 1000 replicates

from the Isis mud volcano, eastern Mediterranean (Schreiber et al. 2010). With respect to retrieved sequences of magnetosomes, we obtained numerous *mamA* clones similar to *Desulfovibrio magneticus* (Nakazawa et al. 2009), *Magnetospirillum* (Okuda et al. 1996), as well as sequences from marine sediment metagenomes (Yooseph et al. 2007).

The MTB detected in Churince Lagoon through the Illumina 16S RNA gene contributed less than 0.01% of the total abundances, making them a part of the “rare biosphere” (Sogin et al. 2006). The sequences were seen to be similar to *Magnetospirillum*, *Magnetococcus*, *Magnetovibrio*, and *Magnetospira* taxa (Fig. 8.2). At CCB, the rare biosphere is implicated in many microbe-driven processes such as those involved in the sulfur cycle, particularly when environmental conditions are changing (Jousset et al. 2017; Lee et al. 2017). In the microbial mats of the Churince Lagoon, several sulfur keystone taxa have previously been recognized as components of the rare biosphere (De Anda et al. under review).

In another study (Chapter 8 by De Anda et al.), we observed that, in addition to marked local seasonal effects, there is an important anthropogenic effect on microbial biodiversity at CCB due to water overexploitation for intensive agriculture. As the aquifer goes down, diversity declines, especially for the anaerobic microbes that depend on the conditions provided by the deep sulfur- and iron-rich water. This reduction in biodiversity includes, as expected, the MTB guilds (De Anda et al. under review). We hypothesize that MTB will be more resilient to changes than other sulfur-related bacteria because magnetotaxis along with chemotaxis will allow MTB to locate and maintain in vertical chemical concentration gradients in a water column as water declines (Frankel et al. 1997). This vertical alignment may give MTB an advantage in adjusting to environmental alterations. However, this hypothesis remains to be tested.

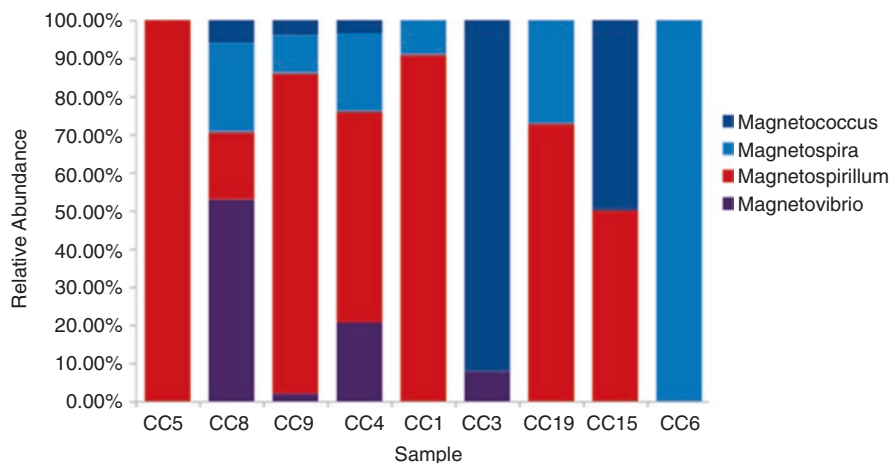


Fig. 8.2 Relative abundance of MTB sequences in sediments of Churince Lagoon, Cuatro Ciénegas

The presence of MTB at Churince sediments is not a surprise. These bacteria inhabit sediments of freshwater, brackish, marine, and hypersaline environments. They flourish in chemically stratified water columns at the oxic-anoxic interface, where a redox gradient is established with different compounds that can be used as substrate, such as sulfur compounds (Bazyliński et al. 2013b; Lefèvre and Bazyliński 2013). Furthermore, the distribution, presence, and abundance of MTB are affected by environmental parameters such as salinity, temperature, nitrate, or sulfur compounds (Lin et al. 2013; Liu et al. 2017). As might be expected, the Churince Lagoon is a biogeochemically suitable environment for development of an extensive diversity of MTB. At CCB, and in particular in the Churince system, the sulfur cycle plays a substantial role as a key biogeochemical gear. Previous studies by our group developed MEBS (Multigenomic Entropy Based Score), an algorithm to measure the impact of the sulfur metabolic machinery. These calculations suggested that microbial communities in mats at Cuatro Ciénegas have among the highest sulfur scores observed, similar to those for hydrothermal vent and marine benthic communities (De Anda et al. 2017).

Conclusion

The sulfur cycle is a fundamental collection of processes in the development of the structure of microbial communities in Churince Lagoon, a relict oasis in Cuatro Ciénegas. The presence of MTB is determined not only by iron but also by other factors, such as sulfur sources. Further studies are required to highlight their ecological function in this desert oasis. Currently, we are studying the whole community of prokaryotes related to MTB in sediments of the Churince Lagoon. These findings will provide us with more information defining the relationships between the important species that assemble the microbial core, the rare biosphere, and keystone taxa of these ancient and diverse communities.

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