Minireview

Life with compass: diversity and biogeography of magnetotactic bacteria

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Summary

Magnetotactic bacteria (MTB) are unique in their ability to synthesize intracellular nano-sized minerals of magnetite and/or greigite magnetosomes for magnetic orientation. Thus, they provide an excellent model system to investigate mechanisms of biomineralization. MTB play important roles in bulk sedimentary magnetism and have numerous versatile applications in paleoenvironmental reconstructions, and biotechnological and biomedical fields. Significant progress has been made in recent years in describing the composition of MTB communities and distribution through innovative cultivation-dependent and -independent techniques. In this review, the most recent contributions to the field of diversity and biogeography of MTB are summarized and reviewed. Emphasis is on the novel insights into various factors/processes potentially affecting MTB community distribution. An understanding of the present-day biogeography of MTB, and the ruling parameters of their spatial distribution, will eventually help us predict MTB community shifts with environmental changes and assess their roles in global iron cycling.

Introduction

Iron is the fourth most common element in the Earth’s crust and a crucial nutrient for almost all known organisms. The cycling of iron is one of the key processes in the Earth’s biogeochemical cycles. A number of organisms synthesize iron minerals and play essential roles in global iron cycling (Westbroek and de Jong, 1983; Winklhofer, 2010). One of the most interesting examples of these types of organisms are the magnetotactic bacteria (MTB), a polyphyletic group of prokaryotes that are ubiquitous in aquatic and sedimentary environments (Bazylinski and Frankel, 2004; Bazylinski et al., 2013). They share a common feature of being able to synthesize magnetosomes, which are intracellular nano-sized iron minerals of magnetite (Fe₃O₄) and/or greigite (Fe₃S₄) (Jogler and Schüler, 2009). Magnetosomes are individually less than 150 nm in size and normally organized into one or multiple chain-like structures within the cell in order to optimize the cellular magnetic dipole moment (Fig. 1). It is widely accepted that magnetosome chain(s) act(s) like a compass needle to facilitate the navigation of MTB using the Earth’s magnetic field (Fig. 1).

Because of their remarkable capacity of assimilation of iron, MTB accumulate up to 2–3% iron per cell by dry weight, which is several orders of magnitude higher than iron in non-MTB cells (Heyen and Schüler, 2003). In most aquatic habitats, the numbers of MTB normally range between 10³ and 10⁶ cells ml⁻¹, while in some microhabitats they can even account for a significant proportion (~10–30%) of the microbial biomass (Spring et al., 1993; Flies et al., 2005b; Simmons et al., 2007). There is great geological significance of magnetosomes formed by MTB; spectacular examples are fossil magnetosomes (so-called ‘magnetofossils’) that may significantly contribute to the bulk magnetization of...
Members of MTB occupy a wide array of ecosystems, including lakes, rivers, ponds, estuaries and salt marshes, lagoons, mangrove swamps, intertidal zones, deep-sea sediments, soils, and even some extreme environments (Fassbinder et al., 1990; Petermann and Bleil, 1993; Flies et al., 2005a; Simmons et al., 2007; Pan et al., 2008; Jogler and Schüler, 2009; Jogler et al., 2009; Wenter et al., 2009; Sobrinho et al., 2011; Lin et al., 2012c; 2013; Martins et al., 2012; Zhang et al., 2012; 2013; Zhou et al., 2012; Bazylinski and Lefèvre, 2013). So far MTB have been globally detected from Asia, Europe, North and South America, Africa, Australia, and Antarctica (Fig. 2). The water depth at which MTB have been recorded ranges from metre scales to those of deep sea environments (~ 3000 m).

Although additional studies are necessary to understand the distribution of MTB in nature, emerging evidence strongly suggests that MTB occur worldwide in aquatic environments. The majority of studies thus far focus on magnetite-producing MTB communities in lacustrine systems. The annual yield of lacustrine magnetite magnetosomes can be estimated using the following formula: (volume in lakes, ponds and impoundments) \( \times \) (average number of MTB cells per mL) \( \times \) (average number of magnetite magnetosomes per MTB cell) \( \times \) (average number of MTB generations per year) \( \times \) (mass of single magnetite magnetosomes).

Global lakes, ponds and impoundments are estimated to cover about 4.6 million km\(^2\) of the Earth’s surface (Downing et al., 2006), and we assume that only 50% of this area harbours MTB cells that live in the upper 10 cm of sediment. If we assume that the lower average number of MTB is \( 10^8 \) cells mL\(^{-1}\), that each MTB cell has 20 magnetosomes, that the generation turnover time of environmental MTB is about 12 h (Moench and Konetzka, 1978) and that the mass of single magnetite magnetosome is \( 6.48 \times 10^{-16} \) g (given the volume of a single magnetosome is approximately \( 50 \times 50 \times 50 \) nm\(^3\)), the annual yield of magnetite by lacustrine MTB is estimated to be no less than \( 2 \times 10^6 \) kg. This conservative estimate is likely to pronouncedly increase to more than \( 10^6 \) kg of magnetite per year if we consider MTB communities in the world’s oceans, although the ecology and distribution of marine MTB are currently poorly understood. In addition, living MTB have been found in soils of a water-rich meadow environment in the southern Bavaria, indicating that MTB may also contribute to the magnetite formation in soils (Fassbinder et al., 1990).

In terms of understanding their ecological functions, the knowledge of to what extent MTB affect local and global
iron cycling would be very useful. Although this represents an area in which there is a paucity of understanding, the earlier estimate strongly suggests that MTB communities play important roles in present-day global iron cycling and the deposition of iron formation through geological history (Fig. 3). Ferrous and ferric ions could be actively taken up by MTB cells in natural environments and accumulate within the cell during the formation of intracellular magnetite or greigite magnetosomes, the biochemical/chemical pathways of which are still not fully understood (Schüler, 2008). When MTB die, parts of, or entire magnetofossils could be dissolved thereby releasing ferrous and ferric ions back to environmental iron cycling (Fig. 3), while other magnetofossils may be deposited into sediments eventually leading to mineral iron formation. On the other hand, some MTB cells can be ingested by their predators, e.g. protozoa (Martins et al., 2007), which causes the iron from MTB to enter into the food chain (Fig. 3). More research involving the distribution and ecology of MTB in nature, especially in marine habitats, will help us better understand the conditions under which and to what extent MTB affect the biogeochemical cycle of iron.

Diversity of MTB

Thanks to their active magnetotactic behaviour, environmental MTB can be magnetically extracted and at least partially purified from water or sediment samples relatively easily. The identification of novel MTB populations has mostly relied on both cultivation-based approaches and 16S rRNA gene-targeting analyses, such as clone library sequencing, fluorescence in situ hybridization (FISH), restriction fragment length polymorphism and denaturing
gradient gel electrophoresis. Recently, newly developed metagenomics (Jogler and Schüler, 2009; Jogler et al., 2009; Lin et al., 2011) and approaches of single-cell separation in combination with whole genome sequencing (Arakaki et al., 2010; Jogler et al., 2011; Kolinko et al., 2012; 2013) have also provided powerful and effective ways to investigate the diversity and metabolic information on environmental MTB.

Through these approaches, MTB identified thus far are phylogenetically associated with the Alphaproteobacteria, Deltaproteobacteria, Gammaproteobacteria classes of the Proteobacteria phylum, the Nitrospirae phylum and the candidate division OP3 (Fig. 4 and Table S1). Magnetite-producing members are affiliated with all known taxa of MTB, while greigite-producing MTB have only been found in the Deltaproteobacteria (Abreu et al., 2011) and perhaps the Gammaproteobacteria (Simmons et al., 2004). MTB that are able to simultaneously biomineralize both magnetite and greigite magnetosomes are thus far exclusively detected within the Deltaproteobacteria (Lefèvre et al., 2011d; Wang et al., 2013) (Fig. 4).

Although MTB of the Alphaproteobacteria represent the dominant populations of MTB in many environments in nature, recent studies have shown that those of other taxa are much more diverse than previously thought (Table S1). For example, MTB in the phylum Nitrospirae were for many years thought as comprising only one uncultivated species, the large rod ‘Candidatus Magnetobacterium bavaricum’ (Spring et al., 1993). However, a number of MTB from this phylum have recently been recovered from Germany (Flies et al., 2005a; Kolinko et al., 2013), China (Lin et al., 2011; 2012a) and the USA (Lefèvre et al., 2010; 2011a), which suggests that the Nitrospirae MTB consist of multiple evolutionary groups (Fig. 4 and Table S1).

Our understanding of the diversity of the Deltaproteobacteria and Gammaproteobacteria MTB has been advanced as well. Novel MTB affiliated with the Deltaproteobacteria have been identified and/or isolated, including iron sulphide-producing multicellular magnetotactic prokaryotes (MMPs) from the North Sea in Central Europe (Wenter et al., 2009), magnetite-producing MMPs from the Yellow Sea in East Asia (Zhou et al., 2011; 2012) and three alkaliphilic vibrioid strains from highly alkaline environments in North America (Lefèvre et al., 2011b) (Table S1). Of note, a number of MTB populations from USA were found to represent two novel groups of sulphate-reducing bacteria in the Deltaproteobacteria (Lefèvre et al., 2011d). Of these MTB, one greigite-
producing strain, known as ‘Candidatus Desulfamplus magnetomortis’ strain BW-1, was successfully cultivated in the lab and found to form greigite and/or magnetite magnetosomes depending on cultivating conditions (Lefèvre et al., 2011d). Recently, a high diversity of Deltaproteobacteria MTB, including one that simultaneously produces magnetite and greigite magnetosomes, was characterized in a single freshwater niche in China (Wang et al., 2013) (Table S1). The first evidence for Gammaproteobacteria MTB was obtained from a coastal salt pond in the USA (Simmons et al., 2004). Two rod-shaped magnetite-producing strains were recently isolated and were identified as belonging to the orders Chromatiales and Thiotrichales, respectively, in the Gammaproteobacteria (Lefèvre et al., 2012) (Table S1). In addition, two populations of Gammaproteobacteria MTB were detected in a freshwater niche in China that coexist with MTB belonging to the Alphaproteobacteria and Deltaproteobacteria (Wang et al., 2013).

It has been shown that MTB are not restricted to the phyla Proteobacteria and Nitrospirae. A large melon-shaped MTB (designated SKK-01) with low abundance was discovered in sediments of Lake Chiemsee, Germany (Kolinko et al., 2012). Cells of SKK-01 contain iron-oxide bullet-shaped magnetosomes organized in multiple bundles of chains.

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**Fig. 4.** Maximum-likelihood phylogeny of nearly full-length 16S rRNA gene sequences representing different groups of representative MTB. This tree shows that all currently known MTB are affiliated within the Alphaproteobacteria, Deltaproteobacteria, Gammaproteobacteria, phylum Nitrospirae and the candidate division OP3. Information of magnetosome composition and morphology is shown for each MTB strain or group. MTB sequences and their magnetosomes information are from literature (DeLong et al., 1993; Abreu et al., 2007; Lefèvre et al., 2009; 2010; 2011a,b,d; 2012; Nakazawa et al., 2009; Wenter et al., 2009; Zhu et al., 2010; Kolinko et al., 2012; Lin et al., 2012a; Zhou et al., 2012).

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<th>MTB Sequences and Magnetosomes Information</th>
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<td>Alphaproteobacteria</td>
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individual cells followed by single-cell genomic and FISH analyses has assigned SKK-01 to the candidate division OP3 belonging to the Planctomycetes-Verrucomicrobia-Chlamydiae superphylum (Kolinko et al., 2012).

There is an interesting and possibly evolutionary important correlation between the composition and morphology of magnetic magnetosome mineral and specific phylogenetic groups of MTB. MTB of the more deeply branching phylogenetic groups that contain MTB of the Nitrospirae and strain SKK-01 of the candidate division OP3 are only known to biomineralize bullet-shaped magnetite crystals that display a great deal of morphological variation (Hanzlik et al., 1996; Li et al., 2010; Jogler et al., 2011; Lefèvre et al., 2011c; Lin et al., 2011; 2012a; Kolinko et al., 2012) (Fig. 4). This is also true of MTB of the deeply diverging class of the Proteobacteria, the Deltaproteobacteria (Lefèvre et al., 2011c), although some species biomineralize greigite magnetosomes in addition to those containing bullet-shaped crystals of magnetite. MTB of the later diverging classes of the Proteobacteria, the Alphaproteobacteria and Gamma-proteobacteria, biomineralize consistent, well-defined cuboctahedral, and elongated prismatic crystals of magnetite (Fig. 4) (Devouard et al., 1998; Lefèvre et al., 2012). Based on this phylogenetic information, it has thus been hypothesized that bullet-shaped magnetite crystals were the more ancient type of magnetic mineral crystals biomineralized within magnetosomes (Lefèvre et al., 2013a).

Magnetosome formation by MTB species in the Alphaproteobacteria is under strictly genetic control through a genomic magnetosome island (MAI) that encodes a group of proteins involving in magnetosome membrane biogenesis, magnetosome membrane chain arrangement and magnetosome biomineralization (Schüler, 2008; Murat et al., 2010; Komeili, 2012). Following comparative genomic analyses have revealed that MAI also exists in genomes of MTB belonging to the Deltaproteobacteria and Nitrospirae, which strongly indicate that this structure is horizontally transferred (Nakazawa et al., 2009; Abreu et al., 2011; Jogler et al., 2011; Lefèvre et al., 2013b). Although several core magnetosome genes are identified in all characterized MTB (Nakazawa et al., 2009; Lefèvre et al., 2013b), the gene content and organization of MAIs differ in distinct MTB groups, which may account for the diversity of composition, morphology and arrangement of magnetosomes. For example, the formation of bullet-shaped magnetosomes in the Deltaproteobacteria MTB is hypothesized to be due to the deficiency of particular magnetosome genes (Nakazawa et al., 2009) or the existence of several specific mad genes currently only found to be present in those MTB that synthesize bullet-shaped magnetosomes (Lefèvre et al., 2013b).

Biomineralization of greigite magnetosomes appears to have originated in the Deltaproteobacteria, the only group known to contain greigite-producing MTB (Abreu et al., 2011; Lefèvre et al., 2011d) and, interestingly, not the most deeply branching groups that contain MTB. ‘Candidatus Desulfumplius magnetormitis’ strain BW-1, the only greigite-producing magnetotactic bacterium currently in pure culture, biomineralizes both greigite and magnetite, and contains two sets of magnetosome genes, one presumably responsible for magnetite biomineralization and the other for greigite biomimeralization (Lefèvre et al., 2011d). Both sets of genes have nine magnetosome genes in common, although they are not identical. Because of the similarities between both sets of magnetosome genes, the second set putatively involved in greigite biomineralization may have originated from gene duplication and/or subsequent mutation or other genetic changes that appears to have only occurred in the Deltaproteobacteria.

Biogeography of MTB

Spatial variation

Microbes were previously thought to be randomly distributed over space and that similarities between microbial communities were independent of geographic distances and environmental gradients between sites because of their great metabolism capacity, large population numbers, long evolutionary history, short generation times and high dispersal capabilities; this being the so-called ‘everything is everywhere’ concept (Baas Becking, 1934; Finlay, 2002; Fontaneto, 2011). If this was true, all kinds of MTB populations should be cosmopolitan and would lack local, regional or global biogeographic patterns.

Building on more than three decades of effort to determine the diversity of MTB in various ecosystems, we have reached a point where comparisons can be made between different environments to identify distribution patterns of MTB. Some specific well-known species of MTB, such as ‘Candidatus Magnetotbacterium bavaricum’-like bacteria and the MMPs that have conspicuous morphologies and are easily distinguished from other MTB and non-MTB, have shown clear biogeographic distributions. So far, all known ‘Candidatus Magnetotbacterium bavaricum’-like MTB appear to be restricted to freshwater or low-salinity ecosystems (Lefèvre et al., 2010; 2011a; Jogler et al., 2011; Lin et al., 2011; 2012a), while MMPs have been exclusively found in saline environments (Martins et al., 2009; Wenter et al., 2009; Zhou et al., 2012). In addition, recent studies using molecular techniques have revealed biogeographic patterns in MTB communities at local and continental scales (Lin and Pan, 2010; Lin et al., 2012c; 2013). In order to address the global distribution patterns of MTB, here, we conducted a
non-exhaustive compilation of MTB community datasets \((n = 27)\) from Asia (China), Europe (Germany), North America (USA) and South America (Brazil) (see legend of Fig. 5 for details). Although the lack of environmental metadata for several datasets prevents in-depth quantitative analyses, our results have clearly revealed that MTB communities from different habitats cluster by salinity (freshwater or saline) along principal coordinate 1 (Fig. 5A). This result indicates that MTB represent biogeographic patterns at the global level as well.

Martins and colleagues (2009), and Sobrinho and colleagues (2011) noted that the abundance and distribution of the greigite-producing MMP, ‘Candidatus Magnetoglobus multicellularis’, are largely affected by water salinity and the ratio of iron and bioavailable sulphur concentrations. Lin and colleagues (2012c; 2013) and the present analysis (Fig. 5A) have revealed that salinity influences the overall phylogenetic diversity of MTB communities across global different ecosystems, i.e. MTB communities from freshwater environments are more phylogenetically similar than those from saline environments. In fact, previous studies have shown that MTB from the two types of environments normally form separate lineages in the phylogenetic tree, which suggests a potential evolutionary separation between saline and freshwater MTB lineages (Spring et al., 1998; Zhang et al., 2010b). These results from MTB are consistent with the observation that salinity is one of the major drivers of global distribution in bacterial diversity (Lozupone and Knight, 2007). Although the mechanisms of salinity-dependent distribution of MTB are not fully understood, the gradients in osmotic pressure and ionic concentration across salinities could be important factors affecting the biogeography of MTB (Lin et al., 2012c). For example, recent genomic analysis showed adaptation of Magnetospira sp. QH-2 to marine habitats, i.e. it possesses genes coding for \(\text{Na}^+\) transporters, \(\text{Na}^+-\text{dependent NADH-quinone oxidoreductase, Na}^+\)-motive force-driven flagellar motors and osmoprotectant synthesis that are absent from genomes of the freshwater Magnetospirillum strains (Ji et al., 2013).

The most unique property of MTB, compared with other bacteria, is their capability to interact with the Earth’s magnetic field. Previous studies have suggested that the strength of the Earth’s magnetic field may influence the morphologies and sizes of magnetosome crystals in MTB, e.g. some MTB in regions of lower geomagnetic field strength appear to contain larger magnetosome crystals (Frankel et al., 1981; Farina et al., 1994; Spring et al., 1998). Recently, variations in the strength of magnetic field have been experimentally found to affect the magnetotactic swimming velocity or cell metabolism of some MTB populations (Wang et al., 2008; Pan et al., 2009; Lin et al., 2012a). By analysing MTB community structures from different ecosystems in East Asia and North America, it is first noted that the \(\beta\)-diversity (variation in community composition) of dominant MTB populations shows a surprising degree in response to differences in the strength of the Earth’s magnetic field in the Northern Hemisphere (Lin et al., 2013). Although the
correlation between biogeography of MTB and the strength of the geomagnetic field is supported by a substantial amount of data, it is still a testable hypothesis that requires additional studies, especially those from areas of high latitude and the southern hemisphere.

Additional environmental factors that could have significant potential effects on MTB biogeography include temperature (Lin et al., 2012b; 2013), redox potential (Simmons et al., 2006; Zhang et al., 2010a; Lin et al., 2013), light (Shapiro et al., 2011), the presence and concentration of sulphur compounds (Postec et al., 2012) and nitrate (Lin and Pan, 2010), and the concentration of total iron (Lin et al., 2013).

Processes that structure MTB biogeography

A central goal of studies of microbial biogeography is to understand the mechanisms that generate and maintain MTB distribution and community composition. Several processes have been assumed to sustain and control biogeography of microbes. The classical niche-based model assumes that the abundance and community composition of microbes are largely determined by environmental parameters (Martiny et al., 2006). For example, a recent study has suggested that the global ocean contains a shared microbial seed bank and that the biogeography of marine microorganisms reflect shifts of rare or dominant taxa depending on environmental conditions (Gibbons et al., 2013). On the other hand, the neutral theory assumes that all species are ecologically equivalent and that community variation arises solely from the spatial process (Hubbell, 2001; Fontaneto, 2011). The latest studies, however, suggest that these two processes may not be mutually exclusive but jointly control microbial communities (Hanson et al., 2012).

For biogeographic analysis of MTB, the niche-based process is much easier to measure than the spatial process. For example, variations of MTB communities are normally explained by changes of local environmental factors as stated earlier (Fig. 6). In addition, recent genomic analysis provides new insights into the molecular adaptation of MTB to ecological niches. For example, TonB protein and TonB-dependent iron transporters widely spread among bacteria and nitrogen fixation have been considered as common features of MTB. However, the intertidal strain *Magnetospira* sp. QH-2 possesses neither TonB/TonB-dependent iron transporters nor the nitrogen fixation pathway (Ji et al., 2013). Mechanisms leading to such environmental specification are still unknown and need further studies.

Besides the niche-based process, a study using a variation partitioning approach has revealed that the spatial process also structure the biogeographic patterns of MTB across a large spatial scale (Lin et al., 2013). Although the niche-based process plays an important role, the contribution of the spatial process to the biogeography of MTB cannot be neglected (Fig. 6). Our analysis on available global MTB community data sets conducted in this study also finds a significant correlation of the variation of MTB communities and the geographic distance between sampling sites (*P* < 0.05, Fig. 5B). This distance–decay relationship indicates that the spatial process may shape the global biogeography of MTB as well. We note several relatively high community similarities (UniFrac similarity

Fig. 6. Conceptual model denoting influences of niche-based and spatial processes on MTB community structure. The Taiji symbol represents that (i) both niche-based process and spatial process jointly control biogeography of MTB community and (ii) their relative contributions to MTB biogeography may vary under different conditions, like across distinct spatial scales.
Concluding remarks and future perspectives

We show in this review clearly that our understanding of diversity and biogeography of MTB has been greatly advanced. MTB represent a valuable model group for addressing some ecological questions in microbial biogeography because of their global distribution, moderate diversity and active magnetotactic behaviours. A deeper characterization of MTB through cultivation-based approaches and advanced cultivation-independent techniques (such as 'omics'-based analyses and single cell-based approach) will allow for future studies of their diversity and biogeography.

Only a small proportion of the community variation of MTB has been explained by characterized factors (Lin et al., 2013), which is likely due to the relatively small amount of data on MTB and the lack of additional important environmental information. Surveys of MTB conducted to date largely focus on mid-low latitudes in the Northern Hemisphere, while the diversity and biogeography of MTB in the Southern Hemisphere as well as high-latitude zones are still poorly characterized (Fig. 2). Standard protocols should be established in MTB diversity analyses that could make results from different labs comparable. Meanwhile, the key factors that influence the microbial biogeography of MTB should be quantitatively determined.

Bacterial populations are dynamic in nature, with their abundance and community structure changing over time. Although a few studies on the temporal variation of particular MTB, such as 'Candidatus Magnetoglobus multicellularis' (Martins et al., 2012) and several dominant populations in a coastal brackish pond (Simmons et al., 2007), have been reported, our knowledge on the variation of MTB communities over time is still very limited. It is thus of great importance for future studies to consider the temporal variation of overall MTB communities in nature.

In a geological context, single-domain magnetofossils preserved in sediments are not only ideal carriers of magnetization for paleomagnetism but also potential biomarkers for retrieving paleoenvironmental information (Kopp et al., 2007; 2009; Roberts et al., 2011; Chang et al., 2012; Larraoaña et al., 2012; Kodama et al., 2013). A better understanding of the present-day biogeography of MTB and its correlation with specific environments will pave the way for reconstructions of past environmental change that will eventually help us predict and assess how MTB communities shift with climate changes. Thus, probing fossil magnetosomes in periods of intensive paleoclimatic changes and geomagnetic field events (e.g. polarity reversals and excursions) will be of particular interest in future investigations.

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References


**Supporting information**

Additional Supporting Information may be found in the online version of this article at the publisher’s web-site:

**Table S1.** MTB strains and populations that have been characterized in the last 5 years (2009–2013).
**Table S2.** Details of the representative locations where MTB have been detected.