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Minireview

Diversity and ecology of and biomineralization by magnetotactic bacteria

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Summary

Magnetotactic bacteria (MTB) biomineralize intracellular, membrane-bounded crystals of magnetite (Fe_3O_4) and/or greigite (Fe_3S_4) called magnetosomes. MTB play important roles in the geochemical cycling of iron, sulfur, nitrogen and carbon. Significantly, they also represent an intriguing model system not just for the study of microbial biomineralization but also for magnetoreception, prokaryotic organelle formation and microbial biogeography. Here we review current knowledge on the ecology of and biomineralization by MTB, with an emphasis on more recent reports of unexpected ecological and phylogenetic findings regarding MTB. In this study, we conducted a search of public metagenomic databases and identified six novel magnetosome gene cluster-containing genomic fragments affiliated with the *Deltaproteobacteria* and *Gammaproteobacteria* classes of the *Proteobacteria* phylum, the *Nitrospirae* phylum and the *Planctomycetes* phylum from the deep subseafloor, marine oxygen minimum zone, groundwater biofilm and estuary sediment, thereby extending our knowledge on the diversity and distribution of MTB as well deriving important information as to their ecophysiology. We point out that the increasing availability of sequence data will facilitate researchers to systematically explore the ecology and biomineralization of MTB even further.

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Introduction

Magnetotactic bacteria (MTB) are motile prokaryotic organisms that biomineralize intracellular, single magnetic domain crystals of magnetite (Fe_3O_4) and/or greigite (Fe_3S_4) in lipid bilayer membranous vesicles called magnetosomes (Bazylinski *et al*., 2013; Uebe and Schüler, 2016). Magnetosomes impart a permanent magnetic dipole moment to the cell causing it to align along magnetic field lines as it swims, a behaviour called magnetotaxis (Lefèvre *et al*., 2011b). Although MTB represent a diverse group in many ways, MTB are ubiquitous in most aquatic environments and global in distribution though appearing to be confined phylogenetically to the Domain *Bacteria* at this time (Lin *et al*., 2014a).

The most widely accepted function of magnetosomes is that they allow MTB to more efficiently locate and maintain an optimal position for survival and growth in habitats with vertical chemical (e.g. O_2) concentration and redox gradients in water columns and sediments, generally at or near the oxic/anoxic interface (OAI) (Lefèvre and Bazylinski, 2013), although several other possible functions have been considered (Simmons and Edwards, 2007a; Faivre and Schüler, 2008). In natural habitats where they are found, MTB appear to be important in the geochemical cycling of iron, sulfur, nitrogen and carbon based on the geochemical transformations they catalyse in the laboratory as well as on specific genes within their genomes.

In the last two decades, a significant amount of new information has been reported regarding the phylogenetic and ecological diversity of the MTB that appears directly related to the biomineralization process as well as to their ecophysiology. Here we review this new information emphasizing the unexpected ecological and phylogenetic findings regarding MTB.

Diversity and phylogeny of MTB

MTB were independently discovered by Salvatore Bellini in 1963 (Bellini, 2009) and Richard Blakemore in 1974 (Blakemore, 1975). The largest early efforts were directed towards microscope-based surveys and cultivation-based studies. During the first two decades after their discovery, MTB were found in many habitats in the Northern (Blakemore, 1982) and Southern Hemispheres (Blakemore *et al*., 1980; Kirschvink, 1980) and at the geomagnetic equator (Frankel *et al*., 1981), suggesting a global distribution of the microorganisms. During this period, several MTB strains were successfully isolated and cultivated; many of them belonging to the class *Alphaproteobacteria* including *Magnetospirillum magnetotacticum* strain MS-1 (Blakemore *et al*., 1979), *Magnetospirillum magneticum* strain AMB-1 (Matsunaga *et al*., 1991), *Magnetospirillum gryphiswaldense* strain MSR-1 (Schleifer *et al*., 1991) and *Magnetococcus marinus* strain MC-1 (DeLong *et al*., 1993), while *Desulfovibrio magneticus* strain RS-1 (Sakaguchi *et al*., 1993) is affiliated with the class *Deltaproteobacteria*. These organisms have become the model strains for MTB research.

The cultivation-independent approach based on PCR amplification and Sanger sequencing of 16S rRNA genes revolutionized studies of MTB since the early 1990s. This approach, combined with fluorescence *in situ* hybridization (FISH), led to the discovery of novel lineages of MTB not only in the *Proteobacteria* phylum (Spring *et al*., 1992; 1994; DeLong *et al*., 1993) but also in the *Nitrospirae* phylum (Spring *et al*., 1993). Since then, a growing number of MTB populations have been discovered, demonstrating their high morphological and phylogenetic diversity (e.g. Flies *et al*., 2005a,b; Pan *et al*., 2005b; Abreu *et al*., 2007; 2016; Simmons and Edwards, 2007b; Lin *et al*., 2009; 2011; 2012a; Lin and Pan, 2009; Lefèvre *et al*., 2010; 2011a; 2011c; 2012; Kolinko *et al*., 2012; Zhang *et al*., 2012; 2013; Zhou *et al*., 2012; Chen *et al*., 2014; Fuduche *et al*., 2015; Pradel *et al*., 2015; Leão *et al*., 2016). In particular, Kolinko *et al*. (2012) discovered a novel, uncultivated MTB population phylogenetically affiliated with the candidate phylum *Omnitrophica* (formerly candidate division OP3) through single-cell studies and analysis. To date, magnetite-producing MTB have been found in the *Alphaproteobacteria*, *Deltaproteobacteria*, *Gammaproteobacteria* classes of the phylum *Proteobacteria*, the phylum *Nitrospirae* and the candidate phylum *Omnitrophica*, while greigite-producing MTB have thus far only been identified in the *Deltaproteobacteria* and the candidate phylum *Latescibacteria* (Lefèvre and Bazylinski, 2013; Wang *et al*., 2013; Kolinko *et al*., 2014b; Lin *et al*., 2014a; Lin and Pan, 2015). Recently it has been suggested, based on comparative genomic analysis, that MTB in the order *Magnetococcales* represent a novel class (*Etaproteobacteria*) in the *Proteobacteria* phylum rather than the earliest-diverging group within the *Alphaproteobacteria* class (Ji *et al*., 2017). So far only three genomes are available for *Magnetococcales*, more sequencing efforts are required to address the phylogenetic position of this MTB group.

MTB in unusual environments: extremophilic MTB

Although MTB were observed and reported in hemipelagic and deep-sea sediments in the 1980s and 1990s (Stolz *et al*., 1986; Petermann and Bleil, 1993), these organisms were mainly thought to only exist in aquatic and sedimentary environments with pH values near neutral and at the normal range of temperature. More recent findings show this not to be the case and that some MTB occupy extreme environments (Bazylinski and Lefèvre, 2013). Nash (2008) identified a thermophilic MTB from Little Hot Creek (45–55°C) and four from Mono Lake (pH of 9.8 and salinity 80.8 gL^{-1}). This was the first indication that some MTB thrive in extreme environments including hot springs (Lefèvre *et al*., 2010), saline-alkaline lakes (Lefèvre *et al*., 2011c; Sorty and Shaikh, 2015) and deep-sea environments (Dong *et al*., 2016). We recently found many types of MTB in several saline-alkaline lakes in Inner Mongolia, China, with pH ranges between 8.9 and 9.8 and salinity values between 5.5 and 58.0 ppt (Fig. 1). There is evidence that suggests that alkaline lakes may have occurred during the Archean Eon (Stüeken *et al*., 2015), making them one of the first types of non-marine saline environments on Earth. Alkaline lakes are the most productive ecosystems on modern Earth and may have been so in the past (Jones *et al*., 1998). Thus, studies of MTB in these and other extreme environments could provide important information and opportunities to address questions regarding the origin and evolution of magnetotaxis and biomineralization in bacteria.

The unique, salient feature of MTB is their ability to swim along the Earth's geomagnetic field lines, suggesting that they should be free-living organisms. Magnetosome-producing bacteria have recently been found in marine bivalves appearing to live as symbionts (Dufour *et al*., 2014). It was hypothesized that the host's sulfide mining and bioirrigation activities, which produce an OAI along burrow walls, might favour growth and colonization of nearby free-living MTB in near-burrow sediments. These MTB might be further incorporated as symbionts by the host, perhaps as autotrophic organisms (Dufour *et al*., 2014), eventually losing the ability to swim and to construct the magnetosome chain motif of magnetosomes common in almost all MTB. This study raises several interesting questions, for example, whether MTB or magnetosome-containing bacteria are widely distributed in host organisms? Do they become established as

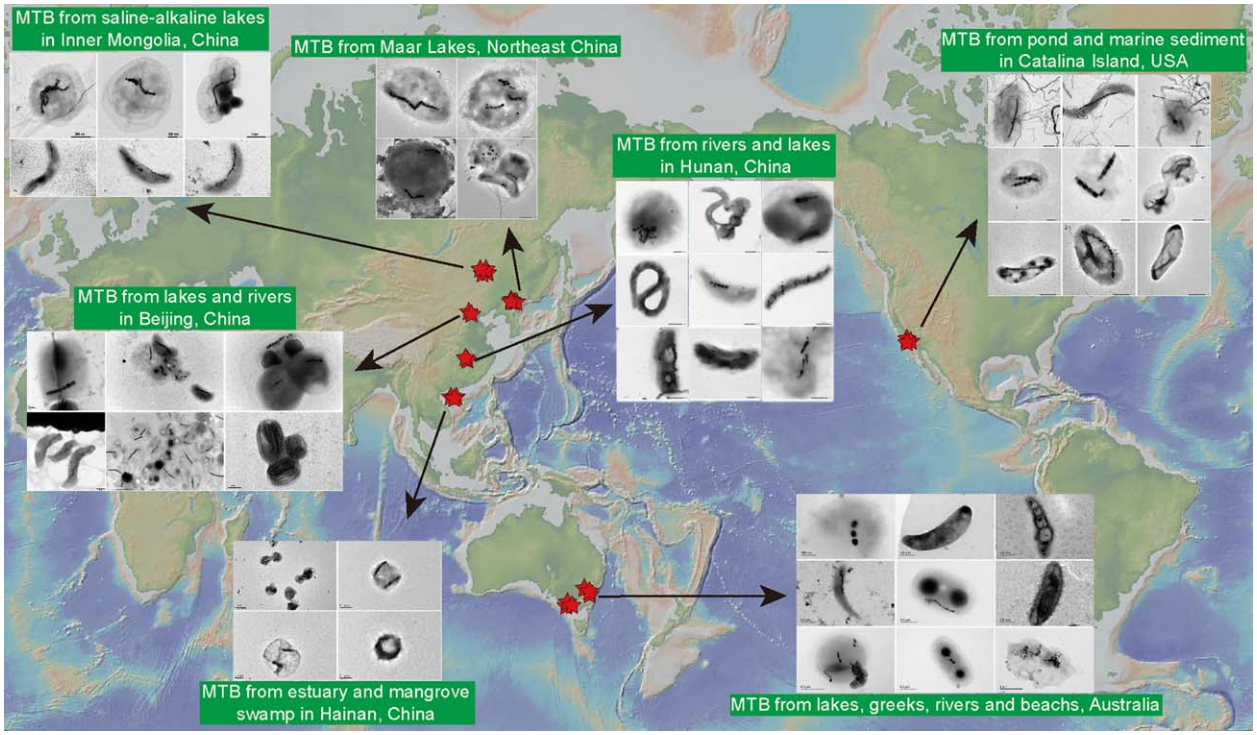

Fig. 1. Various morphotypes of MTB found in different locations in China, USA and Australia.

actual symbionts, and, if so, how? And what are the dynamic metabolisms of magnetosome crystals in the hosts? The finding of endosymbionts that produce magnetosomes will likely have a remarkable impact on our current view of MTB ecology and diversity.

Large-scale biogeography studies

While all initial studies strongly indicated that the MTB were very diverse in numerous ways, large-scale studies of MTB from different environments would facilitate the understanding of their overall diversity and ecology and perhaps their physiology. However, few large-scale studies have been performed involving MTB. The first, to our knowledge, was conducted by Flies and colleagues (2005b) using a combined microscopic, cultivation-independent and -dependent approaches. Sediment samples from more than 50 different sites in Europe were found to harbour diverse MTB communities, in which magnetotactic cocci belonging to the *Alphaproteobacteria* represented the dominant group.

We recently examined the diversity and biogeography of MTB spanning Asia, North America and Australia (Fig. 1) (Lin *et al.*, 2012b,,a). Various morphotypes of MTB, including cocci, rods, vibrios and spirilla, with different arrangements of magnetosomes and magnetosome crystal morphologies were observed. 16S rRNA gene-based phylogenetic analysis revealed that many of these bacteria belonged to the phyla *Proteobacteria* and *Nitrospirae*. Both environmental heterogeneity and geographic distance were found to be significant factors in shaping MTB communities, although the biogeography of MTB was more influenced by environmental factors than geographic distance (Lin *et al.*, 2013). It was also noted that the Earth's geomagnetic field might play a role in the biogeography of MTB.

These large-scale studies confirm the suggestions of early diversity studies and document the occurrence of MTB in many different aquatic environments including lakes, rivers, creeks, ponds, estuaries, lagoons, mangrove swamps, wet soils, intertidal zones and the deep sea. MTB communities in nature are complex and are likely governed by the same processes that shape animals and plants (Lin *et al.*, 2014a). Because of their global distribution and magnetotactic behaviour, MTB represent a valuable model group for addressing ecological questions in microbial biogeography. Due to the decreases in the cost of sequencing and rapid development of computational tools, more large-scale studies of MTB will likely be conducted in the future thereby establishing a broader view of MTB ecology and biogeography.

Magnetosome biomineralization

Although the composition of the magnetosome is well conserved across MTB, i.e. magnetite or greigite,

MTB vary widely with respect to the number of magnetosomes per cell as well as their magnetosome crystal shape, size and arrangement (Pósfai *et al*., 2013). Genetic, genomic, molecular and biochemical studies facilitated the identification of a group of genes involved in magnetosome biomineralization (Grünberg *et al*., 2001). A prominent feature of these magnetosome genes is that many are conserved in all available MTB genomes over a broad taxonomic/phylogenetic range (Jogler and Schüler, 2009; Nakazawa *et al*., 2009; Abreu *et al*., 2011; Jogler *et al*., 2011; Cornejo *et al*., 2014; Lin *et al*., 2014c; Deng *et al*., 2016; Kolinko *et al*., 2016; Barber-Zucker and Zarivach, 2017). In all sequenced MTB genomes, these genes are clustered and in some, the clusters have features (e.g. transposase genes, insertion sequences that flank the magnetosome genes) that suggest they represent a magnetosome gene island (MAI) (Schüler, 2008; Komeili, 2012). Part of a magnetosome gene cluster (MGC) was initially identified in *M. gryphiswaldense* MSR-1 (Grünberg *et al*., 2001). Additional genes clusters were further identified in other *Magnetospirillum* strains, which were transcribed as several operons (e.g. *mamAB*, *mamGFDC* and *mms6* operons) (Arakaki *et al*., 2003; Schübbe *et al*., 2003; Scheffel *et al*., 2008; Murat *et al*., 2012). More recently, in the context of comparative genomics, rather than MAI, the term MGC appears more appropriate because the magnetosome genes in some MTB are not associated with typical features of genomic islands (e.g. *Mc. marinus* MC-1; (Schübbe *et al*., 2009)) and in many MTB (e.g. magnetotactic *Nitrospirae*) the transcriptional structure is not known (Lin *et al*., 2014c). In the best studied systems, those of *Magnetospirillum* strains MSR-1 and AMB-1, $>$ 30 genes located within a 98–130 kb section of DNA have been identified as being involved in magnetosome membrane biogenesis, magnetosome membrane chain arrangement and magnetosome biomineralization (Murat *et al*., 2010; Lohße *et al*., 2011; Nudelman and Zarivach, 2014; Araujo *et al*., 2015).

Comparison of the MGCs in several genomes of MTB that biomineralize both magnetite and greigite (e.g. '*Candidatus* Desulfamplus magnetomortis' strain BW-1 and '*Ca*. Magnetomorum' strain HK-1) revealed two sets of magnetosome genes; one set that is similar to the magnetite gene clusters in *D. magneticus* strain RS-1 and a separate set that is closely related to those in the greigite-producing '*Ca*. Magnetoglobus multicellularis' (Lefèvre *et al*., 2013b; Kolinko *et al*., 2014b). These genomic comparison results strongly suggest that the two sets of MGCs may control the formation of magnetite and greigite magnetosomes separately, which, however, remains to be experimentally proven. Both sets of genes contain several core *mam* genes that play essential roles in magnetosome formation and arrangement (Lefèvre and Wu, 2013). Other types of magnetosome genes, including as *mamGFDC* (Scheffel *et al*., 2008), *mamXY* (Richter *et al*., 2007), *mms* (Arakaki *et al*., 2003; Ullrich *et al*., 2005; Matsunaga *et al*., 2009; Murat *et al*., 2010; 2012; Lohße *et al*., 2011; Staniland and Rawlings, 2016; Yamagishi *et al*., 2016), *mad* (Lefèvre *et al*., 2013b; Rahn-Lee *et al*., 2015) and *man* genes (Lin *et al*., 2014c; Kolinko *et al*., 2016) appear to be involved in important accessory functions in magnetosome biomineralization in different taxonomic groups of MTB. The gene content and the gene synteny within MGCs differ in MTB of different taxonomic groups, indicating that the organization of MGCs is dynamic in evolutionary terms which may account for the diverse morphologies and arrangements of magnetosomes in MTB from various environments.

Even with our increasing information regarding MGCs in different MTB, due to their patchy distribution across different phylogenetic lineages, it has been difficult to infer their origin and evolution. It has been proposed that the magnetotaxis might have arisen independently in phylogenetically distinct groups of MTB (DeLong *et al*., 1993). However, another hypothesis suggests that the MGC evolved only once and may have been distributed, possibly as a genomic island, to different bacteria by extensive horizontal gene transfer (Jogler *et al*., 2009a; Jogler and Schüler, 2009). Recent analyses have shown a general congruence of phylogenetic trees based on 16S rRNA gene and amino acid sequences of some essential magnetosome proteins in the *Proteobacteria* phylum suggesting a monophyletic origin of magnetotaxis in this group (Lefèvre *et al*., 2013a; Zeytuni *et al*., 2015). Using genome-centric metagenomic and phylogenetic analyses of deep-branching MTB from the *Nitrospirae* phylum, it has been shown that the phylogenies based on five core magnetosome proteins from the *Proteobacteria* and *Nitrospirae* phyla and their codon usage patterns similarities to that of the genomic phylogeny and vertically transmitted housekeeping genes, respectively, support an ancient origin of magnetosome biomineralization. In addition, this also suggests that magnetotaxis existed prior to the separation of the *Nitrospirae* and *Proteobacteria* phyla, or that the genes for magnetotaxis were transferred early between organisms at the base of these phyla soon after divergence (Lin *et al*., 2017). A molecular clock analysis places the divergence of the *Nitrospirae* and *Proteobacteria* phyla in the mid-Archean before 3.0 Ga, suggesting that MTB are the earliest geomagnetic field-sensing and biomineralizing organisms on Earth (Lin *et al*., 2017).

Although results from recent studies indicate an ancient origin of magnetotaxis and biomineralization in bacteria, the latter evolution, transfer and rearrangement of MGCs among different phylogenies remain unclear. The consistent phylogenies between core magnetosome

proteins and 16S rRNA genes strongly suggest a general coevolution between core *mam* genes and their genomes; however, the evolution of accessory magnetosome genes (e.g. *mms*, *mad* and *man*) is still unknown. In addition, magnetosome genes may horizontally transfer between some MTB species. For example, a small 'magnetosome islet' containing several homologues of *mam* genes was identified in *M. magneticum* strain AMB-1 was probably acquired independently through HGT (Rioux *et al*., 2010). Comparative metabolic network analysis suggests a metabolic potential that may support the biosynthesis of magnetosomes in some MTB conferred by HGTs (Ji *et al*., 2017). Taken together, it appears that magnetosome biomineralization is an ancient metabolic pathway and the core magnetosome genes tend to be coevolved with their genomes. During evolution, genes in MGCs underwent genetic variation events (e.g. gene duplication (Hershey *et al*., 2016), acquisition and loss (Ji *et al*., 2017)) and in some cases, might transfer horizontally between particular MTB populations. Therefore, the evolution of MGCs in bacteria is more complicated than previously assumed. Additional sequence data of MGCs and genomes from different MTB phylogenies are required to better understand this dynamic process.

MGCs from public databases

The unexpected discovery of a MGC from the previously published genome of a *Latescibacteria* has led to the proposal that bacteria with the ability to biomineralize magnetosomes may be more diverse and ubiquitous than previously thought (Lin and Pan, 2015). Due to advances in sequencing technology, the amount of metagenomic data deposited in public databases continues to increase at an accelerating rate. Consequently, sequences that contain MGCs are relatively easily retrieved from these databases. To test this possibility, we performed a non-exhaustive search of MGCs from public metagenomic databases of GenBank (Benson *et al*., 2005) and IMG/ER (Markowitz *et al*., 2014). Here we define an assembled contig as the MGC-containing contig (MGC-C) as it harbours at least two orthologues of known magnetosome genes. In this case, we identified six MGC-Cs from different environments, including marine oxygen minimum zones (contigs I-1 and I-2 in Fig. 2), groundwater biofilm samples (contig I-3), estuary sediments (contigs G-1 and G-3) and deep marine subsurface sediment (contig G-2).

Of these 6 MGC-Cs, four contigs (I-1, I-2, I-3 and G-3) contain genes that are most similar to magnetite-producing magnetosome genes, suggesting that they are from bacteria that biomineralize magnetite magnetosomes (Fig. 2 and Table S1). The content and order of magnetosome genes in contigs I-1 and I-2 represent high similarity to the MGC from the gammaproteobacterial MTB strain SS-5 (Lefèvre and Wu, 2013). The phylogeny based on concatenated magnetosome protein amino acid sequences also indicates their close relationship with strain SS-5 (Fig. 2B), suggesting that these two contigs are novel MTB belonging to the *Gammaproteobacteria*. Contig I-3 from groundwater biofilm samples and contig G-3 from estuary sediment show a conserved gene order and high protein identity to the MGCs from '*Ca*. Magnetobacterium casensis' (Lin *et al*., 2014c) and '*Ca*. Magnetobacterium bavaricum' (Kolinko *et al*., 2016) in the *Nitrospirae* phylum (Fig. 2), suggesting that these contigs likely originate from magnetotactic *Nitrospirae*. In fact, the contig G-3 belongs to a draft genome of 'Nitrospira bacterium SG8–35-4' that was assembled from sulfate-rich zone estuary sediments (sediment depth 8–12 cm) of the White Oak River in North Carolina (Baker *et al*., 2015).

Contigs G-1 and G-2, on the other hand, contain magnetosome genes closely related to greigite-producing *mam* genes from '*Ca*. Desulfamplus magnetomortis' strain BW-1 and '*Ca*. Magnetomorum' strain HK-1 (Fig. 2). Interestingly, contig G-1 is from a draft genome belonging to the phylum *Planctomycetes* from the sulfate-methane transition zone estuary sediments (sediment depth 16–26 cm) in the White Oak River, North Carolina (Baker *et al*., 2015). Members of *Planctomycetes* are ubiquitous in freshwater, marine, oceanic abyssal sediments and soils and possess an unusual intracellular compartmentalization (Fuerst and Sagulenko, 2011). The *Planctomycetes* have previously been grouped with the phyla *Verrucomicrobia*, *Chlamydiae*, *Lentisphaerae* and *Ca*. Omnitrophica (OP3) that now form the PVC superphylum (Kamneva *et al*., 2013). Interestingly, a magnetite-producing MTB within the phylum *Ca*. Omnitrophica has been described (Kolinko *et al*., 2012). Considering the presumptive identification of greigite magnetosome genes from the phylum *Planctomycetes* in this study, it is therefore likely that some members in the PVC superphylum biomineralize magnetosomes and are magnetotactic. This finding, together with the recent discovery of a MGC from the candidate phylum *Latescibacteria* (Lin and Pan, 2015) suggests that our knowledge on the diversity of MTB, particularly of greigite-producing MTB, is still very limited.

Another intriguing finding is that contig G-2, although short, was retrieved from deep-sea subsurface sediments (0.8 m below seafloor) in the northwestern Pacific (water depth: 1,180.5 m) (Kawai *et al*., 2014). This is, to our knowledge, the first finding of magnetosome genes from organisms present in the deep subseafloor, suggesting that greigite-producing MTB survive in the organic-rich subseafloor sedimentary biosphere and

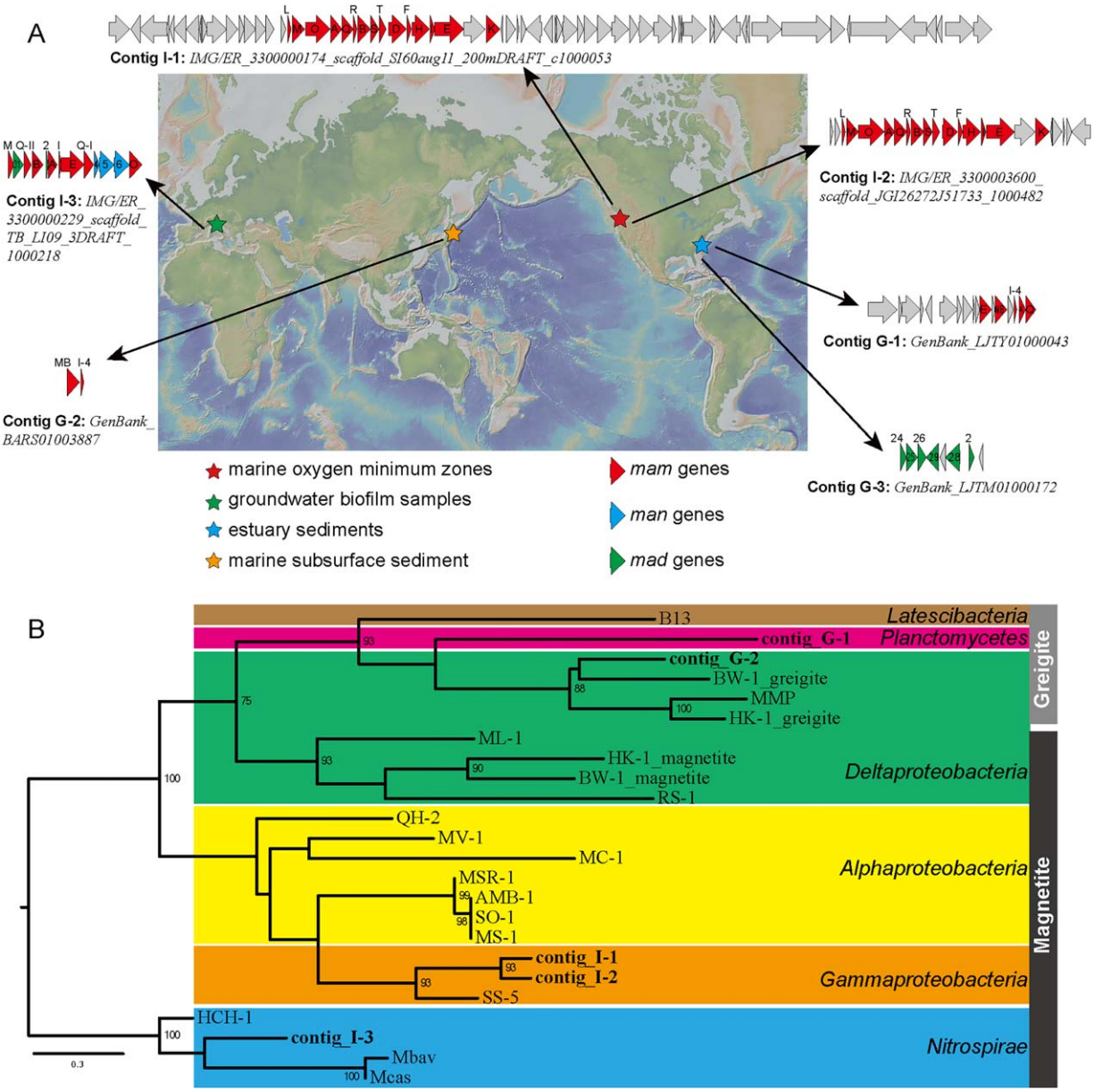

Fig. 2. A. Six magnetosome gene cluster-containing contigs (MGC-Cs) identified from public databases and their retrieval locations. B. Maximum-likelihood phylogenetic tree based on a concatenation of protein sequences of MamI and MamM. The amino acid sequences of magnetosome proteins were aligned using MUSCLE (Edgar, 2004), and poorly conserved regions were trimmed using Gblocks (Castresana, 2000). ProtTest v3.4 (Darriba *et al.*, 2011) was used to estimate the best model of evolution for the protein sequences. The tree was built using RAxML v8.2.8 (Stamatakis, 2014) with LG + G model, and 100 bootstrap replicates were estimated. MTB of *Nitrospirae* were used as outgroups to root the tree, and only bootstrap values of more than 75% are shown.

may catalyse some important geochemical transformations in this deep-sea environment. Overall, this case study indicates a hidden world of MTB information in published datasets and illustrates the actual ubiquity of MTB in both temperate and extreme ecosystems.

Omics-based analyses of MTB

Most of the previous ecological studies on MTB were based on cultivation-independent 16S rRNA gene-targeting analyses, such as clone library sequencing and FISH, which are powerful approaches to characterize the diversity and biogeography of MTB in nature. However, these approaches are somewhat limited in the physiological detail they can provide because they are based only on a single gene. To better understand the evolution, biomineralization and environmental function of MTB it is crucial to decipher their metabolic and ecological potentials from their genomes. Full genomic

sequences are available from some MTB in pure culture including *M. magneticum* AMB-1 (Matsunaga *et al*., 2005), *M. gryphiswaldense* MSR-1 (Richter *et al*., 2007; Wang *et al*., 2014), *Mc. marinus* MC-1 (Schübbe *et al*., 2009), *D. magneticus* RS-1 (Nakazawa *et al*., 2009), *Magnetospira* strain QH-2 (Ji *et al*., 2014) and marine magneto-ovoid strain MO-1 (Ji *et al*., 2017).

Recent technological and computational advances have driven the discovery of draft genomes from uncultivated MTB lineages, mainly through two methods that include single-cell genomics and metagenomics. Single-cell genomics is particularly important in that the DNA from a single cell from environmental samples can be amplified and sequenced (Lasken and McLean, 2014). It is thus a powerful tool to sequence the genome of microorganisms that are in very low abundance in samples but can be separated from other organism, in this case, magnetically. Using this approach, several novel MTB populations and their draft genomes have been characterized (Arakaki *et al*., 2010; Jogler *et al*., 2011; Kolinko *et al*., 2012; 2013; 2014b; 2016). In contrast to single-cell genomics, metagenomics has allowed for the assembly and analysis of entire genomic sequences from complex microbial communities, providing an efficient approach to explore their overall microbial diversity and genomic information (Riesenfeld *et al*., 2004; Simon and Daniel, 2011). The use of metagenomics resulted in the first discovery of MGCs from uncultivated MTB (Jogler *et al*., 2009b). In addition, a metagenomic survey identified several 16S rRNA gene-containing contigs from novel lineages of magnetotactic *Nitrospirae* (Lin *et al*., 2011). Targeted (meta)genomics enabled the reconstruction of draft genomes from the uncultured deltaproteobacterial MTB '*Ca*. Magnetoglobus multicellularis' (Abreu *et al*., 2011; 2014) and magnetotactic *Nitrospirae* 'Ca. Magnetobacterium casensis' (Lin *et al*., 2014c).

The rapid development of metagenomic methods, high-throughput DNA sequencing and efficient computational tools now allows for the rapid assembly of reliable DNA reads and binning of genomic contigs/scaffolds directly from metagenome datasets (Brown *et al*., 2015; Evans *et al*., 2015). It is now even possible to extract not only genomes of individual species but also low-abundance strain-level genomes from the metagenome data (Albertsen *et al*., 2013; Cleary *et al*., 2015). This metagenome-based genome recovery has recently been successfully applied to studies of MTB (Lin *et al*., 2017). A high-quality nearly complete genome of an uncultivated *Nitrospirae* MTB '*Ca*. Magnetominusculus xianensis' strain HCH-1 (HCH-1) was recovered from a metagenome of environmental MTB through a combination of similarity- and composition-based binning approaches (Lin *et al*., 2017). The 16S rRNA gene of HCH-1 shares 100% sequence identity with the *Nitrospirae* MTB fosmid MY3–11A previously identified from the same location, the cells of which were coccoid-to-ovoid that were much smaller (1–2 $\times$ 0.5–1 μm) than their *Nitrospirae* counterparts (e.g. '*Ca*. Magnetobacterium casensis' and '*Ca*. Magnetobacterium bavaricum') (Lin *et al*., 2011). This genome expands our view of genomic diversity and microevolution in magnetotactic *Nitrospirae*. In sum, these studies demonstrate the great opportunity provided by using high-throughput metagenomic approaches to deep our knowledge of genomic and metabolic potential of uncultivated MTB.

MTB are important in driving the global iron cycle on earth

MTB are recognized as having a great potential in the global geochemical cycling of a number of important elements including sulfur, nitrogen and carbon (Cox *et al*., 2002; Lin *et al*., 2014b). Here, because of the biomineralization of magnetosomes, we address the role of MTB in global iron cycling. As the most abundant element in the Earth overall and the fourth most abundant element in the crust, iron is an essential nutrient for nearly all organisms. However, iron, as unchelated Fe(III), is largely insoluble under oxic conditions such as those found on most of the oxygenated Earth. This is recognized to limit primary productivity in oceans (Kendall *et al*., 2012). It has been reported that the increased supply of iron to some regions of the ocean (e.g. areas of high-nutrient and low-chlorophyll) would stimulate phytoplankton growth and result in lowering atmospheric CO_2 (iron fertilization or the iron hypothesis) (Martin and Fitzwater, 1988; Martin *et al*., 1994). Therefore, iron plays a key role in Earth's ecosystems and climate change. It is now clear that microbes act as important engines that drive global iron cycling (Melton *et al*., 2014). The key reason that MTB are likely to contribute to global iron cycling is their ability to synthesize magnetosomes that contain nano-sized crystals of magnetite and/or greigite (Bazylinski and Frankel, 2004; Bazylinski *et al*., 2013). As a result of magnetosomes, the intracellular iron content of MTB is about 100- to 1,000-fold higher than that in other microorganisms. Because of their ubiquity and sometimes high cell numbers in aquatic and sedimentary environments, they account for a significant proportion of the local microbial biomass (Simmons and Edwards, 2007a; Faivre and Schüler, 2008). Based on this information, it was estimated that MTB could generate $> 10^8$ kg of magnetite per year (Lin *et al*., 2014a), compared with about 10^9–10^{10} kg of dissolved iron produced annually through mid-ocean ridge axial hydrothermal venting (Li *et al*., 2014). The stability of iron within magnetosomes, whether in cells or

released from lysed cells in the environment, is also important to consider as magnetite and greigite might represent either sources of bioavailable iron or unavailable sequestered iron depending on whether these minerals are stable or dissolve under environmental conditions where they were deposited (Roberts, 2015). Where magnetosome magnetite has shown to be stable, the crystals have been referred to as magnetofossils and have been used, even in ancient sediments ~2 Gya as evidence for the previous and/or current presence of MTB (Kopp and Kirschvink, 2008; Roberts *et al*., 2013; Roberts, 2015). These general findings indicate a significant role for MTB in present-day global iron cycling and likely in the deposition of iron in sediments across geological history.

Concluding remarks

It is now well established that MTB play an important role in global iron cycling and represent a significant contribution to natural remanent magnetism of sediments (Pan *et al*., 2005a; Roberts *et al*., 2011; 2013; Lin *et al*., 2014a). Ecological and database surveys document the occurrence of MTB in both temperate and extreme habitats, making them truly ubiquitous in aquatic and sedimentary ecosystems. After more than four decades of research, however, there is still very much to be learned about MTB. The discovery of MGCs from novel phyla (e.g. *Latescibacteria* and *Planctomycetes*) turns our view of MTB diversity in new directions. Moreover, focussed studies of MTB from extreme environments will hopefully shed light on the origin and evolution of magnetotaxis and biomineralization. An in depth understanding of MTB diversity and ecology is clearly required for the accurate assessment of their environmental functions and roles, particularly in geochemical cycling.

The increasing availability of 16S rRNA- and omics-based surveys provides promising opportunities to better investigate the ecology and biomineralization of MTB. In the near future, due to the advances in sequencing method and computational technology, large-scale metagenomic sequencing from a range of environments will provide valuable genomic information on uncultivated MTB. These omics-based analyses will provide information on the genetic and metabolic potentials of environmental MTB that will undoubtedly be useful in the isolation and cultivation of new strains. We also predict that novel magnetosome genes or MGCs, identified by omics-based approaches, may be useful in generating new, synthetic magnetosome minerals by transfer of gene fragments to model MTB strains and even non-MTB strains (Kolinko *et al*., 2014a).

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Author contributions

All authors conceived of the study, wrote the manuscript and approved it for publication.

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Supporting Information

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

Table S1. Details of coding sequences (CDSs) from the 6 magnetosome gene cluster-containing contigs.