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Diversity and Taxonomy of Magnetotactic Bacteria

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Abstract Studies of the diversity of magnetotactic bacteria (MTB) benefit from the unique advantage that MTB can be readily separated from sediment particles and other bacteria based on their magnetotaxis. This is the reason why current knowledge on MTB diversity relies to a lesser extent on the isolation and characterization of pure cultures, the classical tool of microbiology, than in other groups of microorganisms. Microscopy of magnetotactic enrichments retrieved from various environmental samples has consistently revealed significant morphological and ultrastructural diversity of MTB. However, of the many morphotypes detected, including spirilla, cocci, vibrios, ovoid, rod-shaped and even multicellular bacteria, only few bacteria could so far be brought into pure culture. The taxonomy of MTB is therefore heavily based on comparative sequence analysis of their 16S rRNA genes which can be investigated without prior cultivation. Based on 16S rRNA sequence similarity MTB are polyphyletic. Most of the MTB pure cultures and many of the so far uncultured phylotypes cluster within the *Alphaproteobacteria*, but MTB have also been affiliated to *Deltaproteobacteria*, to the phylum *Nitrospira*, and, tentatively, also to *Gammaproteobacteria*.

1 Introduction

The studies on the diversity of magnetotactic bacteria (MTB) benefit from the unique advantage that MTB can be readily separated from sediment

particles and other bacteria based on their magnetotaxis. Because of this, current knowledge on MTB diversity relies to a lesser extent on the isolation and characterization of pure cultures, the classical tool of microbiology, than in other groups of microorganisms. Also, the microscopy of magnetotactic enrichments retrieved from various environmental samples has consistently revealed significant morphological and ultrastructural diversity of MTB. However, of the many morphotypes detected, including spirilla, cocci, vibrios, ovoid, rod-shaped and even multicellular bacteria (Fig. 1), only few bacteria could so far be brought into pure culture. The taxonomy of MTB is therefore heavily based on comparative sequence analysis of their 16S rRNA genes which can be investigated without prior cultivation (Amann et al. 1995). Based on 16S rRNA sequence similarity MTB are polyphyletic. Most of the MTB pure cultures and many of the so far uncultured phylotypes cluster within the *Alphaproteobacteria*, but MTB have also been affiliated to *Deltaproteobacteria*, to the phylum *Nitrospira*, and, tentatively, also to *Gammaproteobacteria* (Fig. 2). In the following we summarize the current knowledge on MTB diversity along the groupings suggested by 16S rRNA.

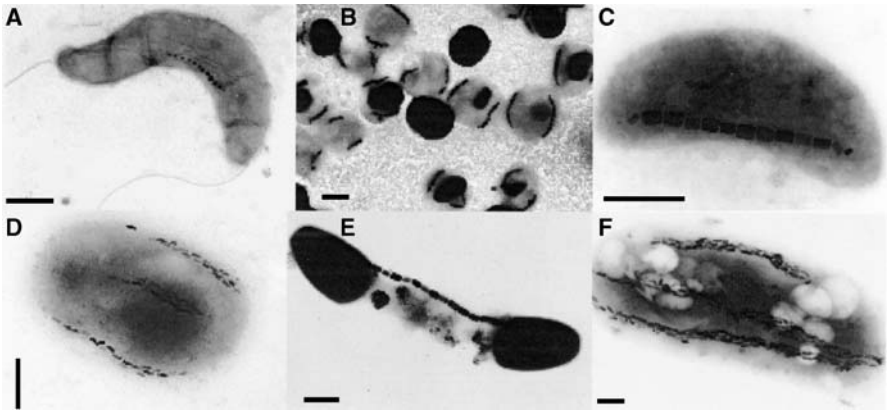

Fig. 1 Transmission electron micrographs showing characteristic cell morphologies of various magnetotactic bacteria. The diversity of abundant morphotypes includes spirilla (**A**), cocci (**B**), vibrios (**C**), ovoid forms (**D**), and large rods (**E**,**F**). *Scale bar* represents 0.5 μm (part (**D**) courtesy of Christine Flies)

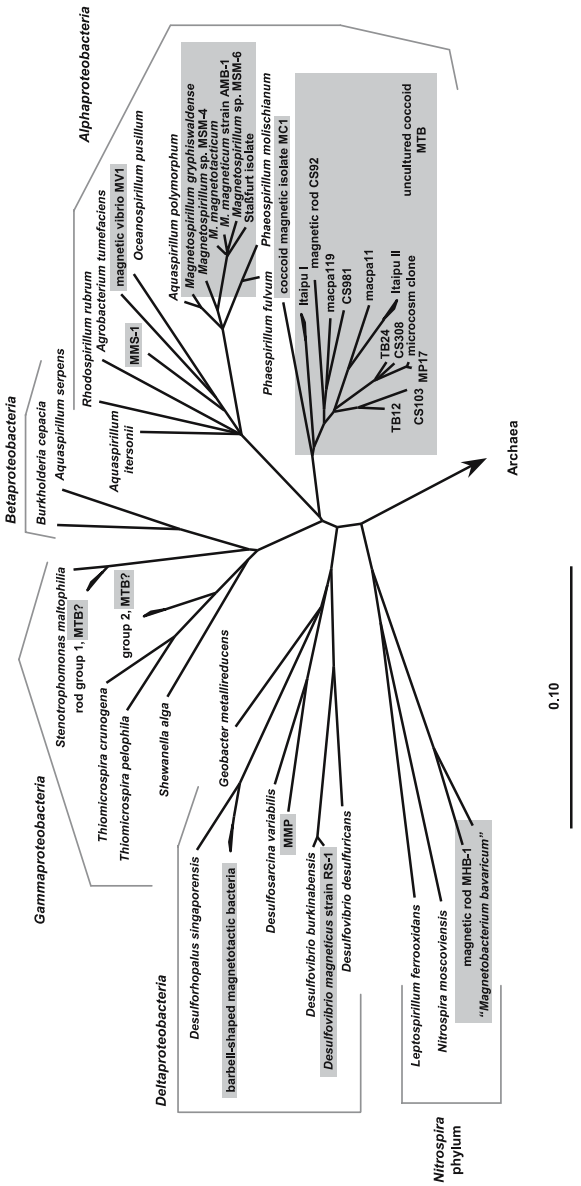

Fig. 2 16S rRNA-based tree reconstruction showing the phylogeny of magnetotactic bacteria (*grey boxes*). The tree is based on neighbor joining analyses and was corrected according to the results of maximum likelihood and maximum parsimony methods using the ARB program package (Ludwig et al. 2004). Multifurcations were drawn whenever branching orders were not stable. The tree topology is based on almost full-length 16S rRNA sequences. The partial sequences of strains CS103, MC-1, MV-1, and MMP have been added with the parsimony tool without allowing changes of the overall tree topology (Ludwig et al. 2004). *Bar* = 10% estimated sequence divergence

2
Alphaproteobacterial MTB

2.1
The Genus *Magnetospirillum*, Encompassing Heterotrophic Culturable MTB

The first MTB isolate had originally been named "*Aquaspirillum magnetotacticum*" (Blakemore et al. 1979). In 1991 Schleifer, Schüler and coworkers (Schleifer et al. 1991) studied the two pure cultures available at that time. Both are magnetospirilla of a width of 0.2–0.7 μm and a length of 1–3 μm. The ultrastructure is also highly similar with respect to the arrangement (single chain of up to 60 magnetosomes), size (diameter approximately 40–45 nm) and cubo-octahedral crystal structure of magnetosomes as well as flagellation (single flagella at each pole). The 16S rRNA sequences were closely related to each other (94%) and clustered with that of *Alphaproteobacteria* whereas the 16S rRNA sequence of the type species of the genus *Aquaspirillum, A. serpens*, clusters with that of *Betaproteobacteria*. In parallel, the 16S rRNA sequence of *A. magnetotacticum* was also determined by Eden and coworkers (Eden et al. 1991). Consequently, the genus *Magnetospirillum* and the two species *Magnetospirillum magnetotacticum* (formerly "*Aquaspirillum magnetotacticum*") and *Magnetospirillum gryphiswaldense* were created (Schleifer et al. 1991; Schüler and Schleifer 2005).

In 1993 it was shown (Burgess et al. 1993) that the 16S rRNAs of two facultatively anaerobic strains of magnetic spirilla (AMB-1 and MGT-1) share 98–99% similarity with that of *M. magnetotacticum* but only 95–96% to that of *M. gryphiswaldense*. Further diversity of magnetospirilla was revealed by a study of Schüler, Spring and Bazylinski (Schüler et al. 1999) in which a new two-layer isolation medium with opposing oxygen and sulfide gradients was used for cultivation. With this technique seven strains of microaerophilic magnetotactic spirilla could be isolated from one freshwater pond in Iowa, USA. While the 16S rRNA sequences of five of the isolates (MSM-1,-6,-7,-8,-9) were very similar to either *M. gryphiswaldense* or *M. magnetotacticum* (> 99.7%), two (MSM-3, MSM-4) may represent an additional group. In a recent study, novel magnetotactic spirilla strains were isolated from various freshwater habitats including a ditch and several ponds in Northern Germany (Flies et al. 2005). Again, 16S rRNA analysis affiliated them all with the genus *Magnetospirillum* with highest similarity to strain MSM-6. Although by now only two species have been validly named, the diversity within this genus of culturable MTB is significant. It is likely that an in-depth taxonomic study would result in the valid description of additional species.

The 16S rRNA sequence similarity between *Magnetospirillum gryphiswaldense* and *M. magnetotacticum* of 96% is similar to that shared by *Magnetospirillum* spp. and members of the photoorganoheterotrophic, nonmagnetotactic genus *Phaeospirillum* (formerly *Rhodospirillum*) (Fig. 2). Fur-

thermore, with 98% 16S rRNA similarity the non-magnetotactic *Aquaspirillum polymorphum* is significantly closer to *M. gryphiswaldense* than *M. magnetotacticum*. Recently, more bacteria have been isolated which are based on a 16S rRNA sequence similarity of about 95%, morphology, and physiology similar to *Magnetospirillum* spp., but lack the capability to form magnetosomes (Coates et al. 1999; Shinoda et al. 2000). Based on the different phenotypes in otherwise closely related and physiologically similar strains of *Magnetospirillum* it is tempting to speculate whether either *A. polymorphum* represents a magnetospirillum strain that recently lost genes essential for magnetotaxis, or *M. gryphiswaldense* has recently acquired the set of genes responsible for magnetosome formation. If the former scenario applies, *A. polymorphum* should be renamed *Magnetospirillum polymorphum*. Further taxonomic investigations are required to clarify the evolutionary relationships of these magnetic and non-magnetic spirilli.

Interestingly, spirillum-shaped morphotypes represent only a minority of the mostly coccoid to rod-shaped MTB in primary enrichments obtained from aquatic environments based on magnetotaxis. However, during subsequent attempts of pure culture retrieval the magnetospirilla outcompete the other morphotypes (Spring and Schleifer 1995). Many of the MTB have therefore only been phylogenetically identified based on cultivation-independent 16S rRNA-based comparative sequence analysis and fluorescence in situ hybridization (FISH) of single bacterial cells with 16S rRNA-targeted oligonucleotide probes (Amann et al. 1995).

2.2 Other Cultivated Alphaproteobacterial MTB

Dennis Bazylinski was the first to isolate MTB other than *Magnetospirillum* strains in pure culture, which included a magnetic vibrio (strain MV-1) (Bazylinski et al. 1988), and a magnetic coccus (strain MC-1). Strain MC-1 represents the only so far cultured magnetotactic coccus and was isolated from brackish water collected from the Pettaquamscutt Estuary (Rhode Island, USA). The name *Magnetococcus marinus* is being proposed for this strain (D.A. Bazylinski, personal communication 2006). Comparative 16S rRNA sequence analysis affiliated the two isolates, which both contain iron oxide magnetosomes and can grow either chemoheterotrophically or chemolithoautotrophically, with the *Alphaproteobacteria* (DeLong et al. 1993) (Fig. 2). Isolate MC-1 is grouping with other, yet uncultured magnetococci (discussed in detail below), whereas MV-1 is closer to *Magnetospirillum*.

Two novel magnetotactic marine spirillum strains designated MMS-1 and MMS-2 were isolated (see chapter by Bazylinski and Williams, this volume). Although not fully characterized, preliminary analysis suggest that MMS-1 and MMS-2 represent a new genus within the *Alphaproteobacteria* and have no close phylogenetic relatives (T.J. Williams and D.A. Bazylinski, personal

communication 2006). The new isolate MMS1 warrants further taxonomic studies since it is a new phylotype that based on a 16S rRNA sequence similarity of only 90% species with MV-1 could represent a new genus of culturable MTB.

2.3 Uncultured Alphaproteobacterial MTB

When upper sediment layers of Lake Chiemsee—a large, mesotrophic freshwater lake in Upper Bavaria, Germany—was stored on a laboratory shelf protected from direct light for several weeks, high numbers of magnetotactic bacteria enriched right beneath the water-sediment interface (Spring et al. 1992). Magnetotactic enrichments encompassed four distinct morphotypes: abundant cocci, two big rods of distinct morphology (one slightly bent and therefore originally referred to as "big vibrio" (Spring et al. 1992)), and small vibrios. Partial 16S rRNA genes were PCR-amplified directly from the enriched cells, singularized by cloning in *E. coli*, and sequenced. Most of the retrieved sequences grouped with 16S rRNA sequences of *Alphaproteobacteria*. FISH with three 16S rRNA-targeted oligonucleotide probes constructed complementary to signature regions of the most frequent alphaproteobacterial sequences (CS, for Chiemsee, 103, 308, and 310) identified three discrete subpopulations of the cocci. Simultaneous applications of two differentially labeled probes showed differences in abundance and taxis: magnetococci of genotype CS308 dominated over coccal genotypes CS103 and CS310, and, under the influence of a magnetic field, cells of genotype CS103 were predominantly entrapped nearest to the agarose solution-air interface.

In 1994, Spring and coworkers used the cultivation-independent approach to retrieve another three partial and seven almost full length 16S rRNA gene sequences from freshwater sediments of various sites in Germany (Spring et al. 1994). By FISH all sequences were assigned to magnetotactic bacteria, nine to magnetotactic cocci and one to the rod-shaped magnetotactic phylotype CS92. The magnetotactic rod shared a 16S rRNA similarity of 90–92% with the magnetotactic cocci, indicating affiliation in a new genus. Most cocci shared 16S rRNA similarities of less than 97%, suggesting that they represent different species. All sequences grouped with those earlier retrieved from the uncultured Chiemsee magnetotactic cocci (Spring et al. 1992).

Another rRNA-based study on the phylogeny and in situ identification of MTB addressed enrichments from the Itaipu lagoon near Rio de Janeiro (Spring et al. 1998). These were dominated by coccoid-to-ovoid morphotypes. Some of the cells produced unusually large magnetosomes that with a length of 200 nm and a width of 160 nm are almost twice as big as those found in other magnetotactic bacteria (Farina et al. 1994). Sequencing of 16S rRNA genes revealed two clusters (Itaipu I and II) of closely related sequences within the lineage of magnetotactic cocci (Spring et al. 1992, 1994; Thornhill

et al. 1995). In order to link at high resolution the ultrastructure of the enriched cells with their 16S rRNA sequence a new methodology was applied. In situ hybridizations were performed with digoxigenin- and fluorescein-labeled polynucleotide probes on ultrathin sections of embedded magnetotactic bacteria. For probe synthesis one representative clone of each of the two closely related 16S rRNA clusters was used as a template for in vitro transcription of a 230 nucleotide long variable region at the 5′ end of the 16S rRNA. A bound polynucleotide probe was detected by incubation of the sections with gold-labeled antibodies specific for fluorescein or digoxigenin. The gold labels could then be detected in the electron microscope. This enabled for the first time a detailed description of the ultrastructure of in situ identified single MTB: the unusually large magnetosomes were only found in ovoid magnetotactic bacteria of the Itaipu I 16S RNA genotype.

Cox and coworkers investigated the diversity of magnetotactic cocci in Baldwin Lake (Los Angeles) by restriction fragment length patterns (RFLP) analysis (Cox et al. 2002). They found several 16S rRNA sequences, which reportedly had high similarities to known magnetotactic cocci from the database. In addition, they identified six sequences, which formed a monophyletic cluster (ARB-1 cluster) related to, but distinct from other magnetotactic bacteria (89% similarity to the magnetotactic rod CS92). Unfortunately, these sequences are currently not accessible in public databases.

Recently, Flies and coworkers (Flies et al. 2005) have investigated the diversity of magnetotactic bacteria in various microcosms with freshwater and marine sediments from Germany and Sweden by DGGE and amplified ribosomal DNA restriction analysis (ARDRA) of the 16S rRNA genes. Initially, the sediments contained a highly diverse population of magnetotactic bacteria displaying a variety of different morphotypes. However, the magnetotactic population in the microcosms underwent a rapid succession, which usually resulted after several weeks of incubation in the dominance of a magnetotactic coccus affiliated with the *Alphaproteobacteria*.

While most MTB 16S rRNA sequences were identified after magnetic enrichment, sequences putatively originating from marine MTB have been repeatedly found without magnetic manipulation. For instance, Riemann and coworkers retrieved two sequences when investigating the bacterial community composition in the Arabian Sea by DGGE analysis (Riemann et al. 1999). Both sequences were nearly identical to each other and closely related (95% similarity) to that of an uncultivated magnetotactic coccus from a freshwater habitat. This indicates that MTB may also occur in the water column in significant numbers. Alternatively, these sequences may represent closely related non-magnetotactic species.

3
A Gammaproteobacterial Greigite-Producing Rod?

In 2004, Edwards and coworkers reported preliminary evidence for the existence of magnetotactic gammaproteobacteria in a seasonally stratified coastal salt pond (Simmons et al. 2004). At the sulfide-rich base of the chemocline in the meromictic Salt Pond, Falmouth, Massachusetts, the authors have found morphologically conspicuous, large (approximately 5 μm long, 3 μm wide) slow-moving rods. These were shown by transmission electron microscopy to contain irregular shaped electron-dense inclusions resembling magnetosomes. A single crystal electron diffraction pattern corresponded to that of greigite. A 16S rDNA library obtained from a sample highly enriched in the slow-moving rod contained 42% sequences with affiliation to *Gammaproteobacteria*. Two clone groups dominated, one with 99% similarity to *Stenotrophomonas maltophila*, and a second with about 90% similarity to *Thiomicrospira* spp. To further confirm that the newly identified large rod-shaped greigite-producing bacterium is a gammaproteobacterium the authors performed FISH with the group-specific 23S RNA-targeted probe GAM42a (Manz et al. 1992). Binding of this probe does, however, not allow to unambiguously link either one of the two dominant or one of the other diverse gammaproteobacterial sequences to the large magnetotactic rod. Furthermore, the group-specific probe GAM42a is outdated and should only be used as part of probe sets, but not as a stand-alone tool for phylogenetic assignments (Musat et al. 2006). Although further experiments are clearly required to unambiguously prove the existence of gammaproteobacterial MTB, these findings might suggest that the diversity of uncultivated MTB goes beyond previously identified groups.

4
Deltaproteobacterial MTB: The Isolate *Desulfovibrio magneticus* RS-1, and Two Yet-Uncultured Unusual MTB

The magnetosomes of most MTB contain magnetite (Fe_3O_4), but some MTB collected from sulfidic, brackish-to-marine aquatic habitats are made of greigite (Fe_3S_4). The 16S rRNA sequence retrieved from an uncultured many-celled, magnetotactic prokaryote (MMP) with iron sulfide magnetosomes collected at various coastal sites in New England was specifically related to the dissimilatory sulfate-reducing bacteria within the *Deltaproteobacteria* (DeLong et al. 1993) (see also chapter by Farina et al., this volume). The closest relative at that time was *Desulfosarcina variabilis* with a 16S rRNA similarity of 91% (DeLong et al. 1993). The assignment of MMP to *Deltaproteobacteria* together with the earlier assignments of *Magnetospirillum* spp., isolates MC-1 & MV-1, and the uncultured magnetococci to multiple groups within

the *Alphaproteobacteria* was the first clear evidence for a polyphyletic origin of MTB. The authors also argue that their findings suggest that magnetotaxis based on iron oxide and iron sulfide magnetosomes evolved independently. They state that the biochemical basis for biomineralization and magnetosome formation for iron oxide-type and iron sulfide type bacteria are likely fundamentally different and speculate that in two independent phylogenetic groups of bacteria analogous solutions for the problem of effective cell positioning along physicochemical gradients were found based on intracellular particles with permanent magnetic dipole moments (DeLong et al. 1993).

In 1995 the group of Matsunaga (Kawaguchi et al. 1995) reported the comparative 16S rRNA sequence analysis of a sulfate-reducing MTB pure culture, RS-1, originally described in 1993 (Sakaguchi et al. 1993). This isolate affiliates with the genus *Desulfovibrio* of the *Deltaproteobacteria*. It was accordingly named as *Desulfovibrio magneticus* strain RS-1 and represented the first bacterium outside the *Alphaproteobacteria* that contains magnetite inclusions (Sakaguchi et al. 1993, 2002). It therefore disrupts the correlation between the alpha and deltaproteobacterial magnetotactic bacteria and iron oxide (magnetite) and iron sulfide (greigite) magnetosomes, respectively, suggested by DeLong and coworkers (DeLong et al. 1993).

A barbell-shaped population was recently reported from a narrow layer immediately below the oxygen-sulfide interface in Salt Pond (Falmouth, MA) when enriching for South-seeking magnetotactic bacterium in the Northern hemisphere (Simmons et al. 2006). This morphotype consists of short chains of 2 to 5 cocci. It was shown by 16S rRNA-based sequencing and FISH with a specific oligonucleotide probe to be another deltaproteobacterium affiliated with the genus *Desulforhopalus*.

5 MTB in the *Nitrospira* Phylum: "*Magnetobacterium bavaricum*" and More

MTB are not restricted to *Proteobacteria*. A large (approximately 5–10 μm long, and 1.5 μm wide) rod-shaped magnetic bacterium has been enriched from the calcareous sediments of a few freshwater lakes in Upper Bavaria, including Lake Chiemsee (Vali et al. 1987). Based on its 16S rRNA this conspicuous morphotype, tentatively named "*Magnetobacterium bavaricum*", was affiliated with the *Nitrospira* phylum (Spring et al. 1993). This independent bacterial phylum encompasses few other isolates including the iron-oxidizer *Leptospirillum ferrooxidans* and the chemolithoautotrophic nitrite oxidizer *Nitrospira moscoviensis*. The magnetosomes of "*M. bavaricum*" were shown to consist of the iron oxide magnetite (N. Petersen, personal communication 2006). It contains up to 1000 hook-shaped magnetosomes with a length of 110–150 nm, often arranged in several chains. The large cells are gram-negative, contain sulfur globules, and are mobile by one polar tuft of flagella.

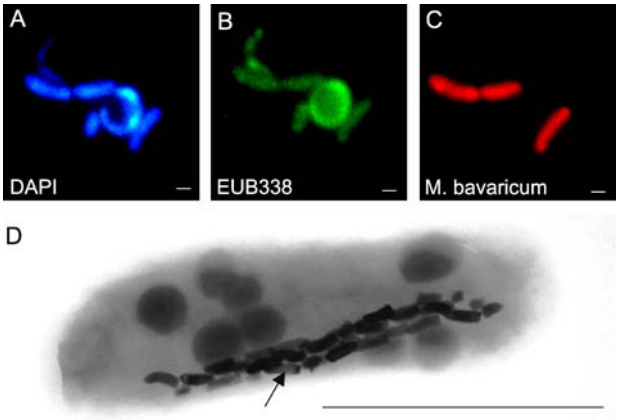

Fig. 3 Micrograph images of MHB-1, a novel magnetotactic rod of the *Nitrospira* phylum, which is closely related to "*Magnetobacterium bavaricum*": DAPI stain (**A**), cells hybridized with a bacterial probe EUB338 (**B**) and a probe for "*M. bavaricum*" (**C**), electron micrograph of MHB-1 (**D**). *Scale bar* represents 1 μm; *arrow* indicates magnetosomes (redrawn after Flies et al. 2005)

As is the case for many other MTB, microbiologists were hitherto unable to grow "*M. bavaricum*" in pure culture. Recently, it was, however, shown that the occurrence of MTB from the *Nitrospira* phylum is apparently not restricted to Bavaria. A conspicuous rod (MHB-1) was magnetically collected from sediment of Waller See, a lake nearby Bremen (Flies et al. 2005). The magnetosomes from MHB-1 display the same bullet-shaped crystal morphology like those from "*M. bavaricum*" (Fig. 3) and are aligned in multiple chains. The cells hybridized with the FISH probe originally used for the identification of "*M. bavaricum*" (Spring et al. 1993). However, unlike the latter organism, MHB-1 has fewer magnetosomes, which form a single bundle. Based on a 16S rRNA sequence similarity of 91% to "*M. bavaricum*", the genotype MTB-1 is a candidate for a new species, "*Magnetobacterium bremense*", if not a new genus, indicating that there is also significant diversity within the MTB of the phylum *Nitrospira*.

6 Final Remarks on MTB Phylogeny

Based on 16S rRNA sequences MTB are phylogenetically diverse, with representatives in *Alphaproteobacteria*, *Deltaproteobacteria* and in the *Nitrospira* phylum. In addition several recent studies suggested that MTB diversity is far from being fully explored. Considering the recent discovery of a potentially mobile magnetosome island (Schübbe et al. 2003; Ullrich et al. 2005) this is, however, not ruling out that biomineralization of magnetite magnetosomes

is still monophyletic, and spread by lateral gene transfer. This hypothesis could be investigated by comparative sequence analysis of the genes involved in the magnetosome formation. Did lateral gene transfer, e.g., from the alphaproteobacterial magnetotactic bacteria to "*M. bavaricum*" contribute to the spreading of magnetite-based magnetotaxis? Or, have mechanisms of magnetosome formation independently developed in the different phylogenetic groups? Studies of this type will not necessarily rely on cultured strains since large DNA fragments are now routinely retrieved from the environment (Stein et al. 1996). The analysis of large contiguous sequences harboring such islands might be an extremely powerful approach to gain further insights in the genetic diversity of biomineralization mechanism of MTB.

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