Unravelling the diversity of magnetotactic bacteria through analysis of open genomic databases

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Magnetotactic bacteria (MtB) are prokaryotes that possess genes for the synthesis of membrane-bound crystals of magnetite or greigite, called magnetosomes. Despite over half a century of studying MtB, only about 60 genomes have been sequenced. Most belong to Proteobacteria, with a minority affiliated with the Nitrospirae, Omnitrrophica, Planctomycetes, and Latescibacteria. Due to the scanty information available regarding MtB phylogenetic diversity, little is known about their ecology, evolution and about the magnetosome biomineralization process. This study presents a large-scale search of magnetosome biomineralization genes and reveals 38 new MtB genomes. Several of these genomes were detected in the phyla Elusimicrobia, Candidatus Hydrogenedentes, and Nitrospinae, where magnetotactic representatives have not previously been reported. Analysis of the obtained putative magnetosome biomineralization genes revealed a monophyletic origin capable of putative greigite magnetosome synthesis. The ecological distributions of the reconstructed MtB genomes were also analyzed and several patterns were identified. These data suggest that open databases are an excellent source for obtaining new information of interest.

Introduction

The amount of data obtained from genome and metagenome sequencing has been sharply increasing for the last several years1. These data are kept in open databases, such as the widely used NCBI2 and IMG3 databases. In the case of IMG, the number of entries for metagenomic data greatly exceeds that for genomic ones3. In most cases, scientists use only a part of the sequencing information uploaded to the databases, leaving large quantities of information essentially unanalyzed. This gives the possibility that the obtained data may contribute to other studies and shorten the time and efforts of other scientists. In the present study, data stored in open genomic and metagenomic databases were used to search for magnetosome biomineralization genes related to magnetotactic bacteria (MtB).

The MtB are a group of organisms characterized by the ability to synthesize magnetosomes, which are crystals of magnetite (Fe₃O₄) or greigite (Fe₃S₄) enveloped by a lipid membrane4. These crystals can be applied in medicine as contrast agents for MRI5 and for treating tumors using magnetic hyperthermia6, and they are also of great interest in geology7–9 and astrobiology10. The synthesis of magnetosomes is controlled by the magnetosome gene cluster (MGC), previously called the magnetosome island or MAI. The MGC comprises genes that control magnetosome biosynthesis and that determine magnetosome morphology and chemical composition. The MGCs are unique and are associated only with MtB. The genes essential to the biomineralization process are called mam (magnetosome membrane) genes. Nine of them (mama, -b, -m, -k, -p, -q, -e, -o, and -i), are present in all MGCs11,12. In addition to the mam genes, genes specific to certain groups may also occur; for instance, mad genes are found in MtB from the Deltaproteobacteria and Nitrospirae, while man genes are present only in the Nitrospirae13.

At present, only about 60 MtB genomes are known, and most are affiliated with the phyla Proteobacteria, Nitrospirae, and Ca. Omnitrophica. Recently, MtB genomes associated with Latescibacteria14 and Planctomycetes15 have been found in open databases, implying that these databases could contain substantial amounts of new information about MtB.

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Table 1. Characteristics of genomes with MGCs obtained from the NCBI and IMG database genomic data.

| Organism | Phylum/Class | Accession in NCBI/IMG | Size (bp) | Scaffolds (no.) | GC (%) | N50 (bp) | CheckM completeness (%) | CheckM contamination (%) |
|----------|--------------|-----------------------|-----------|----------------|--------|----------|------------------------|------------------------|
| Magnetovibrio sp. ARS8 | Alphaproteobacteria | GCA_002868765.1 | 2019305 | 197 | 59.64 | 10605 | 62.87 | 1.00 |
| Elusimicrobia bacterium NORP12 | Elusimicrobia | GCA_002401485.1 | 2913226 | 191 | 54.93 | 19622 | 74.06 | 1.82 |
| Unclassified Nitropina Bin 25 | Nitrospirae | 2651870060 | 4158979 | 431 | 37.69 | 11956 | 92.31 | 4.27 |
| Planctomycetes bacterium SCGC_JGI090-P21115 | Planctomycetes | 2264265205 | 1230646 | 242 | 49.20 | 12722 | 38.87 | 2.19 |

To date, due to the lack of sufficient amounts of genomic data, little is known about the origin and evolution of MGCs\(^{15}\). Thus, additional investigations are needed to determine the mono- or polyphyletic origin of the MGCs, their evolutionary history, and whether the original MGCs were responsible for magnetite or greigite biomineralization.

This article describes the first large-scale search of magnetosome biomineralization genes in open genomic and metagenomic databases. Bioinformatics analysis of the search results allowed new MTB genomes to be obtained. Taxonomic assignments for the studied genomes provided the first evidence of their affiliation to new MTB taxonomic ranks, including three new phyla. These results significantly expanded the knowledge of MTB diversity. The analysis of the ecological distribution of the reconstructed MTB genomes helped to identify several new patterns. Further comparative analysis of MGCs and marker genes of studied genomes allowed new data to be obtained concerning the origin and evolution of magnetosome biomineralization genes.

Results

The search for magnetosome biomineralization genes in open databases. The search for MTB genomes in open databases was guided by detecting MGCs unique to magnetotactic bacteria. Unfortunately, MGC sequences are not annotated as magnetosomal in open databases. This necessitated the use of previously known sequences of MGCs as search targets. The search was further complicated by the low identity values between the sequences of the same MGC gene in different MTB taxonomic groups. To cover the maximum number of new MTB representatives, MGC protein sequences were drawn from all known taxonomic groups where MTB were found previously. For this purpose, a database was created of known MGC protein sequences\(^{12-43}\) (Supplementary Table S1). The database included 67 MGCs from Proteobacteria, Nitrospirae, Ca. Omnitrophica, Latesicibacteria, and Planctomycetes. The sequences of nine Mam proteins present in all MGCs were used to conduct BLASTp with genomic data from the NCBI and IMG databases. This resulted in the detection of four new genomes containing magnetosome biomineralization genes (Table 1, Supplementary Table S2).

The use of all nine Mam proteins in metagenomic databases is complicated by the fact that much more data is kept in metagenomic than in genomic ones. To hasten the search process, one Mam protein out of nine common ones that met the required parameters was chosen for further BLAST analysis. The first chosen parameter was the identity between sequences from different taxonomic groups in each protein. The low values of these identities allowed exclusion of MamE, MamO, and MamP proteins from the analysis. The remaining MamA, -B, -M, -K, -I, and -Q proteins were assessed for sequences with the highest -ln of e-values, in addition to high identities (Fig. 1a). MamI was the least consistent with these requirements and was not used in further analyses. By contrast, MamK was the most consistent.

Each Mam protein has its homologs in non-MTB that are not involved in the magnetosomes biomineralization process. These homologs should be avoided when searching for MGCs. For this, Mam protein was chosen whose identities and -ln of e-values were significantly varied from these parameters in homologs (Fig. 1b). MamK showed the best result in this case, and its minimum identity and -ln e-value between sequences were 30 and 135, respectively. However, part of homologs had identities and -ln of e-values similar to the values found between Mam protein sequences. These homologs were confirmed not to be Mam sequences by verifying their phylogenetic separation (Fig. 1c). The sequences of each Mam protein formed monophyletic clades, while MamK formed two clades. Despite this, no homologs were observed inside the MamK clades. Based on all the investigated parameter results, the MamK protein sequences were chosen for the MGC gene search in the open databases.

The MamK protein sequences were used for BLAST for 10587 metagenomes from water, terrestrial, engineered, and host-associated ecosystems. The analysis revealed 2798 sequences potentially affiliated with the MamK protein (Supplementary Fig. S1a). Their scaffolds were checked for the presence of other Mam protein sequences. After that, 227 MamK sequences referring to 135 metagenomes were obtained (Supplementary Tables S3 and S4). These and previously known MamK sequences were used to construct a phylogenetic tree (Supplementary Fig. S1b), which revealed that the identified MamK sequences were not closely related to previously known sequences. This assumes that they could refer to taxonomic groups in which MTB were not found before.

Metagenome binning, phylogenomic inferences, and MGC reconstruction. The phylogenetic position of genomes to which the MamK sequences belonged was assessed by conducting metagenome binning, and it yielded 14688 metagenome-assembled genomes (MAGs) (Supplementary Table S3). Two metagenomes were also determined to be single-cell amplified genomes (SAGs), so no binning procedures were required for...
them. Of all the MAGs obtained in this study, only 140 contained previously detected MamK sequences. For those of the 140 whose completeness was >45% decontamination was conducted. This left 32 MAGs with completeness >45% and contamination <10% that contained MGCs (Table 2, Supplementary Table S6). The phylogenomic affiliations of the obtained MAGs, SAGs, and genomes were then determined, the MGCs genes were reconstructed, and the ecological distributions were studied.

The identification of the phylogenomic position of the studied genomes revealed, for the first time, their affiliation to the phyla Elusimicrobia, Ca. Hydrogenedentes, and Nitrospinae (Supplementary Fig. S2, Supplementary Tables S2 and S5). One genome was affiliated with the phylum Elusimicrobia and referred to order UBA1565 in the Elusimicrobia class. After MGC reconstruction, the mamI, -B, -M, and -N genes were revealed in the investigated genome (Fig. 2). Two MAGs from Ca. Hydrogenedentes belonged to the same species (98.70% average nucleotide identity), but they were obtained independently from different metagenomes. These MAGs referred to the GCA-2746185 family in the order Hydrogenedentiales. The 16S rRNA gene from the Ca. Hydrogenedentes bacterium MAG_17971_hgd_13044 had 90% similarity with the closest non-MTB Ca. Hydrogenedentes bacterium YC-ZSS-LKJ63. All these data confirmed that the obtained binning results were regular and did not represent a computational error. Only mam genes were found in the MGCs of the studied genomes.

In the Nitrospinae phylum, two MAGs were affiliated with different genera of the order Nitrospinales. Their MGCs revealed the presence of mam and mms (magnetic particle-membrane specific) genes. Samples for the metagenomes of the obtained MAGs were collected from the Gulf of Mexico58 and Arctic Ocean waters. Non-MTB representatives of this phylum were also detected only in marine habitats46,47, indicating that bacteria from the Nitrospinae could prefer to inhabit marine environments.

The 14 reconstructed MAGs belonged to different families of Deltaproteobacteria. Of the 14, three MAGs were affiliated with the UBA8499 genus in the Pelobacteraceae family. In their MGCs, apart from the mam and mad genes, which are typical for Deltaproteobacteria, the man genes were detected for the first time. Previously, the man genes were associated only with MTB from the Nitrospirae. Another two MAGs were affiliated with the Syntrophobacteraceae family, where MTB were discovered previously41. This is further evidence that binning was conducted correctly and that MTB representatives are indeed present in this family.

Three genomes also belonged to the Desulfobulbales order. Of these, the Desulfovibrio bacterium MAG_22309_dsv_0228 contained man3 gene in addition to the mam and mad genes, thereby confirming the routine presence of man genes in Desulfotherbacteria. A further four MAGs were related to the NaphS2 family in the Desulfitoglanales order. Analysis of their MGCs revealed genes responsible for putative greigite magnetosome synthesis. Metagenomic samples of the studied genomes were obtained from marine sediments, as well as all other known non-MTB genomes of this family46,47.

**Fig. 1** The choice of Mam protein for further searching for MGCs in open databases. (a) Correlations between –ln of e-values (x axis) and identities (y axis) among MamA, -B, -M, -K, -I, and -Q proteins sequences. (b) Correlations between identities and –ln of e-values among Mam protein sequences with their homologs. (c) Phylogenetic trees based on investigated sequences. Trees were reconstructed by the maximum-likelihood method with LG + F + I + G4 substitution model. Bootstrap values were calculated based on 1000 resamplings. Bar represents one substitution per 100 amino acid positions.
Organism | Phylum/Class | Metagenome accession in NCBI/IMG | Size (bp) | Scaffolds (no.) | GC (%) | N50 (bp) | CheckM completeness (%) | CheckM contamination (%)  
--- | --- | --- | --- | --- | --- | --- | --- | ---  
Ca. Hydrogenedentes bacterium MAG_17963_hgd_1118 | Ca. Hydrogenedentes | 3300017963 | 3018788 | 288 | 60.18 | 11662 | 71.11 | 1.46  
Ca. Hydrogenedentes bacterium MAG_17971_hgd_130 | Ca. Hydrogenedentes | 3300017971 | 2683901 | 240 | 60.43 | 12541 | 60.01 | 1.16  
Deltaproteobacteria bacterium MAG_00134_naph_006 | Deltaproteobacteria | 330000134 | 1498667 | 692 | 49.54 | 2676 | 71.11 | 3.87  
Deltaproteobacteria bacterium MAG_00241_naph_010 | Deltaproteobacteria | 330000241 | 1547003 | 324 | 49.45 | 6761 | 55.59 | 2.41  
Deltaproteobacteria bacterium MAG_00792_naph_016 | Deltaproteobacteria | 330000792 | 1498667 | 692 | 49.54 | 2676 | 71.11 | 3.87  
Deltaproteobacteria bacterium MAG_09788_naph_378 | Deltaproteobacteria | 3300009788 | 899797 | 137 | 47.24 | 7579 | 49.08 | 0.97  
Deltaproteobacteria bacterium MAG_15370_sntb_261 | Deltaproteobacteria | 3300015370 | 2777907 | 276 | 53.10 | 17193 | 62.13 | 5.10  
Deltaproteobacteria bacterium MAG_15929_sntb_209 | Deltaproteobacteria | 3300015929 | 1691080 | 454 | 53.11 | 4033 | 50.53 | 2.33  
Deltaproteobacteria bacterium MAG_22204_dsfv_001 | Deltaproteobacteria | 3300022204 | 3868622 | 334 | 48.42 | 14397 | 89.68 | 5.59  
Deltaproteobacteria bacterium MAG_22309_dsfv_022 | Deltaproteobacteria | 3300022309 | 2902378 | 66 | 55.15 | 78905 | 91.60 | 1.79  
Gammaproteobacteria bacterium MAG_00150_gam_010 | Gammaproteobacteria | 330000150 | 2847655 | 486 | 49.07 | 8986 | 98.17 | 3.96  
Gammaproteobacteria bacterium MAG_00160_gam_009 | Gammaproteobacteria | 330000160 | 2903803 | 318 | 49.10 | 15339 | 99.39 | 4.88  
Gammaproteobacteria bacterium MAG_00172_gam_018 | Gammaproteobacteria | 330000172 | 2866084 | 274 | 48.97 | 18904 | 96.95 | 3.05  
Gammaproteobacteria bacterium MAG_00188_gam_006 | Gammaproteobacteria | 330000188 | 2866084 | 274 | 48.97 | 18904 | 96.95 | 3.05  
Gammaproteobacteria bacterium MAG_00212_gam_198 | Gammaproteobacteria | 330000212 | 2103212 | 955 | 48.40 | 2901 | 78.43 | 5.08  
Gammaproteobacteria bacterium MAG_00215_gam_020 | Gammaproteobacteria | 330000215 | 2931288 | 507 | 49.02 | 8845 | 95.73 | 5.34  
Magnetococcales bacterium MAG_21055_mgc_110 | Magnetococcales | 3300021055 | 3585593 | 930 | 52.41 | 5203 | 84.82 | 3.65  
Nitrospinae bacterium MAG_09705_ntspn_701 | Nitrospinae | 3300009705 | 2024644 | 120 | 42.63 | 30902 | 67.25 | 2.56  
Nitrospirae bacterium MAG_10313_ntr_311 | Nitrospirae | 3300010313 | 1933163 | 344 | 48.33 | 6818 | 95.12 | 4.19  
Pelobacteraceae bacterium MAG_21601_9_030 | Pelobacteraceae | 3300021601 | 2536371 | 232 | 54.11 | 20074 | 78.15 | 8.39  
Pelobacteraceae bacterium MAG_13126_9_058 | Pelobacteraceae | 3300013126 | 3575652 | 72 | 52.01 | 83631 | 91.61 | 1.29  
Pelobacteraceae bacterium MAG_21600_9_004 | Pelobacteraceae | 3300021600 | 3430740 | 60 | 51.50 | 87052 | 90.32 | 0.65  
Planctomycetes bacterium MAG_11118_pl_115 | Planctomycetes | 3300011118 | 3767441 | 157 | 48.98 | 33372 | 89.44 | 1.24  
Planctomycetes bacterium MAG_17991_pl_601 | Planctomycetes | 3300017991 | 2847655 | 486 | 49.07 | 8986 | 98.17 | 3.96  
Rhodospirillaceae bacterium MAG_04806_dm_210 | Rhodospirillaceae | 3300004806 | 2085124 | 309 | 57.51 | 8435 | 87.64 | 2.12  
Rhodospirillaceae bacterium MAG_05422_2-02_143 | Rhodospirillaceae | 3300005422 | 2281835 | 255 | 61.09 | 11800 | 85.45 | 0.50  
Rhodospirillaceae bacterium MAG_05596_2-02_517 | Rhodospirillaceae | 3300005596 | 1831947 | 329 | 61.19 | 6777 | 76.91 | 0.25  
Rhodospirillaceae bacterium MAG_06104_dm_334 | Rhodospirillaceae | 3300006104 | 3186839 | 353 | 64.25 | 13005 | 89.59 | 2.53  
Ca. Omnitrophica bacterium SCGC AG-290-C17 (SAG) | Ca. Omnitrophica | 3300001513 | 1712617 | 171 | 48.60 | 13921 | 62.84 | 0.00  
Uncultured microorganism SbSrfc.SA12.01.D19 (SAG) | Uncultured microorganism | 3300022116 | 2501480 | 175 | 52.60 | 25257 | 49.13 | 0.00  

Table 2. Characteristics of reconstructed MAGs with MGCs obtained from the IMG metagenomic data.
In Alphaproteobacteria, three MAGs and one genome were related to a 2-02-FULL-58-16 family in the Rhodospirillales order. Metagenomic samples of the studied genomes were isolated from marine ecosystems. The other non-MTB genomes of this family were also detected only in marine ecosystems. For the first time, two MAGs containing MGCs were also detected in Tectonococcus genus. Their metagenomic samples were collected from a freshwater bog. Tectonococcus siberiensis, the only known representative of this genus, was also isolated from freshwater peat soil. Thus, this group possibly tends to inhabit freshwater ecosystems. Reconstruction of the MAGs revealed mam and mms genes in the studied MAGs. One MAG was referred to the Ca. Etaproteobacteria class. Genomes from this class previously were found in both saline and freshwater habitats. The obtained MAG clustered with genomes isolated from freshwater environments. The MGC of the recovered MAG revealed a standard gene set inherent to MTB from this class. A further six MAGs were affiliated with the Gammaproteobacteria. All of these were sampled from one source and had 100% identity between their genes. Only the mam genes were detected in their MGCs.

The Nitrospirae phylum was affiliated with one MAG. A metagenomic sample of this phylum was obtained from a hot spring. Previously, other MTB and non-MTB from this phylum were also detected in hot springs. Three of the recovered MAGs belonged to the SG8-4 order in the Phycisphaeraceae class of Planctomycetes. Apart from the reconstructed MAGs, one SAG was also obtained from the UBA1845 order in Phycisphaeraceae class. The completeness of this SAG was very low (39%), but it was also taken into analyses due to the large number of mam genes detected in the MAG. Another detected SAG was affiliated with Ca. Omnitrophica and was referred to the GWA2-52-8 family in the Omnitrophales order. The MGC of this genome had a set of genes that were specific to all magnetotactic representatives from this phylum.

Reconstruction of the evolutionary pathways for MGCs. The identification of putative genes involved in magnetosome biomineralization allowed investigation of MGC evolutionary pathways. These were analyzed by constructing a phylogenetic tree of concatenated sequences (“Mam tree”, Fig. 3b) and comparing this tree with one based on 120 single-copy marker genes proteins (‘core genome tree’, Fig. 3a). Comparative analysis of the MTB position on the trees revealed some incongruences. For instance, the Deltaproteobacteria group from “core genome tree” was divided into three subgroups on the “Mam tree.” The first subgroup comprised representatives capable of putative greigite magnetosome synthesis, while the other two subgroups included representatives with MGCs for magnetite magnetosome biomineralization. One of the magnetite subgroups included representatives of the Pelobacteraceae, Syntrophia, and Desulfurivibrioaceae families, which clustered with the Nitrospirae. According to the “Mam tree” topology, the mam genes could be assumed to have originated in the Deltaproteobacteria and were inherited by the Nitrospirae through horizontal gene transfer. The compared trees also indicated vertical inheritance in the Alpha- and Ca. Etaproteobacteria groups, although the occurrence of horizontal transfer events was previously established in these groups. These types of transfers have been confirmed to have occurred recently, which is why they cannot be detected through the tree topology analysis.

A further investigation examined whether MGC originated once or more than once. This was done by adding the Mam protein sequences recovered in this study to previously known Mam protein sequences and their non-MTB homologs and then constructing phylogenetic trees (Supplementary Fig. S3). Analysis of the constructed trees confirmed the previous results showing that all Mam protein sequences, except for MamK, formed monophyletic clades and that these clades did not contain any homolog sequences. This indicates that the MGCs for magnetite and greigite synthesis are likely to have a common origin.

The magnetosome chemical composition in genomes of every phylum where MTB were known for the first time were predicted by counting the phylogenetic distances of the concatenated sequences of six essential Mam proteins (MamA, B, K, M, P, and Q) and conducting a principal component analysis (Fig. 4). All values clustered to three groups. First was the group that comprised Planctomycetes, and Latescibacteria, which are known to have genes for putative greigite magnetosome synthesis. The NaphS2 family of Deltaproteobacteria, Ca. Hydrogenedentes, and Elusimicrobia also fell into this group. The second group comprised representatives with magnetite magnetosome synthesis genes. The first magnetite group included Nitrospinae and all classes of Proteobacteria where MTB were known. The exception was the remaining studied classes of Deltaproteobacteria, which clustered with the second magnetite group, together with Nitrospirae.

Discussion

This study represents the first large-scale search of magnetosome biomineralization genes in open databases. Bioinformatic analysis of the gathered data almost doubled the number of MTB genomes from the 60 previously known; 4 genomes, 2 SAGs, and 32 MAGs were obtained as a result of this research. Besides, analysis of the database of collected MGC protein sequences revealed MamK as the most appropriate protein for MGC searching in open databases. This finding will allow the use of these putative protein sequences as markers for MTB detection in environmental samples.

This study also provides the first description of magnetosome biomineralization genes in the genomes of Elusimicrobia, Nitrospinae, and Ca. Hydrogenedentes. Non-MTB representatives of Elusimicrobia phylum were previously found as free-living and ecto- and endosymbionts of multicellular eukaryotes. MTB living symbiotically with eukaryotes have been detected previously. Further investigations are needed to solve the enigma of whether MTB from Elusimicrobia free-living or symbiotic organisms are.

To date, little is known about Ca. Hydrogenedentes, except for its genome presence. More is known about Nitrospinae, where one axenic culture was previously described. However, these reports do not give an extensive understanding of the capabilities of this phylum’s representatives. Thus, the detection of MGCs in genomes that belong to these phyla significantly supplements the knowledge of MTB diversity and evolution, while also providing new information about these phyla.
This work also gives much new information about groups where MTB were previously recognized. For instance, the relatively few genomes were affiliated with Alpha- and Ca. Etaproteobacteria, while the current belief is that representatives of these classes dominate among MTB in all natural environments. In addition, within the Alphaproteobacteria class, the presence of MGCs was discovered for the first time in genomes belonging to the "Tematospirillum" genus. This may indicate a common origin for magnetosome biominalization genes among the Magnetospirillum, Magnetotispira, and Magnetovibrio genera.

Furthermore, for the first time the presence of man genes was revealed in MGCs of the Deltaproteobacteria. Previously, these genes were found only in Nitrospinae. Whether horizontal gene transfer events occurred...
between representatives of these phylogenetic groups or their MGCs shared a common origin is not known. Further studies are required to determine which possibility is correct.

The genomes with magnetosome biomineralization genes obtained in this study allowed the investigation of the origin and evolution of the MGCs. A comparison of the "core genome" and "Mam" trees revealed clustering of the Deltaproteobacteria greigite subgroup sequences with the Planctomycetes, Latescibacteria, Ca. Hydrogenedentates, Ca. Omnitrophica, and Elusimicrobia phyla. Of these, Latescibacteria and Planctomycetes were already known to have MGCs for putative greigite synthesis. Note that Ca. Omnitrophica was also associated

Fig. 3 Maximum-likelihood phylogenomic trees of MTB genomes. Trees were inferred from a comparison of 120 concatenated single-copy marker proteins of MTB genomes (a) and concatenated magnetosome associated protein sequences (MamABKMPQ) (b). Both trees were reconstructed using evolutionary model LG+F+I+G4. Branch supports were obtained with 1000 ultrafast bootstraps. The scale bar represents amino acid substitutions per site.
with the greigite subgroup, although it is believed that they biomineralize magnetite magnetosomes. Such assumptions are based on Ca. Omnitrophus magnesiticus SKK-01 however, this genome is highly contaminated (Supplementary Table S1). Thus, further investigations are needed to study Ca. Omnitrophica magnetosome chemical composition.

In addition to all mentioned findings, the latest version of the bacterial tree of life, based on GTDB R04-RS89 reference data (Supplementary Fig. S4) helped to reveal the most ancient phylum in which MTB representatives were known. It was indicated that the Elusimicrobia phylum is the most closely related to the last universal common ancestor (LUCA). If the MTB of this phylum are assumed capable of greigite magnetosome synthesis, then greigite MGCs could have appeared much earlier than commonly believed, and the first MTB could have greigite, not magnetite, MGCs. The other phyla with MTB representatives in the vicinity of LUCA are Ca. Omnitrophica and Proteobacteria, although Nitrospirae MTB was previously thought to be the most ancient.

Considering the existing data regarding the presence of horizontal transfer events among MTB and analyzing the discrepancies in “core genome” and “Mam” trees, the proposal could be made that horizontal gene transfers occur much more often than previously thought and are of great importance in MGC evolution.

The genomes obtained in this work require further confirmation by morphological identification. Once confirmed, these data will allow a more thorough study of the contribution of vertical and horizontal gene transfer events with respect to MGC inheritance. The data obtained in the present work will allow the study of the environmental and metabolic preferences of newly discovered MTB genomes, which may become the key to isolating them in axenic cultures. Moreover, a detailed MGC analysis could help to find as yet unidentified genes that are involved in magnetosome synthesis and to reveal much about the biomineralization process.

Generally, in this work, it was shown that MamK is the most appropriate protein for MGCs detecting in open databases. The search results allowed to receive 38 new genomes containing MGCs, that were affiliated to both taxonomic groups where MTB were found before and three new phyla. Thus, received MTB genomes permitted to unravel the MTB diversity and can be used in further MTB studies or in receiving new information about these phyla. Also, a comparison of MTB position on “mam tree” and “core genome tree” helped to reveal signs of putative horizontal gene transfers. This led to assumptions that such MGC transfers could occur with higher frequency and probably play a much more important role in MGC evolution than it was previously thought. Moreover, a proposal was made that the origin of MGC probably is more ancient than it was suggested earlier and possibly was capable of greigite magnetosomes biomineralization rather than magnetite.

Thus, all received data allowed the expansion of knowledge about MTB diversity, ecology, and evolution and has opened up new opportunities for further searches for and investigations of magnetotactic bacteria.

Materials and methods
The search for magnetosome biomineralization genes in open databases. The search for magnetosome biomineralization genes was conducted by collecting a database of MGC protein sequences based on currently known MTB genomes (Supplementary Table S1). The search was provided using BLASTp analysis, with identity >30% and e-value >1e-95. Searches of the IMG and NCBI genomic databases used sequences of nine essential Mam proteins from different taxonomic groups as targets. The IMG metagenomic database was searched by BLASTp using MamK sequences. The sequences obtained from BLAST analysis were further checked to separate MGC proteins from their homologs. For this, each Mam protein sequence was checked for joint clustering by BLASTp using MamK sequences. The sequences obtained from BLAST analysis were further checked to separate MGC proteins from their homologs. For this, each Mam protein sequence was checked for joint clustering by BLASTp using MamK sequences. The sequences obtained from BLAST analysis were further checked to separate MGC proteins from their homologs. For this, each Mam protein sequence was checked for joint clustering by BLASTp using MamK sequences. The sequences obtained from BLAST analysis were further checked to separate MGC proteins from their homologs.

Genome reconstruction and analyses. Metagenome assembled genome (MAG) reconstruction was conducted using the Bumpyweb web, Maxbin2, and MyCC with standard parameters. The DAS Tool was used for choosing consensus assemblies for the obtained MAGs. Completeness and contamination values of genomes were obtained using lineage-specific marker genes and default parameters in CheckM v. 1.0.12. RefineM v. 0.0.24 was used to remove contamination based on taxonomic assignments. This process, called ‘decontamination,'
involves the classification of obtained genes and scaffolds in each MAG relative to the gene base with a known taxonomic classification. After that, scaffolds with incongruent taxonomic classifications are removed from the MAGs. The quality metrics were assessed using the QUAST tool. The average nucleotide identity (ANI) was calculated using fastANI. The MAGs were determined using local BLAST and comparison with reference sequences of magnetotactic bacteria.

**Phylogenetic analyses.** Taxonomic assignments for the studied genomes 16S rRNA genes were obtained using the GTDB 16S r89 dataset in IDTAXA. The GTDB-Tk v.0.1.375 'classify_wf' command was used to find 120 single-copy bacterial marker protein sequences, to construct their multiple alignments and to get the taxonomic assignment using the GTDB r86 database. Amino acid sequence sets of the MamA, -B, -M, -K, -P, and -Q proteins were independently aligned using MAFFT, curated with Gblocks with o.91b with an option that allows gap positions within the final blocks, and then concatenated. These Mam protein sequences were also used to build trees with their homologs. Maximum-likelihood trees were inferred with IQ-TREE using evolutionary models selected by ModelFinder. Branch supports were obtained with 1000 ultrafast bootstraps. Trees were visualized with iTOL. The genomes of *Ca. Omnitrophus magneticus* SKK-01, *Ca. Magnetoglobus multicellularis* str. Araruama, *Ca. Magnetobacterium bavaricum* TM-1, and *Ca. Magnetovoom chiemensis* CS-04 were not subjected to phylogenetic analyses because they had failed the quality check (Supplementary Table S1). Taxonomic classification of the obtained genomes on phylum rank was performed using NCBI taxonomy; other ranks were named using GTDB.

**Data availability**

The genomes and metagenomes used during the current study are publicly available in NCBI (https://www.ncbi.nlm.nih.gov/) and IMG (https://img.jgi.doe.gov/cgi-bin/m/main.cgi) databases. Scaffolds of obtained MAGs could be found in Supplementary Table S6, hosted at figshare. All data generated and analyzed in this study are also available in figshare and in supplementary information accompanying this paper. Assembly of Rhodospirillaceae bacterium MAG_01419_mvb_30 could be found in RAST (https://rast.nmpdr.org/) using 'guest' as login and as password.

**Code availability**

The following tools were used for the presented analysis and described in the main text:

Busybee web, Maxbin2, MyCC, and DAS Tool with standard parameters were used for the reconstruction of metagenome-assembled genomes (MAGs).

1. Busybee web https://ccb-microbe.cs.uni-saarland.de/busybee
2. Maxbin2 https://sourceforge.net/projects/maxbin2/
3. MyCC https://sourceforge.net/projects/sh2nhri/files/MyCC/
4. DAS Tool https://github.com/cmks/DAS_Tool
5. CheckM was used to estimate obtained genomes completeness and contamination https://github.com/Ecogenomics/CheckM
6. RefineM was used to remove contamination https://github.com/dparks1134/RefineM
7. QUAST helped to access quality metrics http://cab.spbu.ru/software/quast/
8. fastANI was used to calculate ANI https://github.com/ParBLiSS/FastANI
9. IDTAXA helped to obtain taxonomic assignments for the studied genomes 16S rRNA genes http://www2.decipher.codes/Classification.html
10. GTDB-Tk was used to find 120 single-copy bacterial marker protein sequences, to construct their multiple alignments and to get the taxonomic assignment using the GTDB r86 database https://github.com/Ecogenomics/GTDBTk
11. MAFFT was used for aligning amino acid sequence sets of the MamA, -B, -M, -K, -P, and -Q proteins https://mafft.cbrc.jp/alignment/server/
12. Gblocks helped to curate sequences aligned in MAFFT http://molevol.cmima.csic.es/castresana/Gblocks_server.html
13. Phylogenetic trees were inferred with IQ-TREE http://www.iqtree.org/
14. Obtained trees were visualized with iTOL https://itol.embl.de/

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Author contributions
M.U. and L.A. created MGC protein sequences database. M.U. conducted MGCs search, analyzed obtained data and wrote the manuscript. L.A. reconstructed MGCs of obtained genomes. M.K. conducted metagenomes binning. D.G. had the initial idea for the analysis. V.K. and D.G. discussed and interpreted the results and revised the manuscript. All authors read and approved the final manuscript.

Competing interests
The authors declare no competing interests.

Additional information
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