

Geographical Distribution of Culturable Magnetotactic Bacteria and their Magnetosome Morphology

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Abstract

Magnetotactic bacteria (MTB) play critical roles in environmental iron-cycling and magnetism which are tightly related with their geographical distribution. The geographical distribution pattern of culturable MTB can mirror their ecological function under various niches. In the present study, we analyzed 51 16S rDNA sequences of culturable MTB from the public database and literatures, and accordingly constructed phylogenetic trees to assess the difference among culturable MTB from freshwater and saltwater. Results show that the available culturable MTB are affiliated with Alpha-, Gamma-, and Deltaproteobacteria classes of the *Proteobacteria* phylum. Among them, the bullet-shaped magnetosome producing culturable MTB mainly belong to Deltaproteobacteria. Almost all culturable MTB distribute in the northern hemisphere except IT-1 and the number of culturable MTB decreased with the increase of latitude. Most culturable MTB (about 73%) distribute in freshwater, while others (about 27%) thrive in marine or saltwater environment. The culturable gammaproteobacteria MTB were found to only thrive in saltwater environment. and Fe_3S_4 magnetosome-producing MTB only occurred in the marine environment. These findings reflected that the ecological environment was closely related to the types of MTB.

Keywords: Magnetotactic Bacteria; Pure Culture; Geographic Distribution; Phylogeny; Magnetosome

Abbreviations

MTB: Magnetotactic bacteria; OAI: Oxic-Anoxic Interface

Introduction

Magnetotactic bacteria (MTB) are one of the best examples of microbial magnetic response. Magnetic minerals act as compasses inside them and help microorganisms move to water columns in the oxic-anoxic interface (OAI) [1]. MTB is a general term for microbes that are attracted by magnetic fields and tend to move in magnetic fields [2]. In 1891, Massachusetts first reported that the movement of bacteria was affected by magnetic fields [3]. The Italian scholar Bellini first reported that magnetically sensitive bacteria were found in freshwater in 1963 [4]. In 1975, American scholar Blakemore accidentally discovered and reported prokaryotes that could move along the line of magnetic fields [5]. MTB has no taxonomic significance. Based on the traditional phenotypic characteristics and phylogenetic methods

of 16s rRNA sequences, the diversity of MTB is very rich in nature, which is mainly reflected in morphology, physiology and phylogeny. MTB have been found to be single-celled coccoid, spirilloid, vibrioid, rod-shaped and multicellular magnetotactic prokaryotes [6]. Their physiological and metabolic types include micro-aerobic, facultative or exclusive anaerobic respiratory type, and can be cultivated under either autotrophic or heterotrophic conditions. MTB are associated with the Alpha-, Gamma-, and Deltaproteobacteria classes of the *Proteobacteria* phylum, *Nitrospirae* phylum, *Omnitrophica* phylum and probably with the candidate phylum *Latescibacteria* [5]. But they are all gram-negative bacteria and contain magnetosomes and exhibit magneto-aerotaxis and terminal or tufted flagella [7].

A key characteristic of MTB is that they can synthesize a type of iron compound particles *in vivo*, which is similar to the surface of eukaryotic organelles coated by biofilms-magnetosomes. Magnetosomes have the advantages of nanometer size, high saturation magnetization, and good biocompatibility, so it has a wide application prospect in biomedical, material science and many other fields [8]. Magnetosomes can also be an important carrier for the stable magnetic remanence in deep-sea sediments [9]. The ability of MTB to synthetic magnetosomes makes it play an important model organism for the study of biomineralization, and the research on it can provide important theoretical guidance for biomineralization. Hence, MTB play an important role in geochemical iron-cycling and sediment magnetism [10]. Although MTB have been widely studied, there are still some deficiencies in their geographical distribution and culture condition.

Therefore, the study on the geographical distribution characteristics of culturable MTB is very important to isolate and obtain more culturable MTB and to determine the culture conditions that are more suitable for it. This paper intends to further analyze the similarities and differences of MTB obtained from saltwater and freshwater. In this study, the 16S rDNA sequences of 51 strains of pure cultured MTB were analyzed in order to explore the geographical distribution characteristics of pure cultured MTB by constructing their phylogenetic tree.

Data Sources and Analysis Methods

Data source

The data used in this study come from articles published by authoritative institutions, such as NCBI, CNKI, VIP, Elsevier, Google, etc. and the search keywords include magnetotactic bacteria, *Magnetospirillum*, magnetosome, pure cultivability, geographical distribution and so on. After finding the identified pure culturable MTB, the data were screened strictly, and the cloned, impure culture and non-MTB were excluded.

Data collation and analyses

We found the corresponding taxonomic status and habitat, identified the country and morphological characteristics of the culturable MTB, and preserved the corresponding references. The corresponding strain sequence was downloaded from the gene bank and saved. The phylogenetic tree was constructed by the NnmurJ method with the MEGA7.0 software. Through the classification and comparison of MTB sequences from different countries and waters, the law of geographical distribution was explored.

Results

Distribution of culturable MTB in saltwater

At present, 14 strains of culturable MTB have been reported in saltwater, with the largest number of 11 strains in the United States and one strain each in China, France and Brazil. Alphaproteobacteria are mostly distributed in marine environment, mainly cocci and vibrio. Deltaproteobacteria are mainly isolated from saltwater, mostly bacilli (Figure 1). The average temperature of the isolation site is -4-25°C, with a neutral pH, but there are a few MTB living in extreme environments, such as the AV-1, ZZ-1, ML-1 strains, and their most suitable survival pH is 9.0 [11]. The salinity of culturable MTB living environments varies greatly. It has been found that the separation sites of

Magnetococcus of the Alphaproteobacteria, have relatively high salinity. The salinities of the separation sites of MO-1 and IT-1 are 38% and 55%, respectively [12,13]. Most of the MTB isolated from Gamma- and Deltaproteobacteria prefer a salinity below 5%, but the salinity of Mono Lake, where ML-1 is located, is as high as 75% [11]. Alphaproteobacteria MTB are mainly distributed in marine environments, while Gamma- and Deltaproteobacteria MTB are mostly obtained from saltwater lakes.

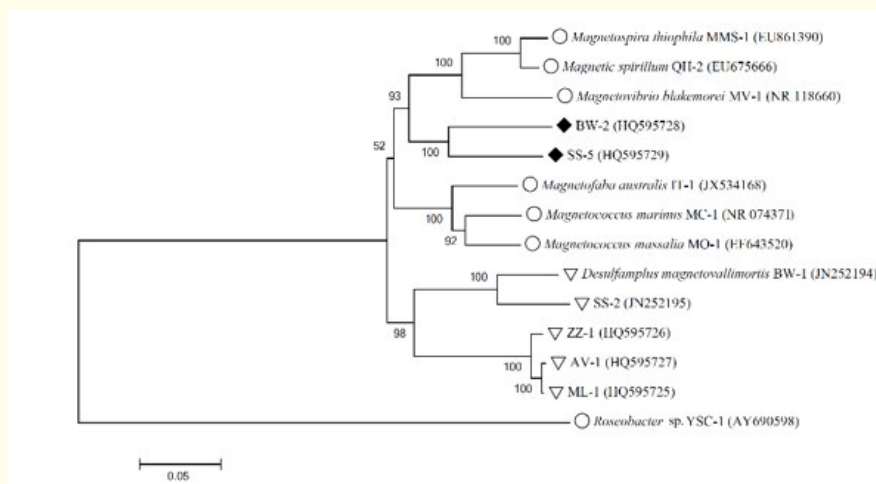


Figure 1: Phylogenetic tree based on partial sequences of 16S rDNA of culturable magnetotactic bacteria in salt water (○: Alphaproteobacteria, ▽: Deltaproteobacteria, ◆: Gammaproteobacteria).

Most cultured species of the Alphaproteobacteria classes grow chemo-organoheterotrophically, such as strain MV-1, which grows chemo-lithoautotrophically using reduced sulfur as an electron source and chemo-organoheterotrophically using organic acids and amino acids as electron and carbon sources [14]. MTB are mostly oligotrophic microorganisms. In pure culture, in order to prevent other non-magnetotactic microorganisms from over propagating, the concentration of organic acid should be controlled at a low level. MTB are known to biomineralize two magnetic minerals, Fe_3O_4 and Fe_3S_4 . For example, there are two different magnetosome gene clusters in BW-1, which is the only MTB that can synthesize two types of magnetosomes [15]. Magnetosomes exist as single or double strands, number about 15, and are between 35 and 120 nm in size, there are bullet, hexahedral and octahedral crystals. Phosphorus, sulfur particles, and lipid particles were also observed in MC-1, MO-1, and BW-2 cells [12,15,16].

Distribution of culturable MTB in freshwater

A total of 37 strains of culturable MTB were isolated from freshwater, mainly Alpha- and Deltaproteobacteria classes *Magnetospirillum* and *Desulfuricans*. *Desulfovibrio* was mainly isolated from Japan, and *Magnetospirillum* was majorly distributed in Russia and China. *Magnetospira* are dominant and include MSR-1, AMB-1, and MGT-1 (Figure 2) [17-19]. The main type of MTB respiration is micro-aerobic. The optimum temperature for the growth of MTB isolated from freshwater is about 30°C, and the optimum pH is between 5.0 and 8.0. All cultured species were either microaerophiles, anaerobes, or both. When this kind of MTB is cultured, a semi-solid or liquid medium is generally used to simulate the oxygen gradient of its living environment as far as possible. The physiological characteristics of pure cultured MTB in freshwater were not perfect. The analyses of the strains that have been identified at present shows that the pure cultured freshwater MTB bacteria are relatively small, about 2 - 4 μm long and 0.3 - 0.4 μm wide, with bipolar flagella. Most of their magnetosomes exist in single strands, but SpK strain magnetosomes exist in clusters or short chains [20].

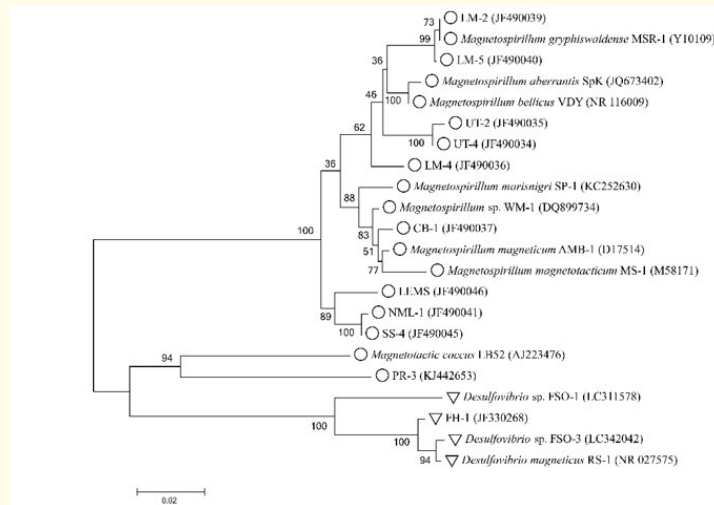


Figure 2: Phylogenetic tree based on partial sequences of 16S rDNA of culturable magnetotactic bacteria in fresh water (○: Alphaproteobacteria, ▽: Deltaproteobacteria).

Because some strains had the same or similar habitats and high similarity, some strains were selected to construct the phylogenetic tree. For example, FSO-1, FSO-2 and FSS-1 are all isolated from freshwater sediments of Otagaya swamp, Saitama, Japan, and have a similarity of 99.87%. LM-5 and KR-1, BB-1, MSM-3, MSM-4 are all *Magnetospirillum* in freshwater sediments and the similarity is 99.59%, 99.58%, 99.65% and 99.58%, respectively. The optimum growth temperature of MTB is about 30°C, and the most suitable pH is between 5.0 - 8.0 in freshwater. There are also weak magnetic MTB in the environment, such as RS-1, whose size and shape are the same as those observed in pure culture [21]. Although they do not have magnetic sensitivity when living in groups, they have the ability to synthesize magnetosomes. RS-1 is a specific anaerobic sulfate-reducing strain isolated from a freshwater river in Japan. It breathes with fumarate as an electron donor and the magnetosome is Fe_3O_4 [22]. The morphological and physiological characteristics of RS-1 are very similar to those of *Burkinensis desulfovibrio* and *Desulfovibrio fructosivorans*. It differs significantly from *Magnetospirillum* in metabolism and morphology. These results strongly suggest that MTB have different evolutionary origins.

Comparison of culturable MTB between saltwater and freshwater

We found that 51 strains of culturable MTB were mainly distributed in America, Japan, Russian and other countries (Table 1). All except IT-1 are located in the Northern Hemisphere, between 5° and 80° north latitude [23]. MTB are distributed from 6° to 145° E Latitude and from 74° W to 130° W Longitude, with the largest number of MTB in the genus *Magnetospirillum*. It can be seen from the phylogenetic tree that the clustering division of MTB in saltwater and freshwater is obvious, but there is also a close relationship between MTB in freshwater and MTB in saltwater; such as PR-3 and MC-1 in the same branch, UR-1 and YSC-1 in the same branch [24]. In saltwater, there are *Magnetovibrio*, *Magnetospirillum*, *Magnetococcus* and *Desulfamplus* in Alpha- and Deltaproteobacteria classes, and the existence of Gammaproteobacteria classes has been found, while in freshwater environment, only Alpha- and Deltaproteobacteria classes MTB, can be classified into *Magnetospirillum* and *Desulfovibrio* (Figure 3).

Taxonomic status	Niche	Total sequence number	Distributed countries
α-Proteobacteria	Freshwater	30	America, Russian, Japan, China, France
	Marine	7	America, China, France, Australia
γ-Proteobacteria	Marine	2	America
δ-Proteobacteria	Freshwater	7	Japan, America, China
	Marine	5	America, France
Total		51	

Table 1: Partial cultured strains of MTB statistics according to the 16S rDNA submitted to the GenBank.

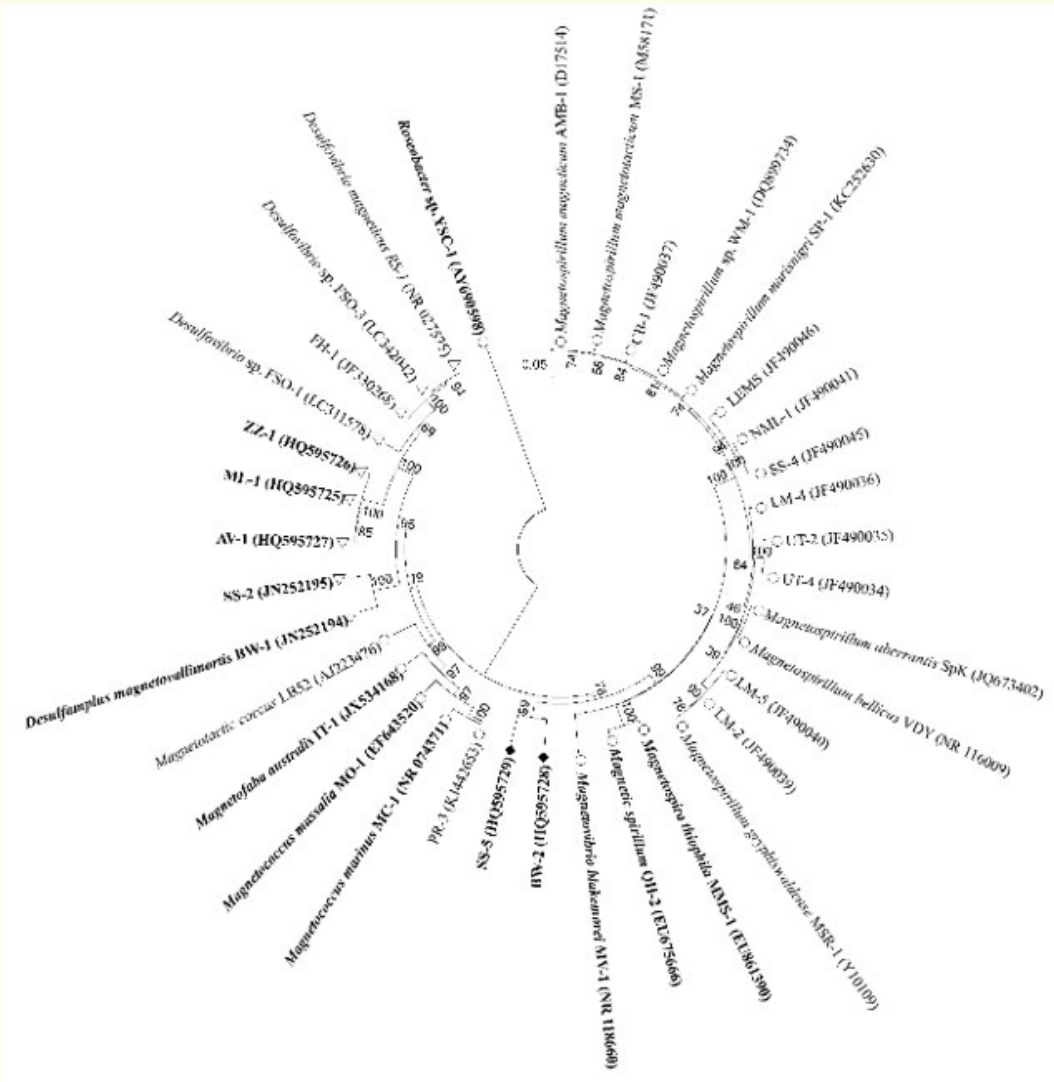
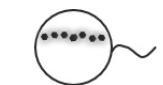


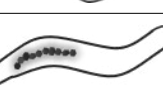

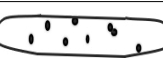


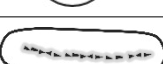

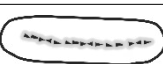
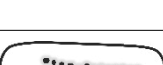
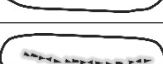


Figure 3: Phylogenetic tree based on partial sequences of 16S rDNA of culturable magnetotactic bacteria (○: Alphaproteobacteria, ▽: Deltaproteobacteria, ◆: Gammaproteobacteria, the bold font is marine magnetotactic bacteria).

From a national point of view, the pure cultured MTB obtained from Russia and Japan are distributed in freshwater environment, among which the MTB isolated from Japan has high similarity, such as AMB-1 and MGT-1 in the same branch, FSS-1, FSO-1 and FSO-2 in the same branch. In terms of cell shape, rod-shaped MTB is mainly distributed in marine environment, vibrio and spiral mostly belong to freshwater environment, only 3 strains of spherical MTB are marine organisms, including MC-1, MO-1 and IT-1 isolated from brackish sediments [25]. In the shape of magnetosome, bullet magnetosome is the most special and mainly exists in MTB in marine environment, such as BW-1, SS-2, AV-1 and ML-1 strains (Table 2) [26]. Generally speaking, most of the MTB in the aquatic environment were isolated from the lower iron concentration environment below the sediment, for example, the abundance of *Magnetococcus* MTB decreased with the increase of iron concentration. Most of the MTB were cultured in semi-solid medium, and 12 kinds of carbon sources such as succinic acid, fumaric acid, acetic acid, malic acid and α -ketoglutaric acid were used for organic heterotrophic growth [35].

MTB	Source	Morphology	Magnetosome morphology	Magnetosome arrangement	Magnetosome composition	Figure illustration	References
<i>Magnetococcus marinus</i> MC-1	Ocean	Cocci	Hexahedron	Chain	Magnetite		[16]
<i>Magnetovibrio blakemorei</i> MV-1	Ocean	Vibrio	Hexahedron	Chain	Magnetite		[26,27]
<i>Magnetococcus massalia</i> MO-1	Ocean	Ovoid	Octahedron	Chain	Magnetite		[12]
<i>Magnetic spirillum</i> QH-2	Ocean	Spiral	Hexahedron	Chain	Magnetite		[28]
<i>Magnetospira thiophila</i> MMS-1	Ocean	Spiral	Octahedron	Chain	Magnetite		[29]
<i>Roseobacter</i> sp. YSC-1	Ocean	Rod	Sphere	Scattered	Iron Oxide Cobalt		[24]
<i>Desulfovibrio magneticus</i> RS-1	Ocean	Spiral	Hexahedron	Chain	Magnetite		[30]
<i>Magnetofaba australis</i> IT-1	Lake	Cocci	Octahedron	Chain	Magnetite		[13]
Strain SS-2	Lake	Rod	Bullet-Shaped	Chain	Magnetite		[26]
Strain SS-5	Lake	Rod	Octahedron	Chain	Magnetite		[15]
<i>Desulfamplus magnetovallimortis</i> BW-1	Lake	Rod	Bullet-Shaped	Chain	Magnetite and/or Greigite		[31]
Strain BW-2	Lake	Rod	Octahedron	Chain	Magnetite		[15]
Strain ML-1	Lake	Rod	Bullet-Shaped	Chain	Magnetite		[11,15,26]







<i>Magnetospirillum gryphiswaldense</i> MSR-1	Lake	Spiral	Hexahedron	Chain	Magnetite		[32]
<i>Magnetospirillum magneticum</i> MGT-1	Lake	Spiral	Hexahedron	Chain	Magnetite		[19]
<i>Magnetospirillum</i> sp. WM-1	Lake	Spiral	Hexahedron	Chain	Magnetite		[33]
<i>Magnetospirillum magnetotacticum</i> MS-1	Pond	Spiral	Octahedron	Chain	Magnetite		[34]
<i>Magnetospirillum magneticum</i> AMB-1	Pond	Spiral	Hexahedron	Chain	Magnetite		[35]
Strain AV-1	Pond	Rod	Bullet-Shaped	Chain	Magnetite		[11]

Table 2: Partial cultured strains of MTB and their magnetosome morphologies.

Discussion

Previous studies confirmed that the dominant group of MTB in pure culture was proteobacteria. Most of the culturable MTB are distributed from 30° to 40° north latitude in saltwater environments. IT-1 is the only culturable MTB isolated from the southern hemisphere. The MTB IT-1 of Alphaproteobacteria in saltwater environments is located in the Western Hemisphere while the rest are distributed in the Eastern Hemisphere, and the Deltaproteobacteria are all located in the Western Hemisphere. The composition of the culturable MTB community differs in water environments with varying levels of salinity, so this biogeographic distribution may be related to water salinity. The geographical location of the separation site affects the salinity of the water bodies. MTB separation sites are mostly located in hot and arid climates near the Tropic of Cancer, resulting in high salinity. Lake water separated by BW-2 and its groundwater flows through fissured metamorphic rocks in the eastern Blake Mountains, SS-5 separated lakes are affected by agricultural runoff [15]. High salinity water environments may affect the survival of MTB, and different salinity levels affect the energy consumption and metabolic pathways of microorganisms [36]. There is evidence that the richness and diversity of MTB in different environments is strongly influenced by salinity although temperature, iron availability and concentrations of nitrogen and sulfur compounds are also clearly important in the distribution of MTB [37]. Some studies have also shown that the competitors or predators of MTB change under different salinities, which will also affect the diversity and distribution of MTB [38]. The MTB species distributed in saltwater lakes and oceans are different, which may be related to differing environmental factors in oceans and lakes. The flow of sea water in the ocean makes changes in environmental factors more violent than in lakes [39]. Alphaproteobacteria MTB may have good adaptability and can survive in rapidly changing environments. Different species have different metabolic adaptability to the environment [40].

Most MTB in marine environments exhibit chemo-organoheterotrophic growth, which may be due to the fact that MTB are oligotrophic microorganisms and organic matter in the ocean is sufficient for MTB growth. Chemolithoautotrophic MTB use sulfides and thiosulfate as electron donors for chemolithoautotrophic growth [15]. There may be a large number of sulfates and sulfides in saltwater environments. The existence of sulfides in different states will have different toxic effects on microorganisms [41]. Therefore, it is possible that MTB have evolved into MTB types adapted to their local environments. At present, of the culturable MTB only BW-1 in saltwater can synthesize Fe₃S₄ [26]. Although its biogeographic distribution cannot be determined, some scholars found that the composition of magnetosomes in BW-1 changed with different culture conditions. When the sulfate content in the medium was less than 0.3 mM, the synthesized magnetosome was the iron oxide type; in contrast, when the sulfate content was higher than 0.3 mM, the synthesized magnetosome was the iron sulfide

type. Studies have shown that the synthesis of Fe_3O_4 seems to be limited to anaerobic environments with sulfide enrichment, and the Fe_3S_4 type is mainly produced in micro-aerobic or anaerobic environments [35,42]. Lipid particles may be a common feature of MTB. It has been reported that lipid granules are formed under the stimulation of stress response and unbalanced growth process of cells as storage compounds for the energy and carbon needed to maintain cell metabolism and synthesis [28].

Culturable MTB in freshwater are all distributed in the Northern Hemisphere and concentrated in latitudes between 30° and 50° . The *Magnetospirillum* MTB of Alphaproteobacteria are mainly distributed in China and Russian, located in the temperate monsoon climate zone, with hot, rainy summers and cold, dry winters. The genus *Desulfovibrio*, belonging to Deltaproteobacteria, is mainly isolated from Saitama Prefecture, Japan, which has a subtropical monsoon climate, four distinct seasons, and abundant precipitation. This climatic condition may have an impact on the distribution of MTB in freshwater. Based on micro cosmological experiments, the change of MTB community structure with the increase of temperature extends to the natural habitat, indicating that climate change may affect the diversity and distribution of MTB in natural environments [43]. According to a large number of studies on MTB in the environment, other scholars think that MTB are mesophilic bacteria [5]. Strains SO-1 and BB-1 can be isolated from Russian freshwater sediments, probably because they are facultative anaerobes and have motor flagella, which allow them to move to deep sediment layers to find suitable living environments. It has been reported that multicellular magnetotactic prokaryotes can carry out seasonal vertical migration. The vertical distribution of multicellular magnetotactic prokaryotes is shallow in summer, deep in winter, and in the middle layer in spring and autumn [44].

The vertical distribution of MTB differs, which may be related to the particle size of the sediment. It has been shown that the electron donor for MTB is in the deep layer of the sediment, while the electron acceptor is on the surface of the sediment. In addition, MTB need to obtain energy through repeated movement. Sediment particle sizes that are too small will hinder the movement of MTB, which may affect the diversity and distribution of MTB [44]. Postec., *et al.* studied the distribution of MTB in the Mediterranean Sea and suggested that the grain size of sediments may be the decisive factor affecting the existence of MTB [45]. When the sediment grain size is large its interstitial water contains more dissolved oxygen, while sediments with small grain sizes contain low oxygen content. MTB are highly sensitive to oxygen; for example, AMB-1 begins to synthesize magnetosomes only in media with low concentrations of dissolved oxygen, and high concentrations of oxygen inhibit magnetosome synthesis [46]. Therefore, MTB may form distinct vertical distribution under oxygen stress for a long time. The magnetosomes in MTB can sense the external magnetic field and act as a magnetic guide to help the bacteria find a suitable micro-aerobic environment. Magnetosomes are generally arranged in chains, causing MTB to move magnetically along the earth's magnetic line of force. Chain arrangement can be explained from a magnetically oriented point of view, but cluster or short chain arrangements are more difficult to explain and may linked to MTB energy storage.

Most of the pure cultured MTB were distributed in the range of 5° to 80° north latitude, the scattered distribution of MTB in the eastern hemisphere was between 6° to 145° east longitude, and the MTB are distributed from 74° to 130° west longitude in the western hemisphere. With the increase of latitude, the number of culturable MTB decreased gradually, which may be due to the decrease of geomagnetic field intensity affecting the growth, metabolism and biomineralization of MTB. It has been reported that when the AMB-1 strain grows in zero magnetic space, the growth rate and the content of magnetosomes in the cell decrease, while a strong constant magnetic field can increase the concentration of bacterial suspensions and the magnetosome content in the cell [35]. The geomagnetic field also acts as an important barrier against cosmic radiation [47]. Areas with relatively weak geomagnetic fields may be affected by cosmic radiation on the earth's surface, which may affect the composition of MTB communities. Compared with other MTB genera, *Magnetospirillum* are more easily isolated and cultured. It may be that after long-term evolution, magnetosome synthesis is more coordinated with cell metabolism. It is speculated that *Magnetospirillum* MTB strains are stronger than other MTB strains with regards to their adaptations to terrestrial environments and cell viability. MTB can be grown through chemolithoautotrophic and chemo-organoheterotrophic growth, mainly

chemo-organoheterotrophic growth, and the best carbon source may be organic acids and some amino acids. No studies have indicated that MTB use any other type of organic compound as a carbon source. Carbon sources provide both carbon and energy for MTB growth, but the availability of different carbon sources to MTB may be different. For example, AMB-1 cannot grow using tartaric acid, sodium acetate, or citric acid as a single carbon source, unlike succinic acid [48].

Based on the phylogenetic analysis of culturable MTB, it is found that there are more species of MTB in saltwater environments, which may be due to the fact that marine environments are more stable than the freshwater environments and have the environmental conditions necessary to produce and breed MTB [49]. The phylogenetic analysis of MTB in different regions shows that environmental factors are greater than geographical factors, that is, MTB with high similarity may live in similar environments, such as AMB-1, MSR-1 and RSS-1 all live in nutrient-rich environments. There is a 97% similarity between QH-2 and MMS-1, which are found in Qingdao Huiquan Bay and off the coast of the United States, respectively [28,29]. It may be that the living environment is affected by human activities and the surrounding environment. This is consistent with the previous view that environmental heterogeneity can better explain the distribution of MTB than simple geographical distance, and environmental conditions are one of the main factors that drives the composition of natural MTB communities [50]. All MTB isolated from different environments have synthetic magnetosome genes. For example, the genome of marine *Magnetococcus* MC-1 contains a magnetosome island 102 kb in length, including many conserved genes in all known MTB, as well as some unique genes. In freshwater, the genes encoding magnetosomes in MS-1 are also located in the magnetosome island, which may be the result of horizontal gene transfer [34].

Conclusion

In this study, the 16s rDNA sequences of 51 culturable MTB published in anywhere were analyzed. MTB widely existed in sediments from freshwater and saltwater; culturable MTB occurred in freshwater more than saltwater; and their similarity is low. Alphaproteobacteria were the dominant MTB group and the class of Gammaproteobacteria were endemic to saltwater. This reflects that environmental factors are an important evolutionary pressure, promoting MTB to evolve in the same direction or in multiple directions in the process of long-term evolution. Future studies will use microbial genomics and metabonomics to reveal the relationship between the ecological distribution of MTB and the environment.

Author Contributions

Conceptualization: Tao Liu, Ziyu Hao; Methodology: Tao Liu, Guojing Zhang; Writing-original draft preparation: Lingzhu Li; Writing-review and editing and supervision: Lei Yan; Funding acquisition: Lei Yan. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement

No applicable.

Conflicts of Interest

The authors declare no conflict of interest.

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