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REVIEW ARTICLE

Magnetotactic bacteria: Characteristics and environmental applications

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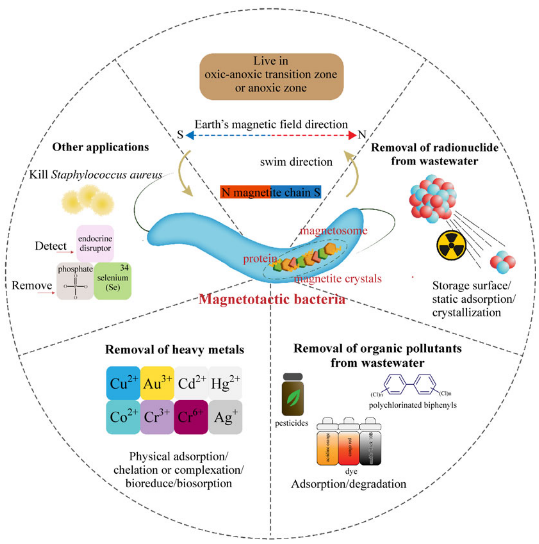
HIGHLIGHTS

- Magnetotactic bacteria (MTB) synthesize magnetic nanoparticle within magnetosomes.
- The morphologic and phylogenetic diversity of MTB were summarized.
- Isolation and mass cultivation of MTB deserve extensive research for applications.
- MTB can remove heavy metals, radionuclides, and organic pollutants from wastewater.

GRAPHIC ABSTRACT



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ABSTRACT

Magnetotactic bacteria (MTB) are a group of Gram-negative prokaryotes that respond to the geomagnetic field. This unique property is attributed to the intracellular magnetosomes, which contains membrane-bound nanocrystals of magnetic iron minerals. This review summarizes the most recent advances in MTB, magnetosomes, and their potential applications especially the environmental pollutant control or remediation. The morphologic and phylogenetic diversity of MTB were first introduced, followed by a critical review of isolation and cultivation methods. Researchers have devoted to optimize the factors, such as oxygen, carbon source, nitrogen source, nutrient broth, iron source, and mineral elements for the growth of MTB. Besides the applications of MTB in modern biological and medical fields, little attention was made on the environmental applications of MTB for wastewater treatment, which has been summarized in this review. For example, applications of MTB as adsorbents have resulted in a novel magnetic separation technology for removal of heavy metals or organic pollutants in wastewater. In addition, we summarized the current advance on pathogen removal and detection of endocrine disruptor which can inspire new insights toward sustainable engineering and practices. Finally, the new perspectives and possible directions for future studies are recommended, such as isolation of MTB, genetic modification of MTB for mass production and new environmental applications. The ultimate objective of this review is to promote the applications of MTB and magnetosomes in the environmental fields.

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1 Introduction

Magnetotactic bacteria (MTB), a group of Gram-negative microorganisms, were initially discovered in 1975 by Richard Blakemore (Ali et al., 2017; 2018), who discovered the bacterial orientation under the geomagnetic field of the earth in both the Northern and Southern Hemispheres (Heslop et al., 2013). MTB are widely distributed in the sediment of freshwater, marine habitats, and soils (Islam et al., 2018). Generally, MTB contain up to 3% iron by dry weight with 10^{-13} to 10^{-15} grams of iron per cell (Lin et al., 2012). The geomagnetical responses of MTB result from the intracellular enveloped magnetic grains or magnetosomes (Acosta-Avalos and Abreu, 2018; Yazdi et al., 2018), which are membrane-bound nanocrystals of magnetic iron minerals such as greigite (Fe_3S_4) or magnetite (Fe_3O_4) in microaerophilic environments (Yazdi et al., 2018). Bacterial magnetosomes offer numerous benefits compared with those chemically synthesized magnetite, such as consistent shape and narrow grain size distribution (Vargas et al., 2018).

The discovery of MTB and magnetosome has led to quest of their potential applications in various fields, including medicine, chemistry, physics, geology, crystallography, mechanics, limnology, mineralogy, astrobiology, food science and biotechnology (Yan et al., 2012; Dieudonné et al., 2019). For example, the bioactive substances can be coupled on the surface of magnetosome envelope, which are important for various medical applications (Dieudonné et al., 2019). MTB magnetite can be used for enzyme immobilization, magnetic antibody formation, and IgG antibody quantification (Yan et al., 2012). MTB magnetite coated with DNA also is used to deliver genes into cells (Vargas et al., 2018). Similarly, MTB was reported to aid the delivery of pharmaceuticals to target tumor (Yan et al., 2012), where traditional drugs are difficult to reach (Stanton et al., 2017). Living MTB can help analyze the domain of soft magnetic materials such as Si-Fe sheet and amorphous Co-based ribbons (Yan et al., 2013). The magnetic pole of rocks containing magnetic minerals could be located using MTB (Lin et al., 2017). MTB could be incorporated into monocytes and granulocytes by phagocytizing and could be magnetically separated from blood (Vargas et al., 2018). In addition, the fossilized magnetosomes store the information for the geomagnetic field origin and magnetic proxy records of paleoclimate (Heslop et al., 2013).

Most previous studies or literature review mainly focused on the biomedical applications of MTB and magnetosome. By contrast, the environmental applications such as wastewater treatment or bioremediation have not been well explored. Removal of contaminants from wastewater is one of the potential environmental applications of MTB. Many works have focused on the use of MTB to eliminate organic pollutants, radionuclides and heavy metals (Wang et al., 2015; Ali et al., 2018; Liu and Wiatrowski, 2018; Dieudonné et al., 2019). Some previous studies evaluated the removal of heavy metals (e.g., Fe, Hg, and Co) and radionuclides from wastewater using MTB (Tajer-Mohammad-Ghazvini et al., 2016; Liu and Wiatrowski, 2018; Dieudonné et al., 2019). The large surface areas of magnetic particles facilitate their adsorption for organic pollutants from wastewater, such as organophosphate pesticides (Ginet et al., 2011). However, there are paramount difficulties in mass cultivation of MTB that hinders their applications.

This article presents a short review on the current state of knowledge about the unique characteristics of MTB, magnetosomes, and their potential environmental applications. Available literature on morphologic and phylogenetic diversity of MTB has been summarized. The isolation and cultivation of natural MTB have been a challenge because of their fastidious lifestyle and strict incubation conditions. Factors such as carbon source, nitrogen source, nutrient broth, and mineral elements affecting the growth of MTB are discussed. Finally, current and potential environmental applications of MTB in the removal or recovery of heavy metals, radionuclides and organic pollutants are critically reviewed. In addition, other broader environmental applications such as pathogen removal and detection of endocrine disruptor are also summarized to highlight new opportunities toward sustainable engineering and practices. Finally, the challenge and future work of MTB's practical applications are discussed.

2 Morphologic and phylogenetic diversity

2.1 Structure, types, and characteristics of magnetotactic bacteria

2.1.1 Structure of magnetotactic bacteria

MTB are a physiologically and morphologically diverse group of Gram-negative and motile microorganisms that are abundant in natural waters (Lin et al., 2017). The most common morphologies of MTB are coccus (spheres), bacillus (short or long rods), vibrios (curved rod), spiral (twisted), and even multicellular magnetotactic prokaryotes (Bazylinski et al., 2014). Figure 1 illustrates a typical cell structure of MTB, which contains magnetosome (magnetic nanoparticles and proteins) and flagellum (Chen et al., 2012). Most MTB contain 10–50 magnetosomes that are composed of magnetic nanoparticles (e.g., Fe_3O_4 and Fe_3S_4) (Vargas et al., 2018). For instance, *Candidatus* Magnetobacterium bavaricum contain between 600 and 1000 crystals composed of magnetite (Fe_3O_4) (Jogler et al., 2010). A majority of MTB biomineralize only one magnetosome mineral (Bazylinski et al., 2014). Most single-celled MTB produce Fe_3O_4

magnetosomes, while only multicellular magnetotactic prokaryotes and a few single-celled rod-shaped bacteria can biomineralize Fe_3S_4 magnetosomes (Zhu et al., 2018). Some MTB (e.g., multicellular magnetotactic prokaryotes) are also able to synthesis both Fe_3O_4 and Fe_3S_4 minerals (Lefèvre et al., 2011; Zhu et al., 2018).

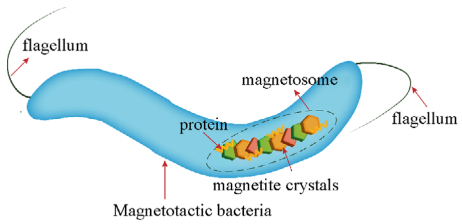

Fig. 1 Typical structure of a magnetotatic bacterium.

2.1.2 Types of magnetotactic bacteria

MTB has unique properties of magnetotaxis, by which MTB orientate themselves within geomagnetic fields of the earth and subsequently swim by their flagellum (Vargas et al., 2018). The magnetotaxis of MTB can be divided into two types: polar and axial (Bazylinski et al., 2014). A polar MTB swims in a preferred direction related to the local field, whereas an axial MTB swims back and forth in all different directions (Bazylinski et al., 2014). Polar MTB are either south- or north-seeking depending on the magnetic crystal forms inside MTB (Bazylinski et al., 2014). North-seeking MTB are mostly found in northern hemisphere and move toward the south magnetic pole of a bar magnet, whereas south-seeking MTB are mainly found in southern hemisphere and move toward the north magnetic pole of a bar magnet (Zhu et al., 2018). The north-seeking and south-seeking MTB are usually observed in the geographic equator and move toward south and north directions (Farzan et al., 2010). The north- and south-seeking MTB with the around same populations exist at the geomagnetic equator (Farzan et al., 2010). However, a population of south-seeking MTB was identified in the northern hemisphere and their swimming direction is opposite from all previously reported MTB (Simmons et al., 2006).

MTB are either microaerophilic or anaerobic and can live from aerobic to anaerobic conditions, seawater to freshwater, and solid to liquid media (Lin et al., 2017). They all require an anaerobic environment and metabolize short chain organic acids as carbon sources (Mathuriya et al., 2015). To date, most discovered MTB belong to Alphaproteobacterial strain with the rest affiliated with Gammaproteobacteria, Deltaproteobacteria, Nitrospirae and candidate phylum Omnitrophica (Lin et al., 2017). Several MTB strains were isolated and cultivated successfully, including *Magnetospirillum magnetotacticum* (*M. magnetotacticum*) strain MS-1 and *Magnetospirillium gryphiswaldense* (*M. gryphiswaldense*) strain MSR-1, *Magnetospirillum magneticum* (*M. magneticum*) strain AMB-1, *Magnetococcus marinus* strain MC-1, *Desulfovibrio magneticus* strain RS-1 (Lin et al., 2017).

2.1.3 Characteristics of magnetotactic bacteria

Despite the diversity of MTB, all known MTB share several similar traits, such as a Gram-negative type of cell walls, presence of flagella, sensitivity to oxygen levels, and biomineralization of magnetosomes (Lefèvre and Wu, 2013; Dieudonné et al., 2019). Magnetosomes of MTB are aligned into a linear chain (Dieudonné et al., 2019). Therefore the total magnetic dipole moment can be calculated by the sum of the moment for each nanocrystal to generate the maximal magnetic dipole moment (Ke et al., 2018). This characteristic results in the rotation of bacterial cell into alignment with a magnetic field (Ke et al., 2018). MTB are inclined to swim in the oxic-anoxic transition zone (OATZ), where oxygen-deficient water mixes with the oxygenated water (Faivre and Schuler, 2008). MTB keep their positions at the OATZ in a vertical gradient system with various oxygen concentrations (vertical arrows) in the Northern and Southern Hemisphere. When MTB are above the OATZ, they move downward along the earth geomagnetic field lines (Chen et al., 2012). While when MTB are under the OATZ, they upend the direction of flagellar rotation, and swim upward along the earth geomagnetic field lines (Chen et al., 2012).

2.2 Isolation and cultivation of MTB

2.2.1 Isolation from the natural environment

Separation of MTB from natural waters for laboratory cultivation are still challenging, despite of the intensive efforts. Up to now only several strains of MTB are separated through the magnetic separation methods or culture media (Prabhu and Kowshik, 2016). The first isolated strain is *M. mgnetotacticum* MS-1 (Lin et al., 2017). After that, *M. gryphiswaldense* strain MSR-1, *M. magneticum* AMB-1 and MGT-1, marine spirillum strain MV-4, vibrios strains MV-1 and MV-2, coccus strain MC-1, and *Desulfovibrio magneticus* strain RS-1 were isolated (Lin et al., 2017). One isolation technique is called orientation magnetic separation (OMS), which separates bacteria from water by an external magnetic field (Prabhu and Kowshik, 2016). OMS process can be used only when MTB are motile and contain a magnetic moment. Nevertheless, many MTB are non-motile or insusceptible to magnetic field (Acosta-Avalos and Abreu, 2018). Channel separator and plate separator based on OMS are widely applied for MTB isolation from water (Prabhu and Kowshik, 2016).

1) Channel separator

Channel separators are widely used for MTB isolation from natural waters (Bahaj et al., 2002). As shown in Fig. 2, water flows through a channel separator with a magnetic field vertical to the flow direction. MTB sense the magnetic field and orientate themselves to move along the magnetic field. MTB accumulate along the channel walls under magnetic attraction (Fig. 2). With surface accumulation, MTB may block the magnetics in the channel separator and prevent bacteria accumulation on the channel walls, especially at high rates of the flowing liquid. To alleviate this problem, metallic wires are used to amplify the magnetic gradients and improve the separation efficiency of MTB.

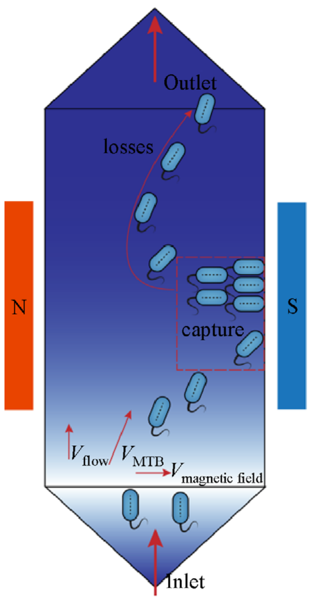

Fig. 2 The principle of orientation magnetic separation method in a channel separator. Graph was regenerated based on ref. (Bahaj et al., 2002) with modifications.

The separation efficiencies of channel separators vary with configurations of metallic wires (e.g., nickel) that creates magnetic fields (Bahaj et al., 2002). For example, smaller sizes or diameters of the nickel wires can increase the separation efficiency for MTB. Compared with the metallic wires that are anchored to the sidewalls of the separator, the nickel pin with a diameter of 250 μm on the sidewalls reduces the separation efficiency. Moreover, increasing the magnetic field had a minor effect on the isolation efficiency.

2) Plate separator

Plate separator is another technique for MTB separation from water. Farzan et al. used a plate separator to isolate two species of MTB from freshwater in Karkheh River and seawater in the Caspian Sea (Farzan et al., 2010). The samples containing mud, water, and MTB were left in a dark condition for approximately one month and were subsequently exposed to a permanent magnet in the plate. Several days later, MTB accumulated at the water surface below the magnetic pole. MTB was collected through a pipette and inoculated on a solid medium. Clearly, this method may also attract some naturally occurring magnetic particles or those released from dead MTB (Prabhu and Kowshik, 2016).

2.2.2 Laboratory cultivation

Although MTB are ubiquitous with high abundance in natural environments, cultivation in the laboratory is still hindered by their strict growth requirements (Bazylinski et al., 2014; Uebe and Schüler, 2016; Ali et al., 2017). MTB obtain energy for growth from oxidants and reductants (e.g., oxygen, reduced sulfur species) in a chemical interface (Faivre and Schuler, 2008; Bazylinski et al., 2014), which is difficult to simulate in laboratory conditions (Zhou et al., 2012). To date, successfully cultivated MTB strains include *M. gryphiswaldense* MSR-1, *M. magnetotacticum MS-1*, *M. magneticum* AMB-1, *Magnetovibrio* MV-1, MV-2, MMS-1 (marine spirillum strain), *Magnetococcus sp.* MC-1, marine magnetic sirillum QH-2, and *Magnetospirillum sp.* WM-1 (Ali et al., 2017). *Alphaproteobacteria* synthesize intracellular magnetite crystals (Prabhu and Kowshik, 2016). Only *Desulfovibrio magneticus* strain RS-1 is sulfate reducing, anaerobic, and magnetite forming, which belongs to the genus of *Deltaproteobacteria* (Prabhu and Kowshik, 2016).

2.2.3 Factors for bacterial incubation and growth

In general, the MTB growth rate and magnetosome formation yield are highly sensitive to many experimental factors, such as dissolved oxygen (DO), carbon source, nitrogen source, nutrient broth, iron source, and mineral elements (Ali et al., 2017).

1) Oxygen concentration

One of the most critical parameters for MTB growth and magnetosome formation is the DO concentration (Lin et al., 2017). A microaerobic level is critical for different strains of MTB to thrive (Lin et al., 2017). For instance, *M. magnetotacticum* strain MS-1 can growth normally at DO concentration of 0.1%–21%, and the optimal DO concentration for the magnetosome formation is 1% (Mathuriya et al., 2015). As the DO level drops to anaerobic conditions, the MTB growth starts to be inhibited. However, when the DO concentration is higher than approximately 3%–5% of the saturation level in the culture medium, the formation rate of magnetosome is inhibited.

2) Culture medium

The MTB culture media require organic acids as carbon sources and nitrate as a nitrogen source (Chandrajit and Prakash, 2011). Many types of organic acids are selected as carbon sources for MTB cultivation, including acetic acid, succinic acid, lactic acid, and malic acid (Liu et al., 2010; Chandrajit and Prakash, 2011). The effect of ferric citrate and sodium lactate concentration on the growth of *M. gryphiswaldense* MSR-1 and formation of magnetosome was reported (Liu et al., 2010). It has been found that 2×10^{-5}–5×10^{-4} mol/L ferric citrate had minor effects on the formation rate of magnetosome (Liu et al., 2010). By contrast, low concentrations of sodium lactate at 2.3×10^{-3} mol/L resulted in much faster bacterial cell growth rates and higher magnetosome yield than high concentrations of lactate at 0.02 mol/L. The addition of nitrate at 0.004 mol/L has significantly promoted the formation of magnetosome (Heyen and Schuler, 2003; Ali et al., 2017). As the nitrate concentration increased to 0.01–0.02 mol/L, the magnetosome yield decreased but the growth of MTB was not affected.

3) Nutrient broth

The growth rate of MTB and the properties of magnetosome are closely dependent on the nutrient broth that provides growth nutrients (Kundu and Kulkarni, 2010). A recent study shows that *M. magnetotacticum* strain MS-1 can successfully grow in the modified magnetic spirillum growth medium (MSGM) (Kundu and Kulkarni, 2010). The cell count obtained at the end of 6 days is 8×10^5 cells/mL, which further significantly increased to 40×10^5 cells/mL when a 25% nutrient broth was added to the medium.

4) Iron source

Iron is indispensable for MTB growth and magnetosome formation (Liu et al., 2010). Previous work compared the effects of two iron sources (ferric chelates and ferrous sulfate) on magnetosome formation (Vargas et al., 2018). Ferric gallate and ferrous sulfate were shown to significantly increase the yield of magnetosome, whereas ferric citrate slightly enhanced the yield of magnetosome (Yang et al., 2001). However, ferric malate and ferric quinate were demonstrated to be not suitable as iron sources (Yang et al., 2001). Liu et al. demonstrated that 2×10^{-5}–5×10^{-4} mol/L ferric citrate exerted no impact on the growth rate of MSR-1 and magnetosome formation (Liu et al., 2010).

5) Mineral elements

Many mineral elements are important for the MTB cultivation, such as Mg, Cu, Co, Mn, Zn and Al (Sannigrahi and Suthindhiran, 2019). Previous study indicated that for the *M. magnetotacticum* MS-1, the properties of magnetosome such as size, number and chain alignment could be changed by the levels of Ni and Zn in the growth medium (Zhou et al., 2012). The size of bacterium increased to 1.85 × 0.3 μm when Zn was present because Zn is a cofactor for many enzymes and stabilize the protein structure.

2.3 Magnetosome and synthesis pathways

2.3.1 Characteristics of magnetosomes

Bacterial magnetosomes are intracellular, membrane-bounded, and magnetic iron-bearing nanocrystals embedded in a lipid vesicle (Chen et al., 2012; Vargas et al., 2018). Magnetosome is a prokaryotic organelle with similar complexity with eukaryotic counterpart (Chen et al., 2012). The morphology, composition, and arrangement of magnetite nanocrystals within magnetosome are subject to species-specific chemical and genetic control (Acosta-Avalos and Abreu, 2018). The size of mature magnetite nanocrystals typically ranges from 35 nm to 120 nm (Lefèvre and Bazylinski, 2013; Vargas et al., 2018). Some large magnetite nanocrystals with lengths up to 250 nm are also formed by uncultured coccus MTB (Descamps et al., 2016). Bacterial magnetosomes with eternal magnetism are stable in the single magnetic domains (SD) at ambient temperature (Barber-Zucker and Zarivach, 2017; Ghaisari et al., 2017). The nanocrystals within the SD size range exhibited the maximal magnetic dipole moment (Barber-Zucker and Zarivach, 2017; Ghaisari et al., 2017). Magnetic nanocrystals with sizes smaller than the SD range are superparamagnetic at room temperature (Vargas et al., 2018). On the contrary, nanocrystals with lengths larger than 120 nm are non-uniformly magnetized due to the formation of domain walls. The domain walls are prone to form multiple magnetic domains with opposite magnetic orientations, thus decreasing the total magnetic remanence of the magnetosomes.

Furthermore, magnetite nanocrystals in magnetosomes have relatively high chemical purity (Yan et al., 2017; Vargas et al., 2018). There are two types of magnetosomes, which are gregite (Fe_3S_4) and iron oxide (Fe_3O_4) (Barber-Zucker and Zarivach, 2017; Ghaisari et al., 2017). The gregite magnetosomes are formed only in the absence of oxygen under the sulphidic condition (Ghaisari et al., 2017; Dieudonné et al., 2019). The MTB synthesizing the iron oxide (i.e., Fe_3O_4) magnetosomes is favored only in the presence of oxygen (Ghaisari et al., 2017; Dieudonné et al., 2019). However, their relative abundance of Fe(II) and Fe(III) in these magnetosome crystals may vary with bacterial species or other factors (Yan et al., 2017). The primary role of magnetosome is to guide MTB to move away from an oxygen-rich environment and seek proper environments for growth and survival (Lin et al., 2017). Magnetic fields can break up the magnetosome chains and may also decrease MTB's stability. Previous study showed that 30 mT magnetic field can break up the magnetosome chains inside the living MTB (Körnig et al., 2014; Blondeau et al., 2018). Magnetosome and nanoparticle chains remain intact and do not rotate in 1 T magnetic field when MTB were freeze-dried (Bender et al., 2019).

2.3.2 Synthesis of bacterial magnetosome

As shown in Fig. 3, for most MTB species, the formation mechanism of magnetosome consists of the following steps (Ali et al., 2018): 1) Invagination of the cytoplasmic membrane and formation of magnetosome vesicle; 2) Iron uptake by MTB and transportation into the magnetosome membrane vesicle through reduction of Fe^{3+} to Fe^{2+} by enzyme; 3) Formation of hydrous ferric oxides with low density via the partial oxidative reaction of a redox enzyme, which are similar to the mineral ferrihydrite; 4) One third of Fe^{3+} in hydrous oxides are reduced and Fe_3O_4 is generated through further dehydration (Bazylinski and Frankel, 2004). For biologically directed magnetite or greigit (Fe_3O_4 or Fe_3S_4) biomineralization in the magnetosome invagination/vesicle (Bazylinski and Schubbe, 2007), co-crystallization with Fe(II) under an iron oxidase results in the generation of Fe(III) ferrihydrite required for the growth of magnetite nanocrystals (Bazylinski et al., 2014; Acosta-Avalos and Abreu, 2018; Dieudonné et al., 2019). Many genes and proteins have been demonstrated to participate in the formation of magnetosome (Bazylinski and Schubbe, 2007). The genes and proteins participated in biomineralization pathway have not been unequivocally resolved (Islam et al., 2018). The syntheses of bacterial magnetosome were mainly studied in *Magnetospirillum* species (Bazylinski et al., 2014).

1) Magnetosome vesicle formation

This step involves the generation of magnetosome membrane invaginations from the cytoplasmic membrane as well as the formation of membrane vesicles (Yan et al., 2012; Bazylinski et al., 2014; Islam et al., 2018). The magnetosome membrane in several *Magnetospirillum* species consists of a lipid bilayer with thickness approximate 3–4 nm composing of fatty acids, glycolipids, phospholipids, sulfolipids, and proteins that are similar to those detected in cytoplasmic membranes (Yan et al., 2012). This exhibits that the magnetosome vesicle may originate from the cytoplasmic membrane (Dieudonné et al., 2019). Magnetosome proteins including, MamB, MamI, MamL, and MamQ are responsible for the magnetosome membrane formation in *M. magneticum* (Murat et al., 2010). MamA gene as a scaffolding protein may coordinate the assembly of oligomeric protein complexes during magnetosome biomineralization and construction of the magnetosome chain (Zeytuni et al., 2011). The magnetosome vesicle could be alkaline to ensure the thermodynamic stability of magnetite (Yan et al., 2012; Bazylinski et al., 2014).

2) Iron uptake in magnetotactic bacteria

This step involves external iron internalization by siderophores and transport proteins, and accumulation into the magnetosome vesicles through the transmembrane iron transporters (Bazylinski et al., 2014; Acosta-Avalos and Abreu, 2018; Dieudonné et al., 2019). Both Fe(II) and Fe(III) are taken up by *Magnetospirillum* for synthesizing magnetite (Bazylinski et al., 2014). Fe(II) is highly soluble (up to 0.1 mol/L at neutral pH) and can be taken up by MTB through nonspecific mechanisms (Dieudonné et al., 2019). By contrast, most microorganisms depend on iron chelators to bind, dissolve, and then uptake Fe(III) because Fe(III) is insoluble (Dieudonné et al., 2019). Siderophore produced by MTB with low molecular weight has high affinity for iron complexation (Bazylinski et al., 2014; Acosta-Avalos and Abreu, 2018). They can enhance the dissolution of Fe(III) by ligand-promoted or proton-promoted iron oxide dissolution mechanisms (Acosta-Avalos and Abreu, 2018; Dieudonné et al., 2019). Thus siderophore increases the contact chance between MTB and Fe(III), and subsequently enhances the uptake of iron by MTB (Bazylinski et al., 2014; Acosta-Avalos and Abreu, 2018; Dieudonné et al., 2019). MTB consist approximate 3% iron measured by their dry weight, which is several orders of magnitude more than that in non-magnetotactic bacteria (Bazylinski et al., 2014). However, no evidence showed that MTB use unique iron-uptake systems. Details regarding iron uptake by MTB for

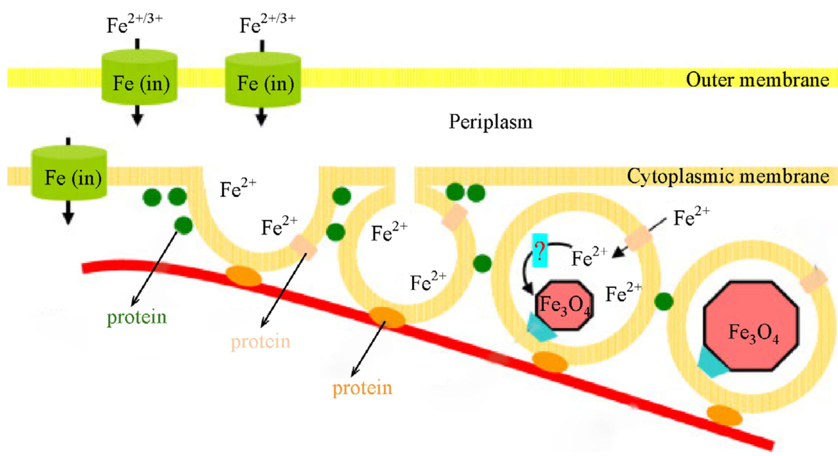

Fig. 3 Hypothesized mechanism of magnetite biomineralization. Graph was cited and reproduced from ref. (Yan et al., 2012) with permission and minor modifications.

magnetosome synthesis are not known, but it seems that several iron uptake systems function in each magnetotactic bacterial species (Dieudonné et al., 2019).

3) Iron transport into the membrane vesicle

Once the dissolved iron is internalized into the vesicle, nanocrystals start to grow regardless of when membrane vesicle is generated (Bazylinski et al., 2014). For example, *M. magneticum* AMB-1 could accumulate as much as 0.01 mol/L iron, which is 200-fold more than that in regular *E. coli* cells (Amor et al., 2018). To achieve such high concentrations of iron, MTB must contain an efficient iron transfer system, whose mechanisms still remain unclear (Amor et al., 2018). However, many membrane proteins regulate the transportation of iron into magenetosomes for biomineralization (Uebe and Schüler, 2016). For example, proteins (MamB and MamM) have been identified in the genomes of all known MTB and belong to cation diffusion facilitator family of metal transporters (Dieudonné et al., 2019). Protein MamV has only been found in some species with the ability of transporting iron to the magnetosome membrane vesicle/invagination (Uebe and Schüler, 2016; Dieudonné et al., 2019).

4) Controlled biomineralization within the magnetosome vesicle

The general biomineralization reaction was proposed as follows (Faivre and Schuler, 2008):

$$Fe^{2+}A + 2Fe^{3+}B + (2x + y + 4)H_2O \rightarrow$$

$$2Fe(OH)_x^{3-x} + Fe(OH)_y^{2-y} + (2x+y)H^+ + A^{2-} + 2B^{3-} + 4H_2O$$

$$\xrightarrow{-A^{2-}\ -B^{2-}} Fe_3O_4 + (2x + y)H_2O + 8H^+ \qquad (1)$$

where Fe^{2+} and Fe^{3+} are ligated by organic substrates of A and B (A is unknown and B is ferritin), respectively, and are released at the interface of magnetosome and compartment (Faivre and Schuler, 2008). A proposed formation mechanism of the magnetosome in the MSR-1 strain is shown in Fig. 4. In the final step, tightly bound magnetosome proteins trigger the nucleation of magnetite nanocrystal (Dieudonné et al., 2019). Specific magnetosome proteins appear to be implicated in magnetosome magnetite crystal maturation (Uebe and Schüler, 2016). Mms proteins direct the nucleation and biomineralization of nanocrystals in the vesicles of MTB (Uebe and Schüler, 2016; Dieudonné et al., 2019). Five Mms-proteins (Mms5, Mms6, Mms7, Mms12 and Mms13) are responsible for the growth of magnetic nanocrystals (Uebe and Schüler, 2016). Magnetic nanocrystals formed by *M. gryphiswaldense* MSR-1 in the presence of Mms6 display similar properties as those generated in MTB cells. However, the nanocrystals formed in the absence of Mms6 exhibited heterogeneous size and shape (Dieudonné et al., 2019). MamX, MamZ and MamH, are involved in the redox control of magnetite biomineralization in *M. gryphiswaldense*, thus probably influencing the size and maturation of magnetosome magnetite crystal. Proteins (MamK and MamJ), which was identified in *M. gryphiswaldense*, was participated in controlling magnetosome chain assembly (Bazylinski et al., 2014). Recently, protein MamY was found to be the membrane-anchored mechanical scaffold that is important to align the motility axis of magnetotactic spirilla and to reconcile magnetoreception with their swimming directions (Toro-Nahuelpan et al., 2019).

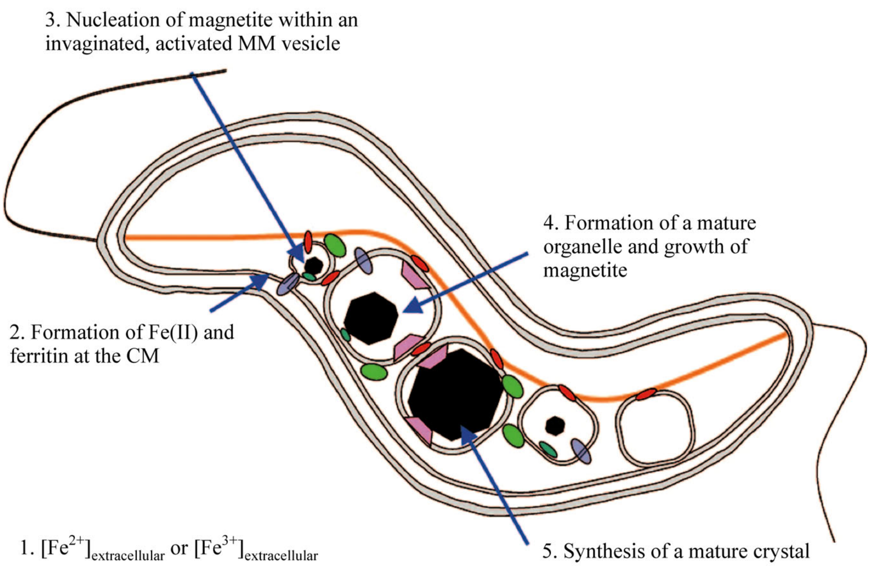

Fig. 4 Role of the proteins in the magnetite biomineralization and chain formation. Graph was cited and reproduced from ref. (Faivre and Schuler, 2008) with permission. MM represents magnetosome membrane, MC represents cytoplasmic membrane.

3 Applications of MTB and magnetosomes in environmental engineering

Water pollution is a major concern among the environmental issues worldwide (Yang et al., 2014; Nguyen et al., 2019). Most recently, nanotechnology has received considerable attention due to its high efficiency and low cost in the remediation of heavy metals, radionuclide and organic pollutants (Singh et al., 2016; de Castro Alves et al., 2019; Ranjan et al., 2019). The large surface areas and magnetic properties of magnetic nanoparticles facilitate their adsorption of pollutants and separation from wastewater, respectively (Ali et al., 2018; Ranjan et al., 2019). MTB and magnetosomes may also find a wide range of potential environmental applications. Because MTB show promising features such as high abundance, large specific surface area, easy operation, and simply separation of the pollutant from water.

3.1 Removal of heavy metals from wastewater

Heavy metals released into natural waters pose threat to organisms as well as human beings (Kiran et al., 2018; Nguyen et al., 2019; Ranjan et al., 2019). Meanwhile the increasing demand for heavy metals leads to their scarcity in natural environment (Yang et al., 2014; Nguyen et al., 2019). Therefore, it is of great importance to recover heavy metals from wastewater to attenuate the toxic effect and recycle valuable metal elements (Yang et al., 2014; Nguyen et al., 2019; Ranjan et al., 2019). Various technologies such as activated carbon adsorption, electrochemical treatment, physiochemical treatment and biological methods have been widely applied to tackle heavy metal wastewater (Kiran et al., 2018; Jiang et al., 2019; Li et al., 2019; Liu et al., 2019). Nevertheless, low recovery rate, toxic/expensive reagent necessities, and difficulty in processing restrict their applications (Liu et al., 2019).

MTB have great bio-adsorption capability to a wide variety of heavy metals in wastewater (Song et al., 2007; Song et al., 2008; Tanaka et al., 2009; Cai et al., 2011). After discovery of MTB, many researchers studied the heavy metal recycle using MTB. As shown in Table 1, different strains of MTB are selected to treat wastewater containing heavy metals with removal rates ranging from 38.6% to 100.0% except for Hg^{2+}. Most published works of heavy metal removal by MTB focused on single heavy metals, especially for Au^{3+}, Cr^{6+} and Cu^{2+}. Only several works focused on evaluating the remove ability in wastewater containing more than one heavy metal.

MTB have been mostly applied to harvest Au^{3+} in contaminated wastewater (Song et al., 2008; Tanaka et al., 2009; Cai et al., 2011; Song et al., 2013). Song et al. isolated a magnetotactic bacterium, *Stenotrophomonas sp.* from a municipal sewage treatment plant and used this bacterium to concentrate Au^{3+} in deionized water (Song et al., 2008; Song et al., 2013). The biosorption efficiency decreased from 506 to 308 mg/g dry weight biomass when the solution pH increased from 2.0 to 12.0. The molecular dynamics simulation indicated that the thermal motion and electrostatic attraction exerted impacts on the biosorption of Au^{3+}. A two-stage removal mechanism for Au^{3+} was proposed (Song et al., 2008; Song et al., 2013). First, in the electric field of charged cells, heavy metals were attracted through physical adsorption of multi-molecular layer. Second, heavy metal ions were chelated or complexed with functional groups (including hydroxyl, carboxylate, and phosphoryl groups) on the cell wall. A small portion of Au^{3+} may undergo the ion exchange reaction with alkali metals binding with other functional groups (Song et al., 2013). *M. magneticum* AMB-1 was also found to show high affinity to Au^{3+}, and then successfully precipitate and recover approximately 100% of gold from a mixture of growth medium/plating waste containing 4×10^{-7} mol/L Au^{3+} (Tanaka et al., 2009). *M. gryphiswaldense* MSR-1 remove Au^{3+} in water environment through biosorption (Cai et al., 2011). And more importantly, they reduced Au^{3+} to Au(0) and then accumulated Au(0) into gold nanoparticles on the cell (Cai et al., 2011; Song et al., 2013).

The water contamination of Cr^{6+} is a worldwide problem because of its high toxicity, mutagenicity, and carcinogenicity (Wang and Sun, 2005; Qu et al., 2014). MTB exhibited high adsorption capacity of Cr^{6+} compared with other bacteria (e.g., *Pseudomonas* spp.) (Wang and Sun, 2005; Qu et al., 2014). MTB with 4–100 g/L biomass shows the potential of fast removing Cr^{6+}/Cr^{3+} in less than 60 min (Qu et al., 2014). The adsorbed Cr^{6+} could also be reduced to Cr^{3+} by MTB. The removal rate of Cr^{6+} was higher (41% to 80%) at pH 5.0–6.0 than at high pH (>6.0) because of the highest activity of MTB at the optimal pH of 6.0. Moreover, at high pH>8, Cr^{3+} may form $Cr(OH)_3$ and precipitate, which may interfere the reduction reactions of Cr^{6+} to Cr^{3+}. Since the process of removing Cr^{6+} was enzyme-mediated, the pH value exerted influence on the ionization of enzyme and the conformation of protein, which would influence the enzyme activity to removal heavy metals. The maximum removal efficiency (77%) of Cr^{6+} by MTB was obtained after 10 min of adsorption at 29°C with the initial Cr^{6+} concentration of 34.64 mg/L. Application an external electric field (0.5 V/cm) can significantly improve the removal rate of Cr^{6+} due to the higher interactions between bacteria and heavy metals.

Studies showed that heavy metals such as Cd^{2+}, Pb^{2+}, Ni^{2+}, Fe^{3+}, Fe^{2+}, Mn^{2+}, and Hg^{2+} can be removed by MTB. For example, MTB showed almost 100% recovery of Pb^{2+}, Ni^{2+}, Fe^{3+}, Fe^{2+}, and Mn^{2+} due to the high affinity to those metal ions (Wang and Sun, 2005). *Desulfovibrio magneticus* RS-1 is applicable for removing Cd^{2+} (Arakaki et al., 2002). The removal efficiency remains fast within 50 h for 0.6–1.3 mg/L Cd^{2+} and eventually up to 45.2% at 240 h. Cd^{2+} was removed through precipitation of

Table 1 Literature review for the removal of heavy metals from wastewater by magnetotactic bacteria

Heavy metals	Strain	Initial metal concentration	Wet biomass weight	Time	pH	Removal efficiency	Ref.
Au^{3+}	*Stenotrophomonas sp.*	80 mg/L	10 g/L	60 min	1.0–5.5	100%	Song et al. (2008)
	M. magneticum AMB-1	2×10^{-7} mol/L 4×10^{-7} mol/L	1.5×10^{8} cells/mL	7 days		100% 100%	Tanaka et al. (2009)
	M. gryphiswaldense MSR-1	80 mg/L	10 g/L	60 min	2.5		Cai et al. (2011)
Cr^{6+}	MTB	34.64 mg/L	44 g/L	60 min	6.0	80%	Qu et al. (2014)
		21.51 mg/L	100 g/L	30 min	6.0	68%	Qu et al. (2014)
	MTB	40 mg/L	80 g/L	60 min	6.0–7.0	100%	Wang and Sun (2005)
Cd^{2+}	*M. magneticum* AMB-1	1×10^{-4} mol/L	1×10^{8} cells/mL	24 h	7.4	3.8×10^{6} molecules per cell	Tanaka et al. (2008)
	Desulfovibrio magneticus RS-1	1.3 mg/L	6.9×10^{7} cells/mL	240 h	7.0	58.0%	Arakaki et al. (2002)
Hg^{2+}	*M. gryphiswaldense* MSR-1	2.5×10^{-7} mol/L	250 mg/L biogenic magnetite	120 min		13.53%	Liu and Wiatrowski (2018)
	M. magnetotacticum MS-1	2.5×10^{-7} mol/L	250 mg/L biogenic magnetite	120 min		8.55%	Liu and Wiatrowski (2018)
Cu^{2+}	*M. gryphiswaldense* MSR-1	80 mg/L	10 g/L	60 min	5.0	62.23%	Wang et al. (2011)
	MTB	40 mg/L	80 g/L	60 min	6.0–7.0	100%	Wang and Sun (2005)
Cr^{3+}	MTB	40 mg/L	80 g/L	60 min	6.0–7.0	100%	Wang and Sun (2005)
Fe^{3+}	MTB	40 mg/L	80 g/L	60 min	6.0–7.0	100%	Wang and Sun (2005)
Fe^{2+}	MTB	40 mg/L	80 g/L	60 min	6.0–7.0	100%	Wang and Sun (2005)
Ni^{2+}	MTB	40 mg/L	80 g/L	60 min	6.0–7.0	96.20%	Wang and Sun (2005)
Mn^{2+}	MTB	40 mg/L	80 g/L	60 min	6.0–7.0	50.75%	Wang and Sun (2005)
Pb^{2+}	MTB	40 mg/L	80 g/L	60 min	6.0–7.0	100%	Wang and Sun (2005)
Co^{2+}	*Alphapro- teobacterium* MTB-KTN90	115 mg/L	0.015 g/L of dry biomass	60 min	7.0	88.55%	Tajer-Mohammad-Ghazvini et al. (2016)
Ag^{+}	*M. gryphiswaldense* MSR-1	80 mg/L	10 g/L	60 min	4.0	91.26%	Wang et al. (2011)
Mixture of Au^{3+} and Cu^{2+}	MTB	Au^{3+} (80 mg/L)	10 g/L	10 min	1.0–5.5	99.53%–100%	Song et al. (2007)
		Cu^{2+} (80 mg/L)	10 g/L	10 min	2.0–4.5	98.07%–98.75%	Song et al. (2007)

electron-dense particles on bacteria cell surface that mainly consisted of phosphate and sulfide. *M. magneticum* AMB-1 also have high binding ability for Cd^{2+} (Tanaka et al., 2008). Cd^{2+} can be recovered from cell surfaces by washing twice with EDTA, which is a metal ion chelator. Liu et al. showed that *M. gryphiswaldense* MSR-1 and *M. magnetotacticum* MS-1 reduced Hg^{2+} to Hg(0) at a slow rate because Hg^{2+} was blocked by the cell membrane (Liu and Wiatrowski, 2018). The removal efficiency (8.55%–13.53%) was pretty low compared with other metals (Tanaka et al., 2009; Cai et al., 2011; Liu and Wiatrowski, 2018). However, the removal efficiency increased to 55.07%–64.70% when using biogenic magnetite without magnetosome membrane (Liu and Wiatrowski, 2018).

Many heavy metals commonly co-exist in wastewater from the mining, metallurgical battery manufacturing and printing industries (Wang et al., 2011; Yang et al., 2011; Parisi et al., 2019; Sannigrahi and Suthindhiran, 2019; Yang et al., 2019). Simultaneous biosorption of Ag^{+} and Cu^{2+} by *M. gryphiswaldense* MSR-1 was studied with different molar ratios of Ag^{+} and Cu^{2+} (from 5:1 to 1:5) (Wang et al., 2011). When the molar ratios of Ag^{+} and Cu^{2+} were lower than 4:1, the adsorption efficiency for both heavy metals was improved compared with those in the unitary system with only one metal ions in the solution. For higher ratio of Ag^{+} and Cu^{2+} (5:1 and 4:1), the biosorption capacity for Ag^{+} was enhanced, whereas the biosorption capacity for Cu^{2+} was lower than that in the unitary system. The enhanced biosorption of Ag^{+} on *M. gryphiswaldense* MSR-1 after addition of Cu^{2+} is primarily attributed to different properties of metal ions. Ag^{+} with higher momentum energy probably promote the sorption of Ag^{+} by improving the probability of effective collision between Ag^{+} and the cellular walls, because atomic weight of Ag was higher than Cu (Tanaka et al., 2010; Shi et al., 2012). In addition, Ag^{+} with a much higher reduction potential showed a much stronger ionic interaction with the electron-rich surface of *M. gryphiswaldense* MSR-1. Previous works also demonstrated that the enhanced removal efficiency in the binary metal solution (Chen et al., 2011; Shi et al., 2012). For instance, the removal of Cr^{6+} was enhanced when Co^{2+} or Cu^{2+} was present, because these co-existing metals may stimulate MTB to produce transferase and reductase of Cr^{6+} (Qu et al., 2014).

MTB are capable to removal heavy metals (e.g., Cd^{2+}, Pb^{2+}, Zn^{2+}, Ni^{2+}, and Cu^{2+}) from printed circuit boards wastewater simultaneously (Yang et al., 2011; Sannigrahi and Suthindhiran, 2019). Five bacterial strains including *M. sp.* RJS2 (KJ570852), *M. sp.* RJS5 (KM289194), *M. sp.* RJS6 (KT266803), *M. sp.* RJS7 (KT693285) and *M. gryphiswaldense* MSR-1 were used individually or in consortia to removal heavy metals (Sannigrahi and Suthindhiran, 2019). RJS2 and RJS6 were dominant strains in heavy metal recovery. MSR-1, RJS6, and RJS2 exhibited maximum recovery of Pb^{2+} (100%), Ni^{2+} (99%), and Cd^{2+} (97%), respectively. The mixed strains MAG1 (RJS2, RJS5 and MSR-1) and MAG2 (RJS6 and RJS7) both showed higher recovery rate compared with the average recovery of individual strains. For example, the recovery rate of Ni^{2+}, Zn^{2+} and Cd^{2+} by MAG1 was 100%, 75%, and 90%, respectively. Bacteria consortia exhibited enhanced solubilization of metals, thereby promoting the recovery of heavy metals. The metal recovery batch experiments were conducted in culture media where pH was readjusted to 6.7 or 7, which is an eco-friendly and low-cost process.

3.2 Removal of radionuclide from wastewater

MTB with a high affinity to accumulate radionuclide is shown to remove radionuclide from wastewater (Jacob and Suthindhiran, 2016; Wang and Zhuang, 2019). The large surface areas of iron sulfide produced by MTB provide a suitable storage surface for radionuclide (Yan et al., 2012; Wang and Zhuang, 2019). Bahaj et al. collected MTB from ponds and streams using an OMS system and investigated the removal efficiency of radionuclides from wastewater (Bahaj et al., 1997; Bahaj et al., 1998). High recovery rate (e.g., 40%) of plutonium (Pu) was observed by the separated MTB under the static adsorption. Keim et al. (2009) showed that manganese (Mn) could be accumulated by uncultured MTB collected from Itaipu lagoon, a coastal region nearby Rio de Janeiro, and they found Mn was incorporated into the growing magnetite crystals (Keim et al., 2009). Similarly, tellurium, a mildly toxic metalloid that is applied as component of alloy, is found to be crystallized in *M. magneticum* AMB-1 (Tanaka et al., 2010).

3.3 Removal of organic pollutants from wastewater

MTB have natural binding affinity toward organic matters and can remove pollutants in water under a magnetic field (Ambashta and Sillanpaa, 2010; Vargas et al., 2018). For example, Bahaj et al. (2002) found MTB could be applied in organic pollutant removal from water via enzymatic reactions. Ginet et al. (2011) used functionalized bacterial magnetosomes extracted from MTB to degrade ethyl-paraoxon, a commonly used organophosphate pesticide. Honda et al. (2015) immobilized two close proximity enzymes (e.g., endoglucanase and β-glucosidase) and a cellulose binding domain on magnetosome for the degradation of cellulose. Some magnetically modified bacteria (e.g., *Rhodopseudomonas spheroids*, *Saccharomyces cerevisiae*, *Saccharomyces cerevisiae subsp. uvarum*) were shown to adsorb and degrade dyes such as acridine orange, amido black 10B, and congo red (Safarik et al., 2002; Šafaříková et al., 2005). The modification usually involves the adsorption of magnetic particles or magnetic fluid treatment to enable the modified bacteria to be manipulated through magnetic field (Safarik et al., 2002; Šafaříková et al., 2005).

3.4 Other environmental applications

Other relevant environmental applications related to MTB include pollutant detection, chemical recovery, and pathogen removal (Tanaka et al., 2004; Tanaka et al., 2016; Zhou et al., 2017). For example, Tanaka et al. developed automated immunoassay with bacterial magnetic particles to detect 17-β estradiol (E2), an endocrine disruptor chemical, in water samples (Tanaka et al., 2004). Bacterial magnetic particles garnered from *M. magneticum* AMB-1 acted as the antibody carrier, where the anti-E2 monoclonal antibody was immobilized. This immunoassays system was reported to detect E2 of as low as 20.0 ng/L within 0.5 h. Tanaka et al. employed *M. magneticum* AMB-1 to accumulate and recover amorphous elemental selenium (Se) in an external magnetic field (Tanaka et al., 2016). They found that 68.1% of the Se (1×10^{-4} mol/L) was uptaken by MTB within 7 days and more than 70% of Se was recovered in 20 h after Se accumulation reaching saturated. *M. gryphiswaldense* was genetically manipulated to overexpress the polyphosphate kinase that increases the removal of phosphate from wastewater (Zhou et al., 2017). The recombinant magnetostatic bacterial strain removed approximate 20% of 5×10^{-4} mol/L phosphate after two days, whereas the non-recombinant bacterial only removed 2% of the total phosphate.

Magnetotactic ovoid strain MO-1 was applied to kill a pathogen of *Staphylococcus aureus* (*S. aureus*) under a swing magnetic field (Chen et al., 2017). The killing efficiency improved with the increasing attachment ratio of MO-1 cells onto *S. aureus*. The attached MO-1 cells generated a mechanical pressure of 8 kPa under the swing magnetic field, which could result in the death of *S. aureus*.

4 Future perspectives

MTB have been demonstrated with high potential to be utilized in a broad range of environmental engineering applications such as wastewater treatment and removal of microbial pathogens. For instance, microbial consortia (e.g., *M. sp.* RJS2, *M. sp.* RJS5 and MSR-1) exhibited superior performances in heavy metals removal in laboratory scale studies (Sannigrahi and Suthindhiran, 2019). However, the applicability of MTB in realistic applications must be addressed, where more than one pollutant co-exists in wastewater, such as the printed circuit boards wastewater, coking wastewater, and dyeing wastewater. Whether MTB can tolerate complex stressors such as heavy metals and stay intact to elicit stable adsorbent functions or characteristics deserves further studies. Furthermore, the mass production of MTB at affordable cost must be realized, which requires fundamental understandings of the biomineralization processes and mechanisms of MTB. For example, MamB, MamM, MamH, MamZ, MamK, and Mms6 proteins were found to participate in the in vivo biomineralization process of *M. magneticum* (Firlar et al., 2019). However, the biomineralization mechanisms of magnetic iron minerals for most MTB remain largely elusive. Genetic engineering, proteomics and nano/microfluidic approaches may be used to address these fundamental questions of MTB and guide their environmental applications. Optimization and standardization of MTB culture conditions and growth protocols should be established for those identified and culturable MTB species. Finally, regeneration and reuse of MTB will be desirable, which essentially requires efficient biomass separation and recovery from chemical matrixes through devising chemical washing or rinsing process.

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