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Biomagnetism: Insights Into Magnetic Minerals Produced by Microorganisms

James M. Byrne¹ and Matthieu Amor²

ABSTRACT

Biomagnetism describes the biological origin of magnetism within living organisms. This phenomenon occurs due to the formation of iron-based minerals that exhibit magnetic ordering at room temperature. Perhaps the most studied form of biomagnetism originates in bacteria, especially magnetotactic bacteria producing internal magnetite grains and iron-reducing bacteria producing magnetite nanoparticles externally as a byproduct of iron respiration. They likely contribute to a significant proportion of environmental magnetite. The emergence of biomagnetism remains unclear, although it is thought that magnetotactic bacteria evolved this mechanism several billion years ago. Understanding how and why microorganisms generate biomagnetism is helping to shed light on the origin of life on Earth and potentially on other planets. Biomagnetism is also of broad interest to industrial and environmental applications.

KEYWORDS: biomagnets; magnetite; greigite; biologically induced mineralization; biologically controlled mineralization

BIOMAGNETS AND WHERE TO FIND THEM

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Quite simply, magnetic minerals are everywhere (FIG. 1) and all you need to test this is a small fridge magnet and a few crumbs of dry soil. Crush the crumbs between your fingers and gently move your magnet over the top of the powder and watch traces of magnetic minerals jump out. The origins of these magnetic minerals are diverse, ranging from anthropogenic inputs, such as fossil fuel power stations and the heavy use of brake pads by automobiles, to natural processes including forest fires and detrital inputs from igneous rock or magmatic activity. Among the more enigmatic routes through which magnetic minerals form, however, is through biological activity. Magnetic minerals, such as magnetite ($\text{Fe(II)Fe(III)}_2\text{O}_4$) and greigite ($\text{Fe(II)Fe(III)}_2\text{S}_4$), have been detected in animals, bacteria, and plants (Kirschvink and Gould 1981). The functions of these biogenic magnetic minerals, which we henceforth refer to as biomagnets, have been widely reported to enable navigation along the Earth's magnetic field, especially in migratory birds and pigeons. While a growing body of evidence focuses on the presence of biomagnets among larger organisms, microbes have so far been the most studied systems. Microbially mediated mechanisms of biomagnet formation take advantage of the ubiquity of iron in the environment. The formation mechanisms of biomagnets are broadly termed either biologically induced mineralization (BIM), which describes biomagnets formed by bacteria outside of their outer cell membrane, or biologically controlled mineralization (BCM), which describes biomagnets formed internally within bacteria (FIG. 2). In this article, we present a broad overview of biomagnets, particularly those produced by bacteria. We first briefly explain the mechanisms leading to the formation of the most widely studied biomagnets, magnetite and greigite, then discuss their occurrence in modern and ancient environments, and finally consider their potential biological function(s).

WHAT ARE BIOMAGNETS?

Biomagnets are minerals produced through biological activity, specifically biomineralization, which are sensitive to an external magnetic field such as that of the Earth. Biomineralization can be initiated by many living organisms including microbes that form biogenic mineral phases using inorganic atoms as building blocks. Microbes account for up to a third of all living biomass on the planet (Whitman et al. 1998) and are key drivers of all of the Earth's major biogeochemical cycles, including the carbon, nitrogen, oxygen, phosphorous, and iron cycles (see Kappler et al. 2023 this issue). Iron (Fe) is readily cycled between ferric (Fe(III)) and ferrous (Fe(II)) species. The iron cycle is largely controlled by prokaryotic microorganisms, including Fe(III)-reducing, Fe(II)-oxidizing, and magnetotactic bacteria, which take advantage of the widespread availability of iron in the environment leading to the transformation and precipitation of various iron mineral phases. In particular, Fe-metabolizing bacteria (i.e., Fe(III)-reducing and Fe(II)-oxidizing bacteria) can

induce the formation of the antiferromagnetic (see BOX 1) phases ferrihydrite ($\text{Fe}(\text{OH})_3$), goethite ($\alpha\text{-FeO}(\text{OH})$), and lepidocrocite ($\gamma\text{-FeO}(\text{OH})$), as well as the strongly ferrimagnetic phases magnetite, maghemite ($\gamma\text{-Fe}_2\text{O}_3$), and greigite, which are the major components responsible for environmental soil magnetism (Dunlop and Özdemir 2001). To date, only dissimilatory iron-reducing bacteria (DIRB) (Lovley et al. 1987), iron-oxidizing bacteria (IOB) (Miot et al. 2014), and magnetotactic bacteria (MTB) (Amor et al. 2020a) are known to synthesize nanoparticles of magnetite. DIRB and IOB are referred to as iron-metabolizing microorganisms, and gain energy from using iron as an electron acceptor or donor, respectively, to produce energy and sustain their metabolism. Alternatively, MTB accumulate iron into intracellular vesicles assembled as chains, presumably for navigation purposes. Greigite production has so far been observed in MTB only (Amor et al. 2020a).

The routes of formation of biomagnets by DIRB, IOB, and MTB are distinct from each other. In DIRB and IOB, iron is used either as an electron acceptor or electron donor for sustaining metabolic reactions (FIG. 3). The metabolic activity of these bacteria induces local modifications of the chemical conditions in the extracellular environment, which eventually leads to the precipitation of magnetite (Lovley et al. 1987). In this case, DIRB and IOB do not exert strict control over the mineral phase that precipitates, and distinct mineral phases can form depending on the local chemical conditions. DIRB gain energy from coupling the reduction of Fe(III) to the oxidation of organic compounds (Lovley et al. 1987). Alternatively, iron oxidation by IOB can occur via (i) anoxygenic photosynthesis, in which Fe(II) is used as an electron source for CO_2 reduction (Kappler et al. 2021), and (ii) indirect oxidation by nitrite released from nitrate reduction performed by denitrifying organisms (Miot et al. 2014). The latter has been shown to induce precipitation of dissolved iron into magnetite nanoparticles (Miot et al. 2014).

Contrastingly, no evidence supports that MTB gain energy from metabolizing iron. They are phylogenetically, physiologically, and metabolically diverse and thrive in aquatic environments that show vertical oxygen gradients (Amor et al. 2020a). Magnetite and greigite formation occurs in these bacteria in the intracellular medium. They exert tight control over mineral production through the action of proteins that selectively incorporate iron into organelles called magnetosomes, trigger magnetite or greigite nucleation, and mediate crystal growth to a restricted size to optimize the cell's magnetic properties through the action of dedicated genes (Uebe and Schüler 2016). Biomineralization in these bacteria is thus genetically controlled and is assumed to optimize navigation along vertical oxygen gradients in water columns or at the water-sediment interfaces in aquatic systems (Amor et al. 2020a). Magnetite- and greigite-forming microorganisms are ubiquitous in the environment. They produce ferrimagnetic crystals with unique magnetic properties that can be preserved in sediments and sedimentary rocks. These

fossil biological ferrimagnetic crystals are known as magnetofossils. Accordingly, they significantly contribute to the magnetization of sediments and sedimentary rocks.

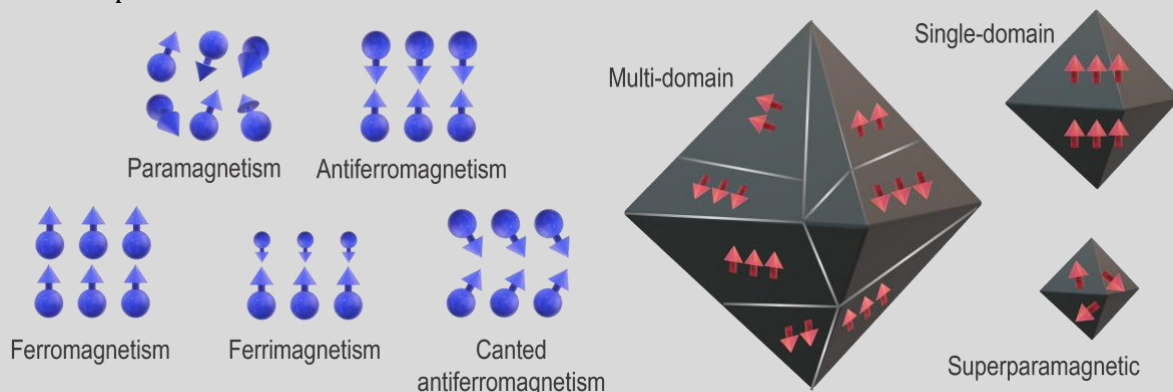
BOX 1 – TYPES OF MAGNETISM AMONG BIOMAGNETIC MINERALS

Almost all iron-containing minerals are magnetic to some degree. Thus, in a sense, all iron minerals precipitated by bacteria via biomineralization can be considered biomagnets. Nevertheless, significant differences exist in the strength of the magnetic response of these minerals depending on the arrangement of atoms within their crystal lattice. Each Fe atom has a magnetic moment, the strength of which depends on the oxidation state: Fe³⁺ and Fe²⁺ atoms have magnetic moments of 5 and 4 μ_B , respectively (μ_B denotes the Bohr magneton). In a crystal, the magnetic moments of each individual atom interact to some extent and give rise to an overall magnetic ordering, the type of which depends on how those atoms interact:

- **Paramagnetism** – Neighboring iron atoms do not strongly interact and thermal effects cause them to randomly orientate, resulting in zero net magnetic moment. Siderite (FeCO₃) exhibits this property. Paramagnets align in an applied field parallel to the applied direction.
- **Ferromagnetism** – Neighboring iron atoms strongly interact and their magnetic moments combine to create a large net moment. Elemental iron is ferromagnetic, although there is little evidence to show it is a biomagnet.
- **Antiferromagnetism** – Arises when two magnetic sublattices are arranged with equivalent but oppositely orientated (anti-parallel) magnetic moments. Examples include goethite and lepidocrocite, although goethite can be described as weakly ferromagnetic.
- **Canted antiferromagnetism** – A form of antiferromagnetism in which magnetic moments within each magnetic sublattice are not perfectly anti-parallel and, hence, result in a net magnetization. Hematite exhibits canted antiferromagnetism, but its occurrence in nature is not typically ascribed to be of biogenic origin.
- **Ferrimagnetism** – Similar to antiferromagnetism in that two sublattices are orientated anti-parallel to each other, but the net moment of the sublattices is unequal and results in a net magnetization. Magnetite is a mixed-valent mineral (i.e., it contains Fe(II) and Fe(III)) with formula Fe(III)_{tet}[Fe(II)Fe(III)]_{oct}O₄²⁻, where tet and oct indicate tetrahedral and octahedral sites, respectively. Thus, the unit formula of stoichiometric magnetite has one Fe(II) ion for every two Fe(III) ions. This imbalance of Fe ions in the sublattices causes ferrimagnetism, where the magnetic moments of Fe(III) ions cancel each other out, but leave an unbalanced magnetic moment of Fe(II) as the main component of the mineral magnetization.

The particle size can also give rise to further magnetic states:

- **Multi-domain** – Occurs in larger magnetic particles (typically >100 nm) when boundaries form between magnetic moments, resulting in multiple domains of magnetization. The net magnetization is the contribution of all the individual domains.
- **Single-domain** – A type of ferro- or ferrimagnetism (typically between 100 and 30 nm) in which the net magnetization does not vary across the particle. Magnetite formed by MTB is frequently observed to be single domain.
- **Superparamagnetism** – A special type of magnetism in which minerals with an extremely small volume behave as a paramagnet above a blocking temperature (T_B), but exhibit a magnetic moment similarly to single-domain particles below T_B . This behavior is typical of magnetite nanoparticles with a particle size below 30 nm and other biomagnets with nanoparticle dimensions.



FORMATION OF BIOMAGNETS

Biomagnet formation by BIM is most notably driven by dissimilatory Fe(III)-reducing bacteria, such as *Geobacter sulfurreducens* or *Shewanella oneidensis*. Under anoxic conditions, Fe(III)-reducing bacteria couple the oxidation of organic carbon (e.g., acetate or lactate) or hydrogen to the reduction of short-range ordered Fe(III) phases such as ferrihydrite, lepidocrocite, akaganéite (β -FeO(OH)) or goethite. This mechanism of reduction leads to the release of Fe(II), which is able to undergo secondary reactions that form mineral phases such as siderite, green rust (mixed Fe(II)–Fe(III) phases composed of $\text{Fe(II)}_{1-y}\text{Fe(III)}_y(\text{OH}_2)^{y+}$ separated by interlayers of anions (CO_3^{2-} , SO_4^{2-} , Cl^-)), or magnetite (Hansel et al 2003). The morphological, stoichiometric (i.e., Fe(II)/Fe(III) ratio), and magnetic properties of the magnetite formed through this route are strongly dependent upon a number of physical and biogeochemical parameters including pH, water content, temperature, organic matter content, Fe(III) mineral concentration, or biomass (i.e., cell number) (Hansel et al. 2003; Byrne et al. 2011). Studies have shown that physical factors such as the Fe(III) mineral surface area (i.e., the interface area between the Fe(III) mineral phase and solution containing substrate) can also affect the formation of magnetite. The particle size of biogenic magnetite also depends on the number of bacteria present during the reaction, with smaller particles (diameter ~ 10 nm) formed when cell biomass is high and larger particles (~ 50 nm) when biomass is low (Usman et al. 2018). Changes to the ratio of electron donor (e.g., acetate) to electron acceptor (e.g., ferrihydrite) also affect the microbial Fe(III) reduction rate and in turn impact the particle size of the magnetite produced. Furthermore, transition metals (e.g., zinc or cobalt) can be substituted into magnetite crystal lattice during formation, affecting the magnetic properties such as magnetization or coercivity (Usman et al. 2018). Ultimately, a wide range of parameters are responsible for the mechanism of formation of magnetite biomagnets and small changes can impact the properties of the mineral that forms.

On the oxidizing half of the microbial Fe-cycle, under neutrophilic microoxic or anoxic conditions, three distinct Fe(II)-oxidizing bacteria are known to occur. These include microaerophilic Fe(II)-oxidizers (Kappler et al. 2021), which require Fe(II) and low concentrations of oxygen, that can often be identified by the presence of enigmatic twisted stalk- or sheath-like features comprising organic matter and iron minerals such as lepidocrocite (Kirschvink and Gould 1981). Nitrate-reducing Fe(II)-oxidizers couple the reduction of nitrate to nitrite with the oxidation of Fe(II) (Miot et al. 2014), although in some cases, an organic co-substrate is required. Different iron biomagnets are produced through this mechanism, but they are typically goethite and lepidocrocite. Photosynthetic Fe(II)-oxidizers use light energy for growth via photosynthesis and oxidize Fe(II) to obtain the reducing equivalents (electrons) for CO_2 fixation (Kappler et al. 2021). To date, relatively few occurrences of magnetite formation by Fe(II)-oxidizing bacteria available

have been reported in the literature (e.g. Miot et al. 2014). This suggests that BIM via Fe(III)-reducing organisms is likely to be more widespread than via their Fe(II)-oxidizing counterparts. The reasons for this have been rarely considered, though potentially could include certain differences such as the presence of ferrihydrite nucleation sites, which are often present during microbial Fe(III) reduction, in contrast to the dissolved Fe²⁺ often used for microbial Fe(II) oxidation. Alternatively, the composition of media may play a role with many Fe(III) reduction experiments performed using pre-grown cells in the absence of nutrients or oxyanions such as phosphate, whereas most Fe(II) oxidation experiments are carried out using growing cells that require complex growth media that can affect mineral precipitation.

Unlike DIRB and IOB, MTB can produce ferrimagnetic nanoparticles, made of either magnetite or greigite, in the intracellular medium. MTB exert strict genetic control over magnetite and/or greigite formation (Uebe and Schüler 2016). The general picture of iron biomineralization in these bacteria, which has been inferred from characterization of a few magnetite-forming model strains, usually assumes four subsequent steps for magnetosome formation (FIG. 4): (i) the biogenesis of magnetosome vesicles from invagination of the inner cell membrane; (ii) the alignment of empty magnetosome vesicles as chains; (iii) iron solubilization, uptake, and trafficking to magnetosomes; and (iv) magnetite and/or greigite nucleation and maturation. All of these four steps require specific sets of genes, most of them being contained in gene clusters called the magnetosome gene clusters (Uebe and Schüler 2016).

Magnetosome vesicles originate from the inner membrane of bacterial cells. Their formation remains unclear, although magnetosome proteins required for the vesicle formation have been identified (Uebe and Schüler 2016). They create a specific environment in which iron is concentrated with basic pH and reductive redox potential conditions that are suitable for magnetite formation. Unlike DIRB and IOB, the chemical conditions of the biomineralization medium in magnetosomes is thus tightly regulated. MTB can take up both dissolved ferric and ferrous iron species from their environment. Upon iron internalization, iron is stored in the intracellular medium as oxidized species, which have been identified as ferrihydrite-like structures likely corresponding to iron bound to ferritin proteins. Iron sequestered in ferritins is then partially reduced into dissolved Fe(II) for delivery to magnetosome vesicles, likely through the magnetosome membrane (Werckmann et al. 2017).

Finally, magnetosomes are aligned in chains in the bacteria, allowing for maximized magnetic anisotropy of the cell (Amor et al. 2022). Such an energetically unfavored configuration is not shared by any other known magnetite-forming organism or environmental source of magnetite and is maintained through the activity of cytoskeletal proteins preventing particle collapse (Amor et al. 2022).

OCCURRENCE IN NATURE

Bacteria that precipitate biomagnets are ubiquitous in aquatic environments (FIG. 4). MTB have been observed in all oceans and on all continents, exhibiting vertical oxygen gradients that generate oxic/anoxic transitions with microoxic conditions (Amor et al. 2020a). These environments include deep-sea sediments, estuaries, lakes, rivers, lagoons, mangroves, and ponds. It was initially thought that MTB were restricted to habitats with circumneutral pH conditions and ambient temperatures. However, they have now been found in extreme environments as well (Lefèvre and Bazylinski 2013).

The density of MTB in the environment usually ranges between 10^3 to 10^6 cells per mL. Given their capacity to sequester large amounts of dissolved iron into the intracellular medium—up to several orders of magnitude higher than most microorganisms—MTB are thought to significantly impact the iron biogeochemical cycling in aquatic environments (Amor et al. 2020b). They could also deplete their environment in iron by transferring it from the dissolved pool to sediments. Indeed, the magnetite and greigite crystals become trapped in sediments when the cells die and can be identified magnetically (see Slotznick et al. 2023 this issue). Moreover, magnetite crystals are stable over geological time scales, with some of the putative oldest being nearly two billion years old (Amor et al. 2020a). MTB thus contribute to the magnetization of sediments and sedimentary rocks. Magnetite originating from MTB have been reported in sedimentary rocks of various ages, mostly from Phanerozoic environments. Fossils of MTB from the Precambrian eon appear to be scarcer. The chain structure of magnetite nanoparticles becomes lost over sediment aging owing to the degradation of proteins assembling magnetosome chains, leading to magnetite agglomeration. Under these conditions, MTB fossils cannot be differentiated from clusters of abiotic magnetite nanoparticles.

DIRB have been found in a wide range of habitats, including wetlands, anoxic sludge, contaminated land, and the deep subsurface (Nixon et al. 2022). Not all of these strains or the habitats in which they have been identified are conducive to the formation of magnetite, although one can speculate that many of these bacteria could be responsible for the magnetic enhancement of soils (Maxbauer et al. 2016). In fact, paleosols in the Chinese loess plateau in north-central China are thought to retain a “magnetic memory” of past rainfall over several hundred thousand years as a result of DIRB. A linear correlation between magnetic susceptibility and mean annual rainfall was reported for several locations in the plateau (Maher et al. 1994). It is thought that DIRB activity was low during glacial dry periods, thus leading to less biomagnetite formation than during interglacial wet periods. This is likely due to the extent of anoxia in soils, which is essential for magnetite precipitation. No studies have yet commented on the formation of biogenic

magnetite in the environment by IOB, but given their ubiquity and suitable geochemical conditions, this contribution should not be overlooked.

FUNCTIONS OF BIOMINERALS

The biological functions of intracellular, genetically controlled biomineralizations are better constrained than distinct types of biomineralizations occurring in the extracellular medium. This statement is also valid in the case of magnetite biomineralization, even though recent advances have shed new light on the potential evolutionary benefits of magnetite precipitation for DIRB and IOB.

The chain assembly of magnetosomes provides a permanent dipole to MTB, which allows the cell to passively align with the geomagnetic field. This behavior is known as “magnetotaxis” and helps MTB to efficiently swim downward or upward along vertical chemical gradients in aquatic environments to reach their preferred microoxic conditions at the oxic/anoxic transition zones (Frankel et al. 1997). Magnetotaxis thus represents a selective advantage for magnetotactic microorganisms by limiting environmental prospection for energy sources and electron acceptors to bidirectional transects instead of a volume. The magnetotaxis hypothesis is supported by field observations where MTB have consistently been observed at oxic–anoxic transitions under microaerophilic conditions (Bidaud et al. 2022). This hypothesis has also received further validation from laboratory studies showing that MTB move rapidly away from advancing oxygen gradients (Frankel et al. 1997), and that such behavior is enhanced in the presence of an external magnetic field (Smith et al. 2006).

Additional biological functions of magnetosomes have also been proposed. It could be speculated that magnetosomes play a role in iron storage. However, no experimental evidence supporting this notion has yet been provided. Alternatively, magnetosomes could be used as energy-storing systems by oxidizing magnetite into maghemite under oxidative conditions, thus releasing electrons that could be used as a source of chemical energy for sustaining the cell’s metabolism (Byrne et al. 2015). According to this picture, maghemite would then be reduced back to magnetite under reductive conditions for electron storage. This “battery” hypothesis has not received experimental support in the case of MTB (see below for DIRB and IOB) and leaves open questions about the cellular machinery that would be required for sustaining metabolic reactions. Finally, the magnetosome membrane exhibits a peroxidase-like activity eliminating reactive oxygen species in the cell (Guo et al. 2012). Magnetosomes could thus be used for overcoming oxidative stress, although the use of magnetite crystals for reactive oxygen species detoxification

remains unclear given that magnetite itself can generate oxidative stress through Fenton reactions.

The type of biomagnets produced by DIRB and IOB strongly depends on the environmental geochemical conditions in which they precipitate. This suggests that no direct function of biomagnets exists for these bacteria. Instead, they can be considered more as a product of electron transfer processes that induce mineral transformation. Exceptions include the aforementioned “battery” hypothesis, which could potentially aid both DIRB and IOB in conditions poor in electron acceptors (DIRB) or donors (IOB). Magnetite has also been suggested to act as a conduit for electron transfer by *Geobacter sulfurreducens* and compensate for proteins known to mediate electron transfers in bacterial cells (c-type cytochromes) (Liu et al. 2015). Neither of these potential functions suggest directed precipitation of magnetite by the bacteria. In terms of the weakly magnetic biomagnets, however, it has been suggested that some nitrate-reducing IOB precipitate goethite as a form of UV protection, although questions remain about the enzymatic capabilities for such bacteria to directly oxidize iron (Kappler et al. 2021).

PROPERTIES OF BIOMAGNETS

Biomagnets harbor specific chemical, isotopic, and magnetic properties distinct from abiotic nanoparticles. This is especially true for those made by MTB because of the specific mineralization pathways in these organisms.

DIRB, IOB, and MTB all produce nanometer-sized ferrimagnetic particles, but biologically controlled mineralization actively maintains the size of the particles to be both large enough to maintain a magnetic moment at room temperature and small enough to prevent nucleation of several magnetic domains in a single particle (typically 30–200 nm depending on the nanoparticle morphology that is strain specific) (Muxworthy and Williams 2009). Thus, magnetite and greigite in MTB correspond to permanent magnets, while the smaller size of DIRB and IOB magnetite (<30 nm) makes it magnetically unstable at room temperature. In addition, the chain arrangement of magnetite and greigite in MTB align the particles’ magnetic moments, thus maximizing the magnetic anisotropy (Amor et al. 2022). Such configuration is not shared by any other source of magnetite and greigite in the environment and is, therefore, a distinctive property that can be used to track the occurrence of MTB in the geological record. Ferrimagnetic particles generated by biologically induced mineralization cannot be distinguished from abiotic nanoparticles using magnetic methods owing to the agglomerated nature of magnetite nanocrystals (Amor et al. 2020a).

In addition to magnetic specificities, controlled mineralization imparts unique chemical properties to biomagnets. MTB sequester iron in magnetosome vesicles for magnetite and greigite precipitation. Consequently, contaminant chemical elements are excluded from the biomineralization process and cannot incorporate into magnetite and greigite. Alternatively, nanoparticles precipitating in the external solution are in contact with contaminant elements, which can thus substitute with iron and incorporate into the crystal lattice. Accordingly, the chemical composition of biomagnets produced by MTB is purer than nanomagnets precipitated either abiotically or by DIRB and IOB (Amor et al. 2020a and references therein). Two exceptions identified to this general picture have been identified: molybdenum and tin show higher affinities for MTB magnetite (i.e., incorporation increased by up to four orders of magnitude) than its abiotic counterpart. The reason for such enrichment in MTB magnetite remains unclear, but could originate from the metabolic importance of these elements, which must be incorporated into the intracellular medium, in contact with magnetite, to sustain the metabolic activity of bacteria (Amor et al. 2020a and references therein). Even though DIRB magnetite shows high incorporation of contaminant trace elements, the partitioning of zinc and nickel has opposite trends when compared with abiotic synthesis: zinc was systematically more incorporated into abiotic magnetite, while nickel can be preferentially incorporated into DIRB magnetite (Han et al. 2021). These results suggest that DIRB can also alter the transfer of trace elements between the external precipitation solution and forming magnetite crystals.

Finally, the iron isotope composition of magnetite has been explored in abiotic syntheses, MTB, and DIRB. During abiotic formation from oxidation of soluble Fe(II), heavy iron isotopes preferentially precipitate into magnetite whereas light isotopes become enriched in the residual soluble fraction (Friedrich et al. 2014). DIRB use ferric mineral phases, such as ferrihydrite, as an electron acceptor to enable cell respiration. This leads to Fe(III) reduction and solubilization into Fe(II). The solubilized iron fraction has been shown to be enriched in light isotopes relative to the ferrihydrite substrate (Crosby et al. 2007). Part of the dissolved Fe(II) then adsorbs onto ferrihydrite, which triggers ferrihydrite transformation into magnetite. The adsorption step further enriches the soluble fraction in light isotopes. Therefore, both abiotic and DIRB magnetite samples possess isotopic compositions favoring heavy isotopes. Again, MTB show a very different picture. They incorporate iron from their environment with a slight enrichment in heavy isotopes, which is then stored in the intracellular medium as Fe(III) species bound to proteins (Amor et al. 2020a and references therein). Such oxidized fraction is then partially reduced into Fe(II) for delivery to magnetosomes and magnetite formation. The reduction step creates large isotope fractionations, with light isotopes being strongly enriched in the soluble Fe(II) pool. Consequently, magnetite in MTB is strongly enriched in light isotopes relative to the external solution (Amor et al. 2020a and references therein). To date, no other mechanism than biologically controlled

mineralization is known to generate magnetite crystals enriched in light iron isotopes when compared with the precipitation solution. In addition, isotopic anomalies have been detected in MTB magnetite. Indeed, the isotope ^{57}Fe is preferentially incorporated into magnetite relative to the three other stable iron isotopes ^{54}Fe , ^{56}Fe , and ^{58}Fe (Amor et al. 2020a and references therein). These so-called mass-independent fractionations have never been observed before and thus constitute a unique feature of MTB magnetite.

CONCLUSION

Biomagnetism and biomagnets are everywhere. Whether precipitated by bacteria or by microorganisms in association with eukaryotes (see Leão and Lefevre 2023 this issue), we are only just beginning to explore and understand the importance of biomagnetism to the natural world. While most studies point to the function of biomagnetism as navigation, questions remain regarding whether other functions exist, such as energy conservation. Regardless, the future directions of biomagnetism are exciting and this issue introduces a wide range of aspects including how magnetofossils are being used to reveal ancient terrestrial and extra-terrestrial life (see Slotznick et al. 2023 this issue), the role of biomagnetism in biogeochemical cycling (see Kappler et al. 2023 this issue), and the applications of magnetic minerals produced by bacteria for catalysis, metal recovery, and in medicine (see Gandarias et al. 2023 this issue).

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FIGURES



FIGURE 1: Magnetite is ubiquitous in the environment and is found with a range of particle sizes including **(A)** nanoparticles from dissimilatory iron-reducing bacteria, **(B)** abiogenic millimeter grains of magnetite from La Serena, Chile, and **(C)** a large crystal of abiogenic magnetite from Russia. PHOTOS: JAMES BYRNE

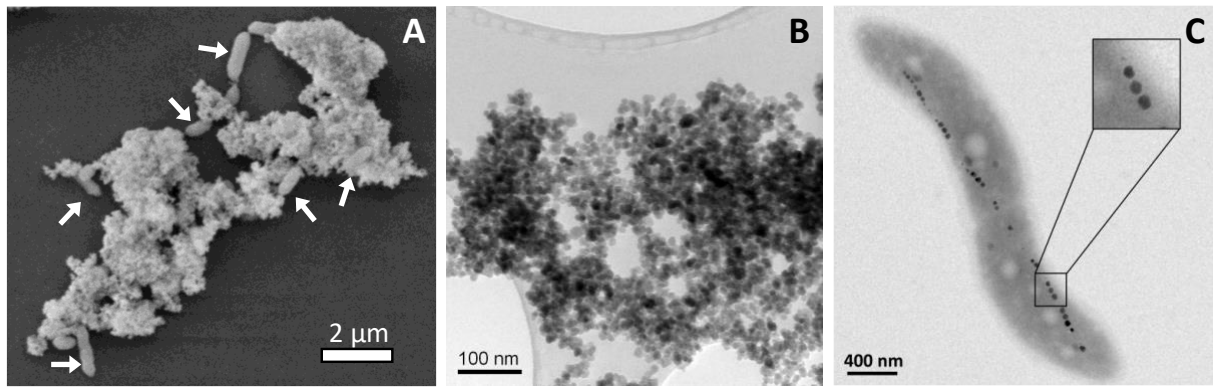


FIGURE 2: (A) Scanning electron microscopy micrograph indicating magnetite associated with *Geobacter sulfurreducens* (arrows). (B) Transmission electron microscopy (TEM) micrograph of magnetite nanoparticles from *Geobacter sulfurreducens*. (C) TEM image of the magnetotactic bacterium *Magnetospirillum magneticum* strain AMB-1 containing chains of magnetite nanoparticles (INSET).

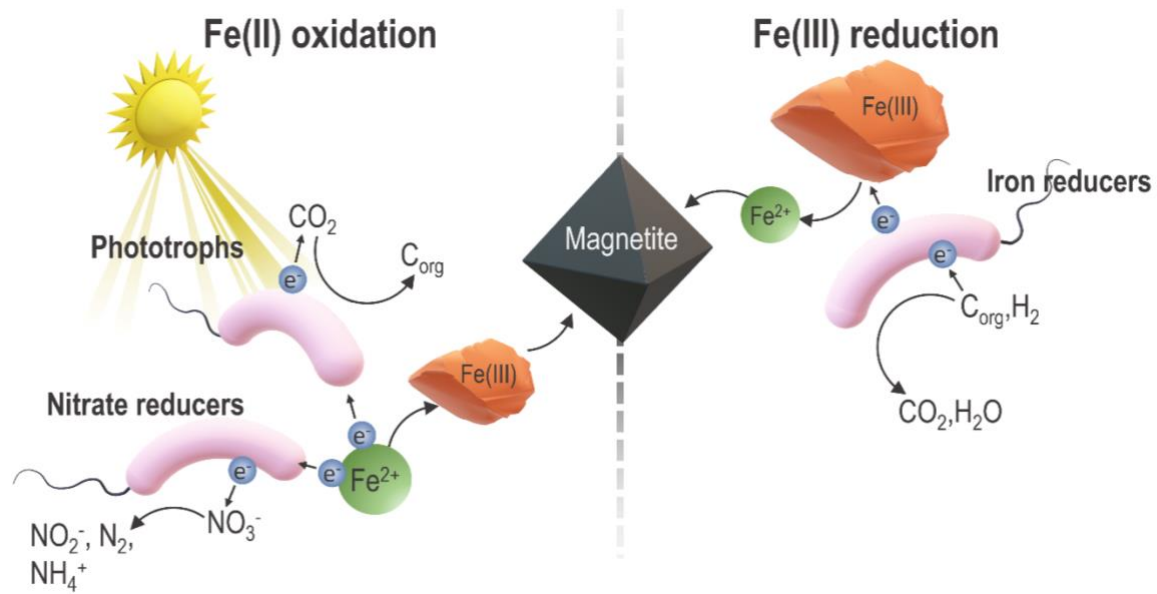


FIGURE 3: Summary of biomagnet (magnetite) formation through biologically induced mineralization either by iron reducers (Fe(III) reduction pathway) or iron oxidizers (phototrophs and nitrate reducers, Fe(II) oxidation pathway). Phototrophic iron oxidizers use sunlight and reduce CO_2 to organic carbon (C_{org}); nitrate reducers use nitrate as an electron acceptor and dissolved Fe^{2+} as an electron donor. Iron-reducing bacteria use short-range-ordered Fe(III) phases as electron acceptors and oxidize C_{org} . Curved arrows denote species transformation; straight arrows denote electron movement.

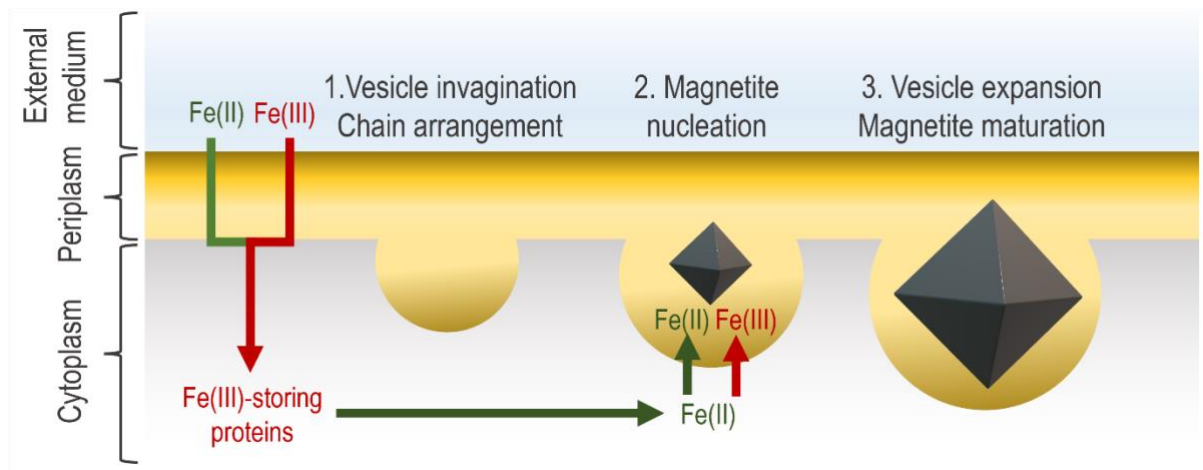


FIGURE 4: Model for magnetosome formation and iron biomineralization in magnetotactic bacteria. First, magnetosome vesicle invaginate from the inner cell membrane. Second, vesicles are arranged in chains and magnetite nucleates in empty magnetosomes. Iron is incorporated as reduced $[\text{Fe(II)}]$ and/or $[\text{Fe(III)}]$ species and stored in the intracellular medium as oxidized iron bound to proteins. Partial reduction of this pool generates Fe(II) for delivery to magnetosomes, in which Fe(II) is partially oxidized for magnetite precipitation. Finally, magnetite size and shape are tightly controlled to provide a magnetic dipole to the bacteria. Green and red arrows point to the reduced $[\text{Fe(II)}]$ and oxidized $[\text{Fe(III)}]$ pathway, respectively.

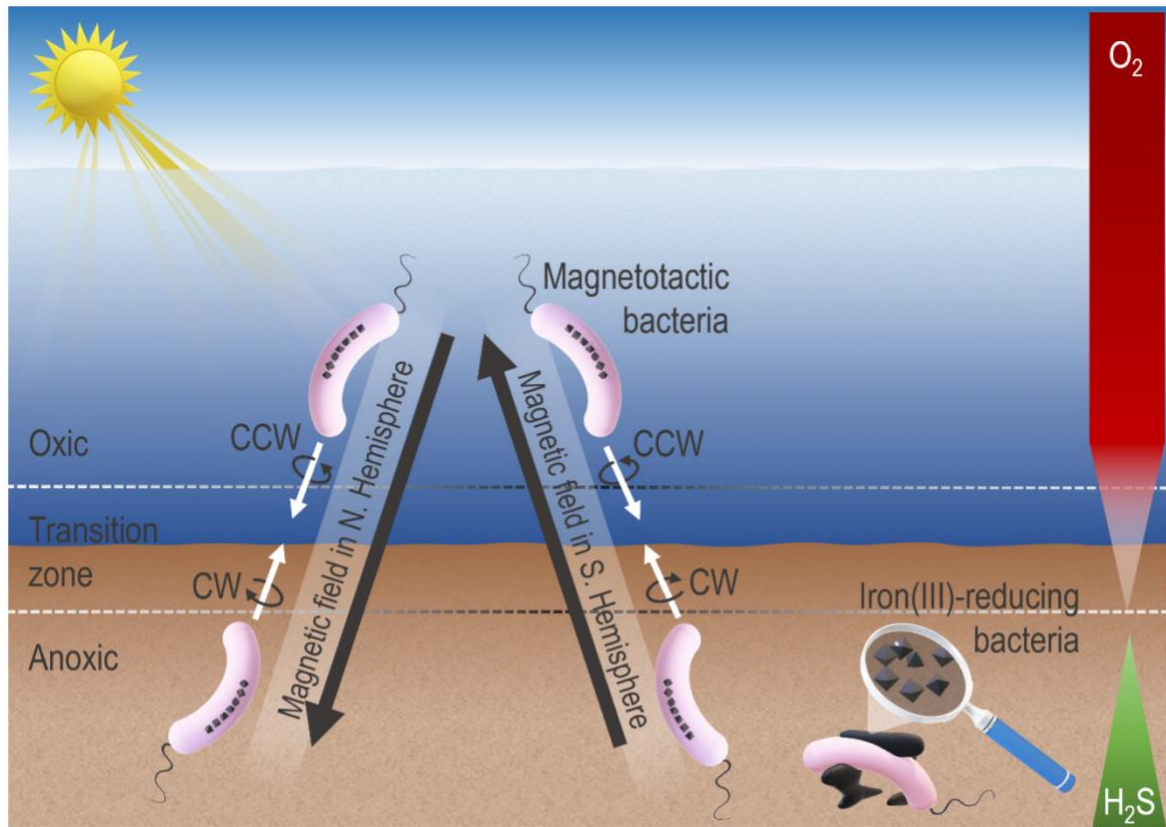


FIGURE 5: Occurrence of magnetotactic bacteria (MTB) and dissimilatory iron-reducing bacteria (DIRB) in nature. MTB traverse along vertical oxygen gradients along the oxic-anoxic transition zone using magnetotaxis to define their direction of travel (white arrows). Depending on the direction of the magnetic field in the Northern or Southern Hemisphere, the bacteria swim clockwise (CW) or counterclockwise (CCW) across the transition between oxic and anoxic zones. DIRB only produce ultrafine magnetite nanoparticles under anoxic conditions via biologically induced mineralization.