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Review

Magnetic microbes: Bacterial magnetite biomineralization

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ABSTRACT

Magnetotactic bacteria are a diverse group of prokaryotes with the ability to orient and migrate along the magnetic field lines in search for a preferred oxygen concentration in chemically stratified water columns and sediments. These microorganisms produce magnetosomes, the intracellular nanometer-sized magnetic crystals surrounded by a phospholipid bilayer membrane, typically organized in chains. Magnetosomes have nearly perfect crystal structures with narrow size distribution and species-specific morphologies, leading to well-defined magnetic properties. As a result, the magnetite biomineralization in these organisms is of fundamental interest to diverse disciplines, from biotechnology to astrobiology. This article highlights recent advances in the understanding of the bacterial magnetite biomineralization.

Contents

1. Introduction

Biomineralization is a process by which living organisms convert chemical elements obtained from the local environment into minerals, producing functional organic–inorganic biocomposites. In biologically induced mineralization, the inorganic phase is formed by adventitious precipitation. In biologically controlled mineralization, proteins and other biological macromolecules are thought to play an important role in controlling the size and shape of the forming biomineral [1]. The products of biomineralization, such as silica shells of diatoms or skeleton in animals, provide a number of benefits to the organism and often exhibit superior physical and chemical properties as compared to their synthetic counterparts.

Iron is the fourth most common chemical element on our planet, as reflected by the abundance of iron-based minerals [2]. Metallic iron, found in meteorites and in the Earth's inner and outer core, is not very common on the planetary surface, as it tends to oxidize to produce a variety of oxides and oxyhydroxides [2]. Due to the presence of iron's unpaired electrons, these compounds are magnetic, with magnetite being the most magnetic of all naturally occurring minerals on Earth. Present in many rocks, small magnetite crystals typically carry the dominant magnetic signature, preserving the record of the geomagnetic history of our planet. This is of great importance to paleogeomagnetism, magnetohydrodynamics, and other scientific fields.

Iron cycling on Earth is an extremely complex biogeochemical process involving both abiotic and biotic components, and magnetite is also common among biogenic materials. It is found as biochemical precipitate in four out of the five kingdoms of living organisms (Monera, Proctista, Animalia, and Plantae), however has not yet been recorded in fungi. Millions of creatures, from fishes and sea turtles, to birds and numerous insects, migrate to spawn and reproduce, often against adverse conditions. Some navigate vast distance to the exactly same place, year after year, while others do this only once and then die. The mechanisms of magnetosensing in these animals, viewed as a trait of complex and highly evolved

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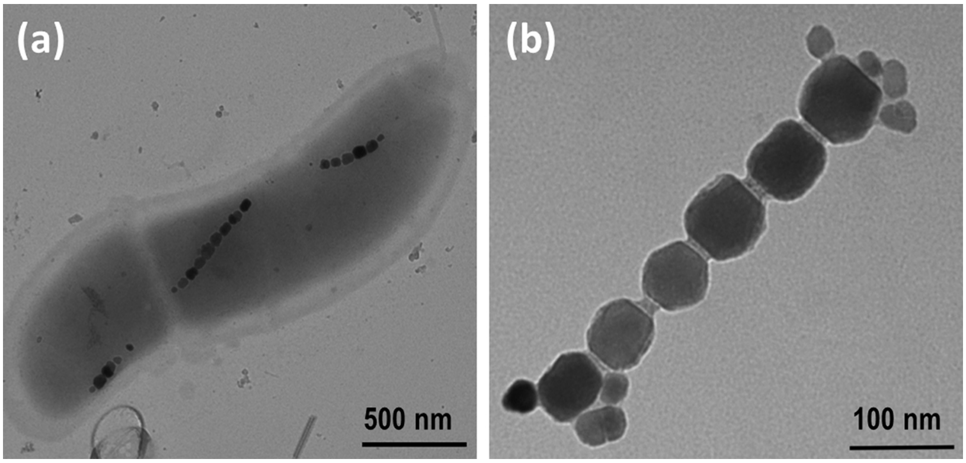

Fig. 1. (a) Transmission electron micrographs of a typical unstained magnetotactic bacterium. Shown is a cell of *Magnetospirillum magneticum* strain AMB-1 with electron-dense magnetite magnetosomes inside. The "broken" appearance of the chain of magnetosomes is brought about by 2D projection of the three-dimensional bacterial cell. (b) Nanocrystalline magnetite chain harvested from lysed bacteria with magnetite nanocrystals. Notably, even after lysis individual magnetite crystals are held together by a thin phospholipid membrane material.

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living systems, continue to fascinate and puzzle researchers [3,4]. But there are other, small and previously thought to be simple organisms responding to the Earth's magnetic field, the subject of this review.

2. Magnetotactic bacteria

The smallest known organisms that respond to magnetic fields are magnetotactic bacteria. The term "*magnetotactic bacteria*" represents a diverse group of fastidious microorganisms with the cellular morphologies ranging from coccoid (ovoid), vibroid (curved rod-shaped) and spirilloid (helical), to multicellular organisms [3,5–7], as exemplified in Fig. 1. These are heterogeneous group of Gram-negative bacteria sharing the ability to orient in magnetic field. These microorganisms, found in freshwater and marine sediments around the world, produce chains of unique intracellular structures called *magnetosomes*, comprised of magnetic magnetite (Fe_3O_4) or greigite (Fe_3S_4) nanometer-sized crystals enveloped in a 2–3 nm thick phospholipid bilayer membrane [5]. Although these microorganisms were discovered more than four decades ago and extensively studied, the exact biomineralization mechanisms of how they synthesize these mineral crystals remain poorly understood, in part because these microbes are notoriously difficult to handle [5,8–12]. Based on the biomineral formed, magnetotactic bacteria can be divided into two general types: the obligate microaerophiles, facultative anaerobes, or obligate anaerobes iron-oxide types that mineralize crystals of magnetite (Fe_3O_4), and the obligate anaerobes iron-sulfide types that mineralize crystals of greigite (Fe_3S_4) [13]. Recently, a greigite-producing magnetotactic bacterium, strain BW-1, was shown to biomineralize greigite and magnetite depending on culture conditions [14]. Common traits of the magnetotactic bacteria as a group include motility by means of flagella, negative tactic and often growth response to atmospheric concentrations of oxygen, respiratory form of metabolism in pure culture, and formation of magnetosomes. The latter is governed by specific gene clusters.

Iron can account for over 2% of the total weight in these bacterial cells, making them highly magnetic [15–18]. Regardless of the type of the biomineral, the magnetosome crystals are in the single magnetic domain size range (35–120 nm), which have the highest possible magnetic moment per unit volume. In most magnetotactic bacteria, the arrangement of magnetosome crystals in chain along the long axis of the cell yields maximal magnetic dipole moment to the cell. This arrangement was long believed to be due to magnetic interactions between individual magnetosomes within the chain. However, cytoskeletal elements have now been shown to play a major role in magnetosome chain formation, thereby anchoring the chain within the cell [12,19,20].

3. Ecology, diversity, genetics, and cell biology

Magnetosome chains act as miniature compass needles, torqueing the bacteria into alignment with the Earth's geomagnetic field lines. This passive alignment allows the cell to efficiently migrate and seek the boundary in liquid known as oxic–anoxic interface, which is characterized by opposing gradients of oxygen from the surface and reduced compounds (usually, sulfur) in water columns or sediments [5]. This phenomenon is known as magneto-aerotaxis, or magnetically assisted aerotaxis. Use of the magnetosome chain, arguably, reduces the random three-dimensional bacterial movement to a one-dimensional search for an optimal oxygen concentration, likely providing an advantage over other non-magnetotactic microorganisms.

Before the advent of molecular phylogenetics, the considerable morphological diversity of magnetotactic bacteria was apparent from light microscopic observations of environmental samples of water and sediment. The phylogenetic diversity of magnetotactic bacteria, based on their 16S rRNA gene sequences, is relatively extensive. Most known cultured and uncultured magnetotactic bacteria belong to the *Alpha*-, *Gamma*-, and *Deltaproteobacteria* classes of the *Proteobacteria* phylum, however several uncultured species are affiliated with the *Nitrospirae* phylum, and one, strain SKK-01, was assigned to the candidate division OP3, part of the *Planctomycetes- Verrucomicrobia-Chlamydiae* (PVC) bacterial superphylum [10,21–27].

In magnetite-producing magnetotactic bacteria, proteins present in the magnetosome membrane control biomineralization of the magnetite crystal. These proteins are encoded by the magnetosome genes present as clusters within the genomes of all examined magnetotactic bacteria so far [21,22,24–26]. The functions of several of these genes and their associated proteins in magnetosome synthesis and construction of the magnetosome chain have been elucidated through bioinformatics and experimental evidence [26]. These clusters are in relatively close proximity to each other within the genomes, and are surrounded or interrupted by certain types of genomic structures. The latter