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REVIEW PAPER

Magnetic Inclusions in Prokaryotic Cells

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Abstract—Prokaryotic cells may contain one of two types of magnetic intracellular structures, either crystalline magnetosomes or noncrystalline magnetic inclusions. In a magnetic field, the locomotor behavior of cells containing magnetosomes is categorized as magnetotaxis, whereas noncrystalline magnetic inclusions cause a passive attraction of cells containing such inclusions to a magnet. This review considers the distribution, structure, and function of both types of magnetic particles in prokaryotic cells.

Key words: magnetotaxis, magnetosomes, noncrystalline magnetic inclusions.

The Earth's magnetic field is believed to have existed before life appeared on the Earth, so that organic evolution took place in the geomagnetic field and under its direct influence [1]. The behavior of living organisms in magnetic fields has long attracted researchers' attention. During the last 30 years, it has been proved that all organisms, from bacteria to vertebrate animals, can respond to changes in geomagnetic or artificial magnetic fields.

It is well known that many insects, fishes, birds, and dolphins can orient in the geomagnetic field. Animals respond to magnetic fields with the aid of magnetoreceptors, i.e., cells containing magnetite crystals either in a single-domain saturation state or superparamagnetic state [2, 3]. Such cells do not form a special organ; magnetite particles were found even in the human hippocampus [4]. Erythrocytes occurring in a strong static magnetic field align along lines of force [5]. Prokaryotic cells were found to contain at least two types of magnetic particles [6, 7].

This review concentrates on crystalline magnetosomes and noncrystalline magnetic inclusions occurring inside prokaryotic cells, without giving consideration to the magnetic iron compound (ferrihydrite) deposited outside or on the surface of cells of iron bacteria and with the extracellular magnetite particles of iron-reducing bacteria [8].

THE GENERAL MAGNETIC PROPERTIES OF BACTERIAL CELLS

The magnetic properties of chemical elements and substances are determined by the small magnetic moments of electrons in their atoms. Most organic substances are diamagnetic; consequently, the magnetic susceptibilities of most living cells, including bacterial, are negative. The susceptibility magnitudes of cells are highly variable, due to different concentrations of paramagnetic compounds in the cells [9].

The paramagnetic compounds of cells are bacterioferritin, chromoproteins (cytochromes), ferredoxins, other metal-containing proteins, as well as short-lived free radicals, which are perpetually produced in cells in various redox reactions [9]. The magnetic properties of cells, which are determined by the proportion between cellular dia- and paramagnetic compounds, considerably depend on cultivation conditions, particular metabolic characteristics of cells, and their ability to transform ferromagnetic, particularly iron-containing, compounds [10].

The magnetic properties of cells can be studied by nuclear magnetic resonance and by measuring their magnetic susceptibility by the Faraday method. The physiological role of iron metabolism in heterotrophic bacteria is to provide their biosynthetic requirements with necessary iron compounds and to protect cells from excess iron by transforming it into nontoxic forms. The Fe(III) compounds present in nutrient media dissociate with the formation of monomeric hydrate complexes, which are transported across the cell wall and reduced by iron reductases. The reduction products penetrate the cytoplasmic membrane and are oxidized in the cytoplasm to low-density hydroxides [10]. The latter are dehydrated to form ferrihydrite. The accumulation of magnetically aligned crystals of ferrihydrite in the cytoplasm increases the paramagnetism of cells. This process is most active under unfavorable growth conditions. The para- and diamagnetism of cells and the amount of magnetically aligned compounds in cells considerably depend on the physiological and biochemical peculiarities of microorganisms [10].

The magnetic properties of cells determined by the processes described above are too weak to provide for

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the motion of the cells in an external magnetic field. However, there are two types of intracellular structures, crystalline and noncrystalline magnetic inclusions, which make such motion possible. In this case, the noncrystalline magnetic inclusions are responsible for the attraction of cells to the magnet, whereas the crystalline inclusions are responsible for magnetotaxis, i.e., the orientation and active motion of bacterial cells along magnetic field lines.

MAGNETOTACTIC BACTERIA WITH CRYSTALLINE MAGNETIC INCLUSIONS (MAGNETOSOMES)

The mechanism of the magnetic susceptibility of magnetotactic bacteria was studied in detail by Blakemore [6]. Magnetotactic bacteria are a diverse group of microorganisms capable of producing magnetosomes, i.e., ferrimagnetic crystals of magnetite or greigite bounded by a three-layer membrane. Due to the presence of magnetosomes, each magnetotactic cell represents a magnetic dipole, which, when in a magnetic field, behaves as a magnetic compass needle. In the Northern Hemisphere, most cells in a population of magnetotactic bacteria are oriented and migrate northward (toward the magnetic North Pole). In contrast, most magnetotactic cells from Southern Hemisphere habitats seek the south. In either of the Hemispheres, the nonzero vertical component of the geomagnetic field selects bacterial cells of the respective polarity, causing them to sink. On the Earth's magnetic equator, where this vertical component is equal to zero, magnetotactic cells move along the horizontal component of the geomagnetic field [11].

The Physiological and Morphological Characteristics of Magnetotactic Bacteria

Magnetactic bacteria are very diverse both morphologically and physiologically. Spring and Schleifer described magnetotactic bacteria in the form of rods of different size, cocci, vibrios, and spirilla [12]. Rodgers *et al.* [13] reported on a very specific many-celled magnetotactic prokaryote, which is made up of 10–30 rounded cells connected by an intercellular membrane. All of the known magnetotactic bacteria are gram-negative cells with monotrichous, amphitrichous, or lophotrichous flagella. The magnetotactic many-celled prokaryotes have flagella on the outer surface of each constituent cell. Magnetotactic bacteria with lateral or peritrichous flagella are presently unknown [14].

Magnetotactic bacteria are difficult to isolate and maintain in pure cultures, which explains why only a few pure strains of such bacteria have been described. Among them, there are two species of the genus *Magnetospirillum*, *M. magnetotacticum* and *M. gryphiswaldense* [15], and several strains with unknown taxonomic affiliation (microaerophilic cocci, facultatively anaerobic vibrios [12], and the sulfate-reducing dissimilatory obligate anaerobe RS-1 [16]). Most of these strains are chemoheterotrophic. Marine magnetotactic cocci, which can be grown only in the counter gradient of oxygen and sulfide, are capable of chemolithoautotrophic growth with sulfide or thiosulfate as electron donors [14].

Magnetosomes

Bacterial magnetosomes represent single crystals of magnetite or greigite bounded by a three-layer membrane. The size, shape, and alignment of magnetosomes inside cells are species- or even strain-specific [11]. Table 1 summarizes data on the chemical composition, size, shape, and intracellular localization of magnetosomes in some magnetotactic bacteria.

Magnetite and greigite crystals have an inverse spinel structure, with Fe^{2+} and half of the Fe^{3+} ions occurring at the octahedron vertices and the remaining Fe^{3+} ions occurring at the tetrahedron vertices. This structure is ferrimagnetic, since the parallel magnetic moments of the octahedron atoms are antiparallel to the magnetic moments of the tetrahedron atoms [17]. Such a structure of the crystalline lattice allows the existence of crystals of different morphology. Indeed, magnetotactic bacteria were found to contain magnetosomes in the form of truncated octahedrons, parallelepipeds, hexagonal prisms, teardrops, floc, arrowheads, bullets, and beans [16, 18]. At the same time, abiogenic magnetite crystals usually have a cubic–octahedral form [14].

Most of the magnetosome crystals have narrow-range sizes (35–120 nm for magnetite and 67–100 nm for greigite [19]), which correspond to the theoretical size of single-domain magnetic particles, possessing the properties of a permanent magnet [20]. The failure of attempts to demagnetize magnetotactic bacteria or the magnetite crystals isolated from them confirms the supposition that biogenic magnetite crystals consist of a single domain [17]. The existence of unusually large magnetosomes from 120 to 200 nm in size (these correspond to the theoretical size of two-domain magnetite crystals) can be explained by the fact that the theoretical size of a magnetic domain calculated for the zero strength of a magnetic field may not correspond to the actual size of such domains under the conditions typical of the cell interior [20].

The limited sizes of magnetosomes and the existence in magnetotactic bacteria of crystalline magnetic structures (such as hexagonal prisms and arrow-like crystals) that are not encountered in abiogenic magnetic minerals allowed Stolz to suggest that the magnetosomes are formed under the stringent control of the bacterial cell [21]. Most relevant studies were performed on available pure cultures of *Magnetospirillum* bacteria [22]. It was found that at least three groups of genes are involved in the regulation of magnetite formation in the *M. magnetotacticum* strain AMB-1,

Table 1. Some characteristics of magnetotactic bacteria and their magnetosomes

Magnetotactic bacteria	Relevance to oxygen	Composition, structure, and localization of MSs	Taxonomic position according to [23]	Ref.
"*Magnetobacterium bavaricum*," 1.5–2 × 8–10 μm	Presumably microaerophile	Up to 1000 bullet-shaped magnetite MSs, 110–150 nm in size, arranged in several chains	Phylogenetic group *Nitrospirae* phy. nov. Class "Nitrospirae"	[12]
Magnetospirillum magnetotacticum	Obligate microaerophile	One chain of 15–40 magnetite MSs with the CO structure, 40 nm in diameter	Phylogenetic group *Proteobacteria* phy. nov. Class "*Alphaproteobacteria*"	[13]
M. gryphiswaldense	Obligate microaerophile			[13]
"*Bilophococcus magnetotacticus*"	Presumably microaerophile	15–40 magnetite MSs in the form of HP, 60 × 100 nm between the bundles of flagella		[12]
Marine coccus MC-1	Obligate microaerophile	Extended magnetite HPs		[20]
1.4-μm cocci and rods, 2.2 × 2.4 μm in size	Presumably microaerophile	Two chains of unusually large magnetite MSs in the form of truncated RP, 160 × 200 nm in size		[20]
Marine vibrios MV-1 and MV-2, and spirilla MV-4	Facultative microaerophiles	One chain of 10 magnetite MSs in the form of RP, 40 × 60 nm		[21]
Sulfate-reducing bacterium RS-1	Obligate anaerobe	Magnetite, beanlike inclusions	Phylogenetic group *Proteobacteria* phy. nov. Class "*Deltaproteobacteria*"	[25]
MMP composed of 10–30 cells, 0.6–0.8 × 0.8–1.4 μm in size, the total length 12.5 μm	Presumably obligate anaerobe	2 to 65 greigite and pyrite particles, 50–90 nm in size, of irregular shape and arrangement		[13]
Marine curved MTB, 1.4 × 3.9 μm in size	Presumably anaerobe	Pleiomorphic particles localized along one side of the cell	ND	[19]
Marine rodlike bacterium, 1.3 × 3 μm in size	Presumably anaerobe	Two chains of 30–40 magnetite MSs in the form of arrowhead and 20 greigite MSs in the form of truncated RP	ND	[19]
Freshwater rodlike bacterium, 2–4 × 7–15 μm in size	Presumably microaerophile	Thousands of bullet-shaped magnetite MSs throughout the cytoplasm	ND	[18]
Bacterium, 1.8–2.8 × 2.2–3.4 μm in size	Presumably microaerophile	Hundreds of bullet-shaped magnetite MSs arranged in radial or central chains	ND	[18]

Note: MC, magnetosome; CO, cubic–octahedral; HP, hexagonal prism; RP, rectangular prism; MMP, magnetotactic many-celled prokaryote; MTB, magnetotactic bacterium; ND, no data available.

although the entire genetic mechanism of magnetite formation was not clearly understood [11].

All magnetite-based magnetosomes are single crystals of Fe_3O_4 surrounded by the amorphous hydrate of ferric oxide (the ferrihydrite $5Fe_2O_3 \cdot 9H_2O$). At neutral pH and a redox potential equal to about 100 mV, ferrihydrite undergoes a phase transition into magnetite, about one-third of the Fe(III) ions being reduced to Fe(II) ions [21].

Supposedly, the magnetosome membrane originates from the cytoplasmic membrane of bacterial cells and remains bound to this membrane, due to which magnetosomes in the cells are arranged in the form of chains. The magnetosome membrane vesicles exist in *Magnetospirillum* cells before the mineral phase begins to form and can be detected when there is iron deficiency in the cultivation medium [11]. The three-layer membrane of a growing magnetosome provides for its growth in a certain direction (due to the anisotropic penetration of ions into the magnetosome compartment and the spatial interaction between the membrane and the growing magnetosome [17]), thus determining the specific shape and orientation of the crystal. The mechanisms underlying these processes remain poorly understood [11].

Most of the known magnetotactic bacteria contain magnetosomes that are similar in size, arrangement, and composition (but not in number) and specific for particular species (or even strains) [14]. Some magnetotactic bacteria, however, contain magnetosomes that are very inhomogeneous in size, shape, and chemical composition. In areas with a high content of sulfides, there occur many-celled magnetotactic prokaryotes, which contain single or double chains of greigite-based

magnetosomes and nonmagnetic pyrite particles in their cytoplasm. Each of these chains may contain crystals of different morphology but similar sizes (within 50–90 nm). Particles of pyrite prevail over the greigite particles. How the greigite and pyrite particles alternate in a chain and the function of pyrite particles in magnetosomes is unknown [21]. Some greigite and pyrite particles of many-celled magnetotactic prokaryotes contain copper, and the magnetite crystals of one of the nonculturable magnetotactic cocci contain titanium in trace amounts [12]. The magnetotactic bacteria described by Bazylinski *et al.* [19] produce both magnetite- and greigite-based magnetosomes. The chains of magnetosomes formed by these two ferromagnetic minerals differ in the morphology and crystallographic orientation of constituent crystals [17].

Magnetosomes occurring in a cell are most commonly arranged in one or several chains along the long axis of the cell, the direction of the easy magnetization of crystals being parallel to the axis of these chains. Due to such an arrangement of magnetosomes and the single-domain structure of crystals, magnetotactic bacterial cells represent magnetic dipoles and behave in an external magnetic field like a compass pointer, passively orienting along the magnetic field lines [11].

The recognized function of magnetosomes is to provide for the magnetotaxis of cells. However, there is a supposition that the crystalline forms of iron maintain the necessary level of this element in cells, regulate the redox potential, and are even involved in energy metabolism [11].

The Systematics of Magnetotactic Bacteria

The 16S rRNA gene sequencing showed that all of the presently known magnetotactic bacteria belong to two phylogenetic groups, *Nitrospirae* and *Proteobacteria*, of the *Bacteria* domain [12, 23] (Table 1).

The bacterium *"Magnetobacterium bavaricum,"* which is able to accumulate more than one thousand magnetite crystals and form large sulfur inclusions, falls into the phylogenetic group *Nitrospirae* phy. nov. of the class *"Nitrospira"* of the order *"Nitrospirales"* of the family *"Nitrospiraceae"* [23]. All of the culturable representatives of this group are strictly chemolithoautotrophic bacteria [11].

Magnetospirillum bacteria are close to nonsulfur purple bacteria and, according to Bergey's Manual of Systematic Bacteriology, 2nd ed. [23], belong to the phylogenetic group *Proteobacteria* phy. nov., the class *"Alphaproteobacteria,"* the order *Rhodospirillales*, the family *Rhodospirillaceae.* The magnetic vibrio MV-1 is closest to the species *Rhodospirillum rubrum.* Nonculturable magnetotactic cocci, the culturable marine magnetotactic coccus MC-1, and magnetotactic bacteria with anomalously large magnetosomes comprise a monophyletic group within the class *"Alphaproteobacteria"* [12, 23, 24].

The phylogenetic analysis of magnetotactic bacteria producing iron sulfide crystals showed that the strains MMP 1990 and MMP 1991 of many-celled magnetotactic prokaryotes, like sulfate-reducing bacteria, belong to the class *"Deltaproteobacteria"* and are closest to the species of the genus *Desulfosarcina*, the order *"Desulfobacterales*," the family *"Desulfobacteraceae"* [23, 24].

According to the 16S rRNA gene sequence data, the sulfate-reducing bacterium RS-1 forming magnetite crystals belongs to the same class *"Deltaproteobacteria"* and is closest to the species of the genus *Desulfovibrio*, the order *"Desulfovibrionales,"* the family *"Desulfovibrionaceae"* and to the species *Geobacter metallireducens*, of the order *"Desulfuromonadales,"* the family *"Geobacteraceae"* [23, 25]. It should be noted that the species *G. metallireducens* is not magnetotactic and is able to form extracellular magnetite.

The phylogenetic position of bacteria capable of producing both magnetite- and greigite-based magnetosomes is unknown. The occurrence of magnetotactic bacteria in different phylogenetic groups gives grounds to believe that the capability for producing magnetosomes and the related capability for magnetotaxis are of multiple evolutionary origin in bacteria [21]. The data presented show that there is no correlation between the phylogenetic position of magnetotactic bacteria and the composition of their magnetosomes [12].

It should be noted that the phylogenetic position of almost all magnetotactic bacteria was determined by the methods of 16S rRNA gene sequencing and *in situ* hybridization, without isolating them in pure cultures [20].

The Ecology of Magnetotactic Bacteria

Magnetotactic bacteria are widespread in nature and have been detected in lacustrine and marine sediments, soils, and stratified waters. Different species of magnetotactic bacteria dwell in water at different depths, forming distinct layers. There is a correlation between the concentration of iron ions in water and the amount of magnetotactic bacteria. At low iron concentrations, the population of magnetotactic bacteria is proportional to the iron concentration, leveling off at 30–50 μM of iron. The vertical distribution of magnetotactic bacteria correlates with the concentrations of oxygen and sulfides. The upper layers of biotopes are inhabited by microaerophilic magnetite-forming bacteria, while facultatively anaerobic magnetite-forming bacteria live in deeper layers, beginning from the zone with trace amounts of oxygen and ending with the sulfide zone. Anaerobic greigite-forming bacteria inhabit the biotopes where the concentration of sulfides is on the order of micromoles to millimoles [21].

Due to the relatively high abundance of magnetotactic bacteria, which reaches 200 to 10000 cells per ml of seawater, and their ability to accumulate up to pico-

Table 2. Some bacteria that contain noncrystalline magnetic inclusions

Bacteria	Relevance to oxygen	Taxonomic position according to [23]	Strain designation in VKM	Intracellular localization of inclusions
Domain *Archaea*				
Haloarcula vallismortis	Facultative aerobes	Phylogenetic group *Euryarchaeota* phy. nov., class *Halobacteria*, order *Halobacteriales*, family *Halobacteriaceae*	B-1791^T	Rounded inclusions (regular or flattened spheres) in the central part of cells
Halococcus morrhuae			B-1772^T	
Halococcus salifodinae			B-2108^T	
Haloferax mediterranei			B-1748^T	
Haloferax volcanii			B-1768^T	
Halorubrum sodomense			B-1771^T	
Domain *Bacteria* Phylogenetic group *Proteobacteria* phy. nov. Class "*Alphaproteobacteria*"				
Caulobacter maris	Obligate aerobe	Order *Caulobacterales* family *Caulobacteraceae*	B-1510^T	Rounded inclusions (regular or flattened spheres) along the long axis of cells
Rhodopseudomonas palustris	Aerotolerant anaerobe	Order "*Rhizobiales*" family "*Bradyrhizobiaceae*"	B-1620^T	
Class "*Gammaproteobacteria*"				
Ectothiorhodospira shaposhnikovii	Obligate anaerobe	Order "*Chromatiales*" family *Ectothiorhodospiraceae*	B-1525^T	Rounded inclusions (regular or flattened spheres) along the long axis of cells
Escherichia coli	Facultative anaerobe	Order "*Enterobacteriales*" family *Enterobacteriaceae*	B-126	Rounded inclusions along the long axis of cells and irregular structures associated with the cytoplasmic membrane
Pseudomonas aeruginosa	Obligate aerobe	Order *Pseudomonadales* family *Pseudomonadaceae*	B-552 B-558^T	
Class "*Deltaproteobacteria*"				
Desulfomicrobium baculatum	Obligate aerobe	Order "*Desulfovibrionales*" family "*Desulfomicrobiaceae*"	B-1378^T	Rounded inclusions randomly distributed over the cytoplasm
Phylogenetic group *Firmicutes* phy. nov., class *Bacilli*				
Bacillus cereus	Facultative aerobes	Order *Bacillales* family *Bacillaceae*	B-504^T	Small 10-nm globules near the cytoplasmic membrane
Bacillus thuringiensis			B-439	
Lactobacillus plantarum	Aerotolerant anaerobe	Order "*Lactobacillales*" family *Lactobacillaceae*	B-2209	Small (<10 nm) globular structures near the cytoplasmic membrane
Lactococcus lactis subsp. *lactis*	Aerotolerant anaerobe	Order "*Lactobacillales*" family *Streptococcaceae*	B-978	

Note: VKM, All-Russia Collection of Microorganisms. The superscript T marks the type strains.

grams of iron per cell, these bacteria exert a considerable impact on the environment and play an important part in the biogenic iron cycle. Large magnetotactic cells may contain more than 100 greigite crystals [21] or, in the case of "*Magnetobacterium bavaricum,*" more than 1000 magnetite crystals per cell [12].

When magnetotactic bacteria die out, their magnetosomes accumulate in sediments, causing their magnetization. The single-domain size of biogenic magnetic particles makes them excellent fossil recorders of paleomagnetic fields. Such particles can easily be identified due to their unique crystalline structure in the form of hexagonal prisms, teardrops, and arrowheads, which are not encountered in abiogenic magnetic minerals [17]. Fossil magnetosomes in the form of chains could be detected in the sediments of the Oligocene, Miocene, and Tertiary Periods. Their analysis can provide insight into the evolution of magnetosomes and the orientation of the Earth's magnetic field in the past [21].

Friedmann *et al*. [26] detected chains of magnetite crystals in the meteorite ALH84001 and found that their characteristics (the size and morphology of crystals, their length-to-width ratio, the crystallographic perfection, the chemical purity, the arrangement of crystals in the form of chains, and the extension of crystals along the axis of easy magnetization) are not typical of abiogenic magnetite. This allowed the authors to suggest that these magnetite chains are of biogenic origin and may serve as an indication of the existence of life on Mars in the distant past.

The small size of bacterial magnetite particles and the absence of an aggregation of magnetosomes possessing an intact membrane provide for their high surface-to-volume ratio. This is a prerequisite for the use of magnetosomes in immobilizing various biologically active substances, enzymes, antibodies, and genetic objects [11].

NONCRYSTALLINE MAGNETIC INCLUSIONS IN PROKARYOTIC CELLS

In 1997, Vainshtein *et al.* [7] reported on a new type of noncrystalline magnetic inclusions differing from crystalline magnetosomes. These intracellular inclusions, which were detected in the photosynthesizing purple bacteria *Ectothiorhodospira shaposhnikovii*, *Rhodopseudomonas palustris*, and *R. rutila*, looked like spherical particles from 20 to 150 nm in size and arranged in the form of a chain along the long axis of these bacteria. The particles were formed when the bacteria were grown under microaerobic conditions in media with the metal chelate complex EDTA-Fe(III). Such cells could be attracted to either of the magnet poles but not to nonmagnetized iron [7].

Such noncrystalline magnetic inclusions were also detected in cells of halophilic archaea and eubacteria from different systematic groups, their intracellular localization, size, and number depending on the particular bacterium (Table 2) and cultivation conditions [27, 28].

The electron microscopic studies of cells with such magnetic inclusions and isolated inclusions showed that they are composed of an electron-transparent nucleus and an electron-opaque matrix surrounded by a single-layer envelope about 10 nm in thickness [7]. This envelope is homogeneous, has a low electron density, and is not typical of the known intracellular inclusions and structures. In the process of cell disintegration, noncrystalline magnetic particles lose their membrane envelope, forming either chains or conglomerates of particles. Cells may contain both large and small inclusions. Large inclusions presumably result from the fusion of small inclusions, as is evident from the inhomogeneous density of the nuclei of large inclusions. External magnetic fields may enhance such fusion [7].

The X-ray analysis of the elemental composition of cell sections showed that iron is concentrated in the matrix of magnetic inclusions and that the matrix does not contain sulfur and phosphorus. The absence of sulfur (a typical constituent of greigite) implies that amorphous iron sulfide is not involved in the formation of noncrystalline inclusions and that these inclusions do not contain greigite. This fact, together with the observation that these inclusions do not contain magnetite either, explains why the cells with such noncrystalline inclusions do not interact with nonmagnetized iron. The absence of phosphorus in the inclusions suggests that they are not iron-containing polyphosphates. This suggestion is confirmed by the fact that the cultivation of bacteria in media with a decreased content of phosphates affects neither the amount nor the size of magnetic inclusions [7].

Noncrystalline magnetic inclusions differ from the magnetosomes of magnetotactic bacteria in morphology (noncrystalline spherical particles), heterogeneous structure (electron-transparent nuclei in the iron-enriched electron-opaque matrix), and the membrane structure of the envelope (one-layer envelope instead of the three-layer envelope typical of magnetosomes).

The motion of bacterial cells with noncrystalline inclusions in a magnetic field differs from that of magnetotactic bacteria. This motion represents a passive attraction of the cells (irrespective of whether they are motile, nonmotile, living, or dead) to either of the poles of the magnet [27], whereas magnetotaxis is a combination of the active motion of cells and their passive orientation along the magnetic field lines. Dead magnetotactic cells retain the ability to align along the magnetic field lines [14].

Another feature that distinguishes crystalline magnetosomes from noncrystalline magnetic inclusions is that the former contain only iron and, as a rule [12], do not contain the other metals present in the cultivation medium [11, 17], whereas the noncrystalline magnetic inclusions may be fully composed of either chromium or cobalt if these metals were substituted for iron in the cultivation medium [29]. It should be noted that X-ray microanalysis detected metals (iron, chromium, and cobalt) only in the inclusions and not in the cytoplasm [27, 29]. The behavior of bacterial cells with noncrystalline inclusions in a magnetic field (the attraction of the cells to either pole of a magnet but not to nonmagnetized iron) did not depend on the kind of the metal present in the inclusions (iron, chromium, or cobalt).

It is suggested that the formation of noncrystalline magnetic inclusions in prokaryotic cells is a protective response of bacteria to an increased content of metal ions in the medium. In addition, iron-containing inclusions may serve as a depot of iron or (in the case of sulfate reducers, lactic acid bacteria, and photosynthesizing bacteria) may perform the same function as magnetosomes, i.e., provide for the motion of bacteria toward zones with a decreased content of oxygen [29].

CONCLUSIONS

Prokaryotic cells may contain at least two types of intracellular magnetic structures, magnetosomes and noncrystalline magnetic inclusions. Magnetosomes contain single-domain crystals of magnetite and greigite, whose chains impart a dipole magnetic moment to the cells and make them capable of magnetotaxis, i.e., orientation and active migration along the magnetic field lines. Magnetotactic bacteria were found to belong only to the domain *Bacteria* (the phylogenetic groups *Nitrospirae* and *Proteobacteria*).

Noncrystalline magnetic inclusions are structures with an organic nucleus in an iron-enriched matrix bounded by one layer envelope, which is not typical of the other cellular structures. The noncrystalline magnetic inclusions and the cells that contain them are passively attracted to either of the poles of a magnet. Bacteria with noncrystalline magnetic inclusions belong to two domains, *Bacteria* and *Archaea*.

It should be noted that after this review had already been submitted to the journal *Mikrobiologiya*, Glasauer *et al.* (*Science*, 2002, vol. 295, pp. 117–119) reported on granules of iron oxide bounded by a three-layer membrane in cells of the dissimilatory iron-reducing bacterium *Shewanella putrefaciens.* The structure of these granules differs from that of magnetosomes and noncrystalline magnetic inclusions. The magnetic properties of the granules were not described.

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