Abstract: Magnetotactic bacteria (MTB) belong to several phyla. This class of microorganisms exhibits the ability of magneto-aerotaxis. MTB synthesize biominerals in organelle-like structures called magnetosomes, which contain single-domain crystals of magnetite (Fe₃O₄) or greigite (Fe₃S₄) characterized by a high degree of structural and compositional perfection. Magnetosomes from dead MTB could be preserved in sediments (called fossil magnetosomes or magnetofossils). Under certain conditions, magnetofossils are capable of retaining their remanence for millions of years. This accounts for the growing interest in MTB and magnetofossils in paleo- and rock magnetism and in a wider field of biogeoscience. At the same time, high biocompatibility of magnetosomes makes possible their potential use in biomedical applications, including magnetic resonance imaging, hyperthermia, magnetically guided drug delivery, and immunomagnetic analysis. In this review, we attempt to summarize the current state of the art in the field of MTB research and applications.

Keywords: magnetotactic bacteria; magnetosome; magnetite; magnetofossils; biomedicine; biotechnology; biogeoscience

1. Introduction
The formation of iron minerals due to biochemical processes has been known for several decades. Many organisms are able to synthesize various magnetic iron compounds such as magnetite (bacteria, protozoa, mollusks, arthropods, and chordate molds), ferrhydrite (bacteria, fungi, plants, animals), lepidocrocite (sponges, mollusks), goethite (bacteria, protozoa, annelids, mollusks), and some others [1,2]. Bacteria, in particular, are able to form intra- and extracellular grains of iron hydroxides, silicates, phosphates, sulfates and sulfides [3], and a wide range of nanosized particles of noble metals and semiconductor compounds [4].

The greatest interest, academic as well as including potential applications, is attracted by bacterial magnetite formed by a complex genetically mediated process [5–7] and localized in intracytoplasmic membrane vesicles—magnetosomes, responsible for magnetoreception of magnetotactic bacteria (MTB) [8]. These bacteria were first observed in samples of marine sediments, where they moved at a speed of about 100 μm/s [9].
a geomagnetic field having a strength of the order of 0.5 Oe, and the direction of movement was changed when the magnet polarity was reversed. Further studies revealed that MTB are widespread in marine, fresh, and extreme water environments of both hemispheres [10,11]. The optimal zone for MTB growth is usually the oxic–anoxic transition zone in the area of bottom sediments (Figure 1), and crystals of magnetite and greigite from dead bacteria make a significant contribution to remanent magnetization of sediments [12]. Fossil magnetosomes (magnetofossils) in most cases carry a reliable paleomagnetic signal in sedimentary rocks [13].

![Figure 1. Scheme of chemical gradients vs. typical depth optimal for the growth of various types of magnetotactic bacteria and magnetite transformations. Magnetite (greigite) crystals provide the bacteria with a net magnetic moment, which they employ for magnetotaxis, movement directed by the local magnetic field. Many magnetotactic bacteria grow preferentially under specific, narrow redox conditions. Redox gradients can exist on scales from millimeters to meters. Reprinted from [14], Earth-Science Reviews, Vol. 86, Kopp R.E., Kirschvink J.L., “The identification and biogeochemical interpretation of fossil magnetotactic bacteria”, pp. 42–61, 2008, with permission from Elsevier.](image)

Studies of the diversity of biomineralization and fossilization pathways of microorganisms in modern extreme conditions—such as hydrothermal springs, hypersaline and super-alkaline lakes, sea-floor basalts, etc.—can help unravel the microbial activity of the early Earth [15]. The size and quantity of magnetite particles in MTB are relatively constant for a given bacterial species and, in most MTB, there are 10–30 particles per cell that constitute 50–100 nm along the long axis [16]. Morphologically, MTB are diverse including vibrios, rods, cocci, spirilla, and so-called “multicellular” organisms [17]. According to their present phylogenetic position, MTB are classified in the following phyla: *Proteobacteria*, *Nitrospirota*, *Omnitrophota*, *Latescibacterota*, *Planctomycetota*, *Nitrospinota*, *Hydrogenedentota*, *Elusimicrobiota*, *Fibrobacterota*, *Riflebacteria*, *Bdellovibrionota*, UBA10199, *Desulfobacterota* [18–21] (Figure 2).
Figure 2. Phylogenetic distribution of MTB. The maximum likelihood phylogenomic tree was inferred from the concatenation of 120 single copy marker proteins using LG + F + I + G4 model. The analysis was performed on 264 genomes of cultured and uncultured MTB. Question marks indicate a lack of data on cell morphology and/or the shape and composition of magnetosome crystals.

Only a few MTB strains were isolated into a pure culture. Most of them belong to the genus *Magnetospirillum* [22]. MTBs observed in natural samples mostly remain uncultivated, and are studied by molecular biology and microscopic methods [11].

The biocompatibility of an iron biomineral sequestered within a phospholipid membrane is a promising feature for various biomedical and biotechnological applications related to magnetosomes and magnetosome-based complexes [23–26]. Possibilities of altering the chemical composition by substituting foreign metal for iron in magnetosome magnetite nanocrystals are investigated, the biomineralization process serving as a basis for developing new approaches to the synthesis of nanomaterials [27–30], such as e.g., biosynthesis of magnetite using human cells [31].
2. MTB and Magnetosomes

The nature of magneto-aerotaxis remains a subject of active research. According to some models, it reduces the search for conditions with low oxygen content to a one-dimensional rather than three-dimensional problem, the latter usually associated with other mechanisms of cell taxis [32]. Using microcapillary analysis for 12 species of MTB, six variants of magneto-aerotaxis have been revealed [33]. Statistically significant changes in the cell shape of the *Magnetospirillum magneticum* strain occurred when the bacteria were exposed to a magnetic field, as compared with control conditions. However, in the *Magnetospirillum gryphiswaldense* strain, no morphological changes were observed under the same conditions, implying a difference in the arrangement of magnetosomes in two different strains. This emphasizes the importance of choosing the correct source strain of bacterial nanoparticles if a high sensitivity to external magnetic fields is required [34].

One of the most studied MTB are freshwater bacteria of the genus *Magnetospirillum* [35]. *Magnetospirillum magneticum* AMB-1 and *Magnetospirillum gryphiswaldense* MSR-1 are model microorganisms for studying the process of magnetosome biomineralization [36]. For these strains, metabolism and magnetosome formation have been studied under various growth conditions, which included, in particular, varying isotopic composition of iron [37]. For these two microorganisms, a longitudinal study of genetic determinants responsible for the magnetosome formation has been carried out and possible factors involved in the formation of the magnetosome membrane and biomineralization of magnetic crystals were elucidated [7,38]. Recently, it has been shown that MTB can form an additional pool of iron in the cytoplasm outside of magnetosomes [39], and that the process of magnetosome biomineralization requires maintaining the necessary redox conditions, regulating the content of intracellular reactive oxygen species to maintain the intracellular balance of ferric and ferrous iron [40,41]. This can contribute to the survival of MTB in the conditions of low oxygen content and high content of iron [42] and other transition metals [43].

Genomes of many MTB species were sequenced [20,21,44–60], and genes specific for magnetotactic bacteria were found, which control the magnetosome formation [61,62]. These genes are located in a so-called magnetosome genomic cluster (MGC) and are responsible for the formation of the magnetosome membrane, transport of iron into magnetosomes, nucleation and growth of magnetite crystals, and the shape and size of the latter [17,63–69]. Magnetite (greigite) crystals in magnetosomes can take the form of prism, cuboctahedron, bullet, or a combination of a cube and a dodecahedron, which is associated with the process of crystal growth [70] (Figure 3). Magnetosomes in MTB are commonly arranged in one or several parallel chains, although chaotically distributed magnetosomes have also been observed [49,52,71,72]. The mechanism of magnetosome formation [73,74] and their chains [75] in MTB has been investigated experimentally by electron cryotomography. The morphological characteristics of magnetite crystals obtained from some MTB are listed in Table 1.
Figure 3. Shape combinations compatible with magnetite symmetry (Fd3m): (a) [111] (octahedron); (b) distorted [111]; (c) elongated [111]; (d) elongated [110]; (e–g) [110] + [111]; (f) [110] + [111]; (h, i) [110] + [111] + [100]; (j) [100] + [111] (cuboctahedron); (k, m) elongated [100] + [111]. The anisotropy of the environment could derive from an anisotropic flux of ions through the magnetosome membrane surrounding the crystal. The resulting crystals are distorted in a consistent species-specific manner. The cube [100], octahedron [111], and dodecahedron [110] can, with certain distortions, create a wide range of shapes, taking into consideration those observed in magnetosomes. Reprinted from [70], American Mineralogist, Vol. 83, Devouard B., Pósfai M., Hua X., Bazylinski D.A., Frankel R.B., Buseck P.R., “Magnetite from magnetotactic bacteria: Size distributions and twinning”, pp. 1387–1398. 1998. Copyright © 1998, with permission from the authors and The Mineralogical Society of America.
Table 1. Shape, size, and quantity of magnetosomes isolated from magnetotactic bacteria (MTB) of some species

| MTB Species                        | Crystal Shape               | Average Crystal Length (nm) | Average Crystal Width (nm) | Average Magnetosomes Quantity | Refs.          |
|-----------------------------------|-----------------------------|-----------------------------|---------------------------|-------------------------------|----------------|
| *Magnetospirillum magneticum* AMB-1 | prismatic, cuboctahedral    | 30–50                       |                           | 15–20                         | [32,35,73,75–78] |
| Magnetococcales spp.              | prismatic, cuboctahedral    | 70–250                      | 40–200                    | 10–200                        | [49,52,72,79–81] |
| *Magnetovibrio blakemorei* MV-1   | prismatic                   | 50–60                       | 35–40                     | 2–20                          | [74,82]        |
| *Magnetospirillum gryphiswaldense* MSR-1 | cuboctahedral            | 30–50                       |                           | 15–40                         | [43,63,68,83–85] |
| *Desulfovibrio magneticus* RS-1   | bullet-shaped               | 40–70                       | 20–40                     | <10                           | [86]           |
| *Nitrospira bacteria* MYR-1       | bullet-shaped               | 40–45                       | 80–180                    | up to 1000                    | [87]           |
| Ca. *Magnetobacterium bavaricum* TM-1 | bullet-shaped              | 35–40                       | 100–120                   |                               | [88,89]        |

The interaction of proteins associated with magnetosome formation has been an important research subject in recent years [90]. The structure of some of these proteins is well understood [91]; however, the role of individual magnetosome proteins in each stage of the biomineralization process has not been established. Many studies are carried out by directed modification using plasmid vectors [92] to obtain mutant MTB strains, including non-magnetic ones [36,84,93]. A promising direction in MTB bioengineering is inducing biomineralization in initially non-magnetotactic bacteria [94,95], and obtaining mutant strains with a genetically modified membrane [96]. Another one is the possibility of synthesizing biomimetic magnetic particles with faceted magnetite crystals with a narrow size distribution by using a combination of magnetosome proteins MamC and Mms6 [97,98].

The process of obtaining a pure MTB culture is very complicated [99] and industrial cultivation of even the most studied species—e.g., *Magnetospirillum magnetotacticum*—requires the use of large-volume fermenters, reaching 30 [100] and even 50 L [101] (Figure 4). In addition, constant precise control of the dissolved iron content in the nutrient medium and its pH [102], and maintaining oxygen concentration in the gas phase <5% are required [76]. However, recently, a new approach to accelerated production of MTB biomass using fermentation has been proposed, which does not require precise control of the gas environment [103]. Also, a method for controlling the MTB physiology has been developed based on the use of the flow cytometry, so that the process of growing MTB can be significantly simplified [104].
3. Physicochemical Properties and Isolation of Magnetosomes

The magnetic properties of MTB and isolated magnetosomes correspond to magnetostatically interacting magnetite crystals and are described using the model of a chain of spheres [105]. The magnetic characteristics of magnetosomes (saturation magnetic moment at $T = 300$ K $M_{s300K}$, remanent coercivity at $T = 300$ K $H_{c300K}$, remanence to saturation magnetization ratio at $T = 300$ K $M_{rs}/M_{s300K}$ and Verwey transition temperature $T_V$ [82]) isolated from various MTBs are listed in Table 2.

### Table 2. Magnetic characteristics of magnetosomes isolated from MTB of some species

| MTB Species | $M_{s300K}$ 10$^{-3}$ emu$^1$ | $H_{c300K}$, Oe$^2$ | $M_{rs}/M_{s300K}$$^3$ | $T_V$, K$^4$ | Refs. |
|-------------|-------------------------------|--------------------|------------------------|---------------|-------|
| **Magnetospirillum magnetotacticum** AMB-1 | 1.6–4.5 | 128–380 | 0.43–0.50 | 100–118 | [39,77,106–111] |
| **Magnetospirillum gryphiswaldense** MSR-1 | 0.2–1.5 | 96–234 | 0.38–0.50 | | [68,85,112–117] |
| **Magnetovibrio blakemorei** MV-1 | 3.0 | 250–350 | 0.46–0.50 | 100–117 | [82,118] |
| **Ca. Magnetobacterium bavaricum** TM-1 | 1.5–8.0 | 400–460 | 0.32–0.51 | 100–110 | [88,89] |
| **Magnetococcus marinus** MC-1 | – | – | – | 102 | [118] |

$^1$ Saturation magnetic moment at $T = 300$ K. $^2$ Remanent coercivity at $T = 300$ K. $^3$ Remanence to saturation magnetization ratio at $T = 300$ K. $^4$ Verwey transition temperature.

Even for crystals about 30 nm in size, magnetostatic interaction of grains arranged in chains leads to their magnetic moments being in blocked state in a zero external magnetic field [108,119]. Experiments and numerical modeling have revealed that the organization...
of magnetosomes into chains plays a significant role in the process of their maturation, while the effect of chains is small in the process of MTB cell division [120]. Changes in the iron oxidation state and size distribution of magnetosome crystals vs. time have been studied at early stages of the biomineralization process [121]. Growing MTBs in a magnetic field, weakened compared to the geomagnetic field, can affect the size of magnetosome crystals and the expression of some MGC genes [122].

Various electron microscopy techniques, particularly the one using the signal from inelastically scattered electrons, have been applied to study MTB ultrastructure. Examples include observing the shape of magnetosomes and their chains without isolating them from bacterial cells [123], and directly obtaining images of individual magnetosome membranes [124]. Use of energy dispersive X-ray analysis allows mapping the distribution of chemical elements and the energies of chemical bonds within MTB [109,125]. New modifications of transmission electron microscopy using a graphene liquid cell with an encapsulated 1 µL MTB sample allow direct observation of the biomineralization process in high resolution [126].

Images of magnetosome chains, similarly to chain aggregates of synthetic magnetic particles [127], have been also obtained by atomic force [128,129], magnetic force [130,131], and scanning transmission X-ray [125] microscopy. During the formation of chain structures and changes in rheological properties in a suspension, isolated magnetosomes appear quite similar to synthetic magnetic particles [132,133]. Mathematical models have been constructed that describe the mechanical properties of chains of magnetosomes taking into consideration the effect of the filament connecting them in MTBs [134], and energy parameters of magnetosome magnetostatic interaction in a chain [135]. Immobilization of MTB in a gel matrix made of hydrated silica affects the reaction of magnetosome chains to changes in the direction of an external magnetic field and leads to a reversal of chains and disruption of their structure [109]. However, for freeze dried immobilized MTB, application of magnetic fields up to 1 T does not lead to the destruction of chains [85].

According to high-resolution transmission electron microscopy [87], faceting of magnetosome crystals by planes with high Miller indices [136] is apparently determined by a multistage biomineralization process, controlled by anions and organic molecules inside a vesicle and other intra-[80] and extracellular [137] factors, and may differ for magnetosomes within the same chain [81]. Formation of ε-Fe₂O₃ at an intermediate stage of biomineralization in magnetosomes has been hypothesized [138]. This metastable polymorph of iron (III) oxide exists in a narrow crystal size range and, with an increase in the latter, transforms to α-Fe₂O₃ [5]. Adding inorganic manganese [139] or cobalt [111] salts directly to the MTB nutrient medium allows obtaining metal-substituted magnetite crystals with modified shape, size, and magnetic properties.

Isolating magnetosomes from MTB starts with exposure to air, followed by ultrasonic cell lysis or using of a laboratory extrusion cell disintegrator (French press) [140–142], stirring in a shaker, magnetic separation of magnetosomes, or separation by centrifugation with removing cellular debris and multiple rinsing with buffered solutions and deionized water [100,131,143]. An automated MTB cultivation mode with variable oxygen content can be used to control the particle size and, correspondingly, the magnetic characteristics of magnetite in order to adapt them for the desired application [144]. The mass of dry particles obtained from MTB is small and does not exceed 20 µg per 1 mg of lyophilized biomass [145]. The maximum achieved productivity is about 150 mg of dry biomass per 1 L of culture per day [146].

4. Magnetofoils and Their Properties

Studies of marine clays from the western part of Crete [147] and the Pacific Ocean [148], deep-sea sediments from the Atlantic [149] and Pacific [150,151] oceans and the Black Sea [152], microbial mats [153] and sapropels of the Baltic Sea [154], stromatolites in coastal waters [155], sediments from freshwater lakes and rivers of central Russia [156], stratified ferruginous lakes [57] and a Cisalpine lake [157] have shown that single-domain mag-
netite or greigite from MTB is a major carrier of stable remanent magnetization in these rocks. Methods used for the analysis included thermal and alternating field demagnetization of natural remanent magnetization, measurement of hysteresis loops, and curves of isothermal saturation remanent magnetization and anhysteretic remanent magnetization. More advanced methods such as construction of first order reversal curve (FORC) diagrams [77,158] and ferromagnetic resonance spectroscopy (FMR) [159] have been applied to selected samples.

Chemical stability of submicron magnetite particles in marine sediments is due to slightly alkaline conditions and may differ in the case of freshwater reservoirs [157]. Relative proportion of maghemite formed as a result of magnetite oxidation can vary from 0 (in the initial magnetosomes) to 100%, depending on the geography of the sediments [79]. Increased oxygen content in freshwater lake sediments leads to a greater tolerance to oxygen in MTB; the magnetosomes they form commonly have lower coercive force [160]. Environmental conditions also affect the shape of magnetite crystals in magnetofossils, isotropic crystals dominating in an oxic medium, and anisotropic crystals in a reducing one [161]. The relationship between magnetofossil properties and the alternation of glacial cycles has been observed, probably mediated by changes in the oxygen level in pore water [14] and other global climatic changes [162].

Extraction of submicron particles of biogenic magnetite from sediments includes the separation of non-magnetic phases and separation of chains formed in MTB, and takes no more than 30–60 min [163]. TEM images of individual magnetofossil crystals show the high degree of structural perfection, which, however, can be destroyed over time due to the dissolution of magnetite in the pore space electrolyte [164]. Oxidation of magnetite to maghemite in magnetosomes when exposed to temperatures above their stability threshold (approximately 300 °C [143]) manifests itself in pronounced nonstoichiometry, resulting in a decrease of the Verwey transition temperature and ultimately in the disappearance of the transition [112]. Alongside the formation of magnetosome chains [106], effect of magnetite nonstoichiometry can be detected using FMR spectroscopy [113]. This method can be further used to determine the content of magnetofossils in a sample, since the effective g-factor, characterizing the ratio of the magnetic and angular momenta of a particle, and the resonance curve width of synthetic magnetite particles differ significantly from the corresponding characteristics of particles biomineralized by various bacteria [107,115,164,165]. Fields of uniaxial and cubic magnetic anisotropy of crystals of various shapes [86,114,166] have been determined by FMR spectroscopy, electron cryotomography, and measurement of dynamic hysteresis loops. FMR curve parameters of magnetofossils have been found to change along the length of sediment cores, thus yielding paleoclimatic information [167].

The method of magnetic granulometry [168,169], along with other approaches in rock magnetism [88,89,116,165], confirms that the shape and size of bacterial magnetite crystals correspond to a single-domain [170] or pseudo-single-domain [82] (metastable single-domain [167]) state, with the aspect ratio and particle length varying over a wide range, up to one order of magnitude, depending on magnetofossil geography [171], and differs little for cultivated and non-cultivated MTB strains when taking into consideration statistical data [172]. Exceptionally, multi-domain [173] and superparamagnetic [117] magnetite grains originating from magnetofossils have been found in natural conditions. Biogenic single-domain crystals of greigite [174] close in size to magnetite crystals differ from the latter by a 2–3 times lower coercive force [175]. Figure 5 illustrates size range of stable single domain (SSD) bacterial magnetite crystals. The most commonly studied Magnetospirillum genus MTB produce almost cubic particles about 40–60 nm lying squarely in the SSD region. Therefore, fossilized MTB retain stable magnetization and are an important carrier of paleomagnetic signal in sediments.
Figure 5. Diagram of magnetic states of magnetite; the regions of a stable single-domain (SSD) state are indicated for individual grains and for chains with and without taking into consideration Table 60. s below which all grains are considered to be in a superparamagnetic (SP) state where the direction of a magnetic moment of an individual grain is constantly changed by thermal agitation. For non-interacting grains, there is a range of grain sizes marked by $d_{\text{min}}$ and $d_{\text{max}}$, where both SSD and multi-domain (MD) states are possible. Changes in both grain shape and volume contribute to the location of critical boundaries. Reprinted from [119], J. R. Soc. Interface, Vol. 6, Muxworthy A.R., Williams W., “Critical superparamagnetic/single-domain grain sizes in interacting magnetite particles: implications for magnetosome crystals”, pp. 1207–1212. 2009. Copyright © 2009, with permission from the authors and The Royal Society (U.K.).

5. Application of Magnetosomes in Biomedicine and Biotechnology

High biocompatibility of bacterial magnetosomes is confirmed by studies of cytotoxicity (MTT test), hemolytic activity and genotoxicity [176,177], and influences a range of potential applications in biomedicine [178,179], including oncology [180] (Figure 6).

Figure 6. Schematic representation of the biological features of MTB, which determines the prospects for their use as theranostics agents in oncology. At present, only the fundamental properties of MTB
suitable for the biomedical applications, including self-propulsion, magnetotaxis and aerotaxis, are reasonably well studied. At the same time, other possible biomedical applications of MTB include magnetically guided drug delivery, alternate magnetic field (AMF) hyperthermia, magnetic resonance imaging (MRI) or magnetic particle imaging (MPI) and modification of MTB membrane with drugs or superparamagnetic iron oxide-based nanoparticles (SPIONs). Reprinted from [181], J. Appl. Phys., Vol. 128, Fdez-Gubieda M.L., Alonso J., García-Prieto A., García-Arribas A., Fernández Barquin L., Muela A., “Magnetotactic bacteria for cancer therapy”, Article 070902. 2020. Copyright © 2020, with permission from the authors and AIP Publishing.

The possibility of using magnetosomes from magnetotactic cocci [182] and spirilla [183] as contrast agents has been established experimentally, which, in combination with effective control by means of an external magnetic field, can be used for magnetic resonance imaging (MRI) in the positive and negative contrast mode, including that in real time [181]. MRI can be used to create bacterial or hybrid medical nanorobots that can controllably move through the human circulatory system [184,185], as demonstrated in a model system based on a microfluidic chip [186]. When functionalized through genetic modification, magnetosomes may also become tissue-specific, highly sensitive molecular probes for MRI due to their high transverse relaxivities, up to 600 mM$^{-1}$s$^{-1}$ and tropism to tumor tissue [187,188]. Reporter gene expression using magnetosome genes to create endogenous MRI contrast for longitudinal molecular imaging was described [189].

Magnetosomes with an artificially modified membrane are able to selectively bind to monoclonal antibodies [129] and can be used for magnetic separation of cells [190], conducting automated magnetic immunological analysis by immuno-PCR [191], creating new electrochemical sensors for detecting pathogenic bacteria and their secreted toxins [192], and immunomagnetic analysis for anthropogenic pollutants [193]. Modification of magnetosome membranes with aminosilane allows using these for isolation of nucleic acids in PCR diagnostics of whole blood [194], or of bacterial cell culture [195] samples (Figure 7).

A comparative study of the immobilization of enzymes (oxidase and uricase) on the surface of biogenic magnetic particles and particles of synthetic magnetite has shown 30–80 times greater efficiency and an approximately 30-fold increase in enzyme activity in biogenic particles [145]. Genetic engineering of magnetosomes can provide high catalytic activity for a wide range of enzymes, opening a possibility of creating a new class of magnetosome-based magnetic biocomposites [24,196–198]. Use of various organic linkers for modifying the magnetosome membrane provides a wide range of applications in the field of targeted therapy in oncology and in gene therapy [199,200]. Compared to synthetic magnetic particles modified with aminosilane, bacterial magnetosomes are characterized by greater thermal effect when heated by a radiofrequency field, at the same time having a much higher lethal dose converted to the mass of magnetite (up to 480 mg per kg [146]) as compared to synthetic analogs [201]. Bacterial magnetosomes are also toxic at concentrations above 1 mg/mL against 70–100 µg/mL for synthetic magnetite particles [200,202]. Biocompatibility of magnetosomes can be further increased by removing bacterial endotoxins and forming an additional protein coating [203].

The cytostatic effect in vivo and in vitro with respect to human hepatocellular carcinoma HepG2 cells capable of selectively binding to magnetosomes [204] is higher for the magnetosomes modified with anthracycline drugs, than for drugs not bound to nanoparticles [205]. The effect of targeted gene [206] and chemotherapy [207] with functionalized magnetosomes has also been demonstrated on HepG2 cells. Several characteristics of synthetic magnetic nanoparticles and bacterial magnetosomes are compared in Table 3.
Figure 7. Scheme of a functionalized magnetosome according to various biomedical and biotechnological applications. Drug delivery: the association between the surface proteins of the magnetosome and doxorubicin (DOX), an anti-breast cancer drug. Cell separation: modified magnetosomes were bound to anti-murine IgG anti-CD19 and used for separating B-lymphocytes from peripheral blood cells. Food sciences: a capture system with the magnetosome proteins fused using a cross-linking reagent bis (sulfosuccinimidyl) suberate (BS3) for attachment of antibodies to Salmonella and Vibrio species from food samples (e.g., milk, egg, and pork). DNA/Antigen analysis: antibody-functionalized magnetosomes were used for immobilization of HBsAg (hepatitis B antigen) in human serum and enhancement of sensitivity of immunoassay. Image contrast: magnetosomes with specific proteins bound to the surface with high affinity to target cells were used as superparamagnetic contrast agents for magnetic resonance imaging. Hyperthermia: magnetosomes coated with poly-L-lysine (PLL) were used in hyperthermia. Enzyme immobilization and bioremediation: magnetosomes expressing MamC fused with organophosphohydrolase (OPD) from Flavobacterium sp., were used for the degradation of paraoxon. Reprinted from [24], Vargas, G.; Cypriano, J.; Correa, T.; Leão, P.; Bazylnski, D.A. and Abreu, F. Applications of Magnetotactic Bacteria, Magnetosomes and Magnetosome Crystals in Biotechnology and Nanotechnology: Mini-Review. Molecules 2018, 23, Article 2438, license CC BY 4.0.

Table 3. Comparison of the biological properties of synthetic particles of magnetite and magnetosomes

| Characteristic                              | Synthetic Particles | Magnetosomes | Refs. |
|--------------------------------------------|---------------------|--------------|-------|
| Acute toxicity (LD50) in rats, mg/kg       | 135–180             | 480          | [146,201] |
| Cytotoxicity (HUVEC 2 MTT assay), mg/mL    | 0.07–1.0 3          | 0.1–5.1      | [176–178,188,189,200,202] |
| Maximum non-hemolytic concentration, mg/mL | 3.0                 | 1.6–4.0      | [176,189,208] |
| Magnetic resonance relaxivity, mM−1 s−1    | 130–170             | 150–600      | [127,182,187,189,200] |
| Specific absorption rate, kW/g             | 0.6–0.8             | 0.4–1.4      | [132,183,185,209] |
| Minimal biodegradation period, days         | 30                  | 28–42        | [177,200,201,210] |
| Magneto Immuno-PCR limit of detection, ng/mL | 8                   | 0.32         | [191] |
| DNA extraction release, µg/mg              | 1.0–2.2             | 3.0–19.2     | [195] |

1 Dextran coated superparamagnetic iron oxide nanoparticles unless otherwise specified. 2 Human umbilical vein endothelial cell culture. 3 Silica-coated magnetite nanoparticles.
In vitro studies have shown that interaction with an alternating magnetic field allows using magnetosomes conjugated with polyclonal antibodies to bind and destroy pathogen cells, in particular *Staphylococcus aureus*, not via the thermal effect but through the mechanical pressure created by magnetosomes [211]. Due to the ability to biosorb metal ions from an aqueous medium, MTB can be used for environmentally safe biosynthesis of controlled size gold, silver, platinum, and palladium nanoparticles [212].

Chains of magnetosomes provide better inhibition of tumor cells compared to individual magnetosomes due to the absence of aggregates [213]. MRI was applied to monitor the distribution of magnetosomes within the tumor tissue in the course of the therapeutic treatment, and it was shown that inhomogeneous distribution of magnetosomes inside tumor tissue may strongly limit their therapeutic efficacy against glioma [209]. The U87-Luc glioma model was used to demonstrate complete tumor eradication after hyperthermic therapy in 40–50% of cases, while the magnetosomes themselves were subject to biodegradation over time [214,215]. Nevertheless, the clinical use of magnetosomes has not been described so far due to incomplete tests on biocompatibility and pharmacokinetics in vivo [183,216,217].

6. Conclusions

Based on the analysis of scientific publications on the cultivation and the physicochemical and biological properties of magnetotactic bacteria and magnetosomes, we can outline some of the most active research directions in this field.

Despite the long time since the discovery of MTB, many important aspects for understanding the mechanisms of biomineralization such as the kinetics and dynamics of the crystallization of magnetite and greigite, reasons for the predominance of the main types of faceting and the aspect ratio of crystals, the presence of natural alloying elements in magnetite are yet insufficiently studied. Furthermore, these studies have only been carried out for a small number of MTB types. The difference in the magnetic and, generally, electromagnetic properties of magnetosomes isolated from different MTB therefore remains a vibrant research field. There exist considerable differences in the magnetic properties of bacterial magnetosomes and their synthetic counterparts, which are actively studied on the crossroads of rock and mineral magnetism, physics of magnetic materials, and nanotechnology.

Along with the continuing interest in the fundamental physical and chemical properties of MTB and magnetosomes, a growing number of studies is seen to explore their practical applications in biomedicine and biotechnology. This is dictated, on the one hand, by the ability to use magnetosomes as a base element for design of new theranostic agents and their high biocompatibility, which is unattainable for present-day synthetic counterparts, and, on the other hand, by the need for joint efforts of specialists in related fields of knowledge, such as genetic engineering, chemistry of nanosystems, micromagnetism, and microfluidics.

In our view, the most important directions for MTB research in the near future will be the further development of the technology of high-performance automated fermentation of genetically modified strains with improved biocompatibility and, possibly, superparamagnetic properties. Detailed studies of the mechanisms of biomineralization of magnetite would provide a basis for developing methods for the synthesis of biomimetic magnetic nanoparticles providing much higher productivity and maintaining high biological characteristics. In addition, in the field of paleomagnetism, it is important to consider bacterial magnetite in the framework of broad comparative rock-magnetic studies of the biogenic magnetic minerals of bacteria, protists, and other single-celled organisms.

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