



**HAL**  
open science

# Magnetic guidance in multicellular prokaryotes and eukaryotes

Pedro Leão, Christopher T. Lefèvre

► **To cite this version:**

Pedro Leão, Christopher T. Lefèvre. Magnetic guidance in multicellular prokaryotes and eukaryotes. Elements, 2023, 19 (4), pp.234-238. 10.2138/gselements.19.4.234 . hal-04299412

**HAL Id: hal-04299412**

**<https://hal.science/hal-04299412v1>**

Submitted on 23 Nov 2023

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

# Magnetic Guidance in Multicellular Prokaryotes and Eukaryotes

Pedro Leão<sup>1</sup> and Christopher T. Lefèvre<sup>2</sup>

1811-5209/23/0019-0234\$2.50 DOI: 10.2138/gselements.19.4.234

Transmission electron microscopy (TEM) image of a thin sectioned multicellular magnetotactic prokaryote (MMP) biomineralizing magnetite particles.

**S**ome organisms have the unique capacity to geolocate and navigate in response to the Earth's magnetic field lines. Migratory birds and fishes are the best-documented animals that evolved this capacity to guide their movements. In the microbial world, magnetotactic bacteria (MTB) and multicellular magnetotactic prokaryotes (MMPs) have been the only known magnetoreceptive microorganisms for decades. Some microeukaryotes also orient their motility axis along magnetic field lines thanks to the exploitation of MTB magnetism. The magnetic guidance of these prokaryotes and eukaryotes is due to the biomineralization of magnetic crystals. This article provides a brief overview of the current knowledge concerning the different multicellular prokaryotes and micro/macro-eukaryotes capable of magnetoreception. We also discuss the evolution of this unique ability.

**KEYWORDS:** multicellular magnetotactic prokaryotes; magnetotactic protists; animal magnetoreception; evolution

## MULTICELLULAR MAGNETOTACTIC PROKARYOTES (MMPs)

Most studies regarding biomineralization of magnetic minerals are based on the capability of unicellular magnetotactic bacteria (MTB) to synthesize and organize magnetosomes, nanocrystals enveloped by a lipidic-protein membrane, in their cytoplasm (Uebe and Schüler 2016). Magnetosomes are organized in chains inside the cell, providing the ability to use the geomagnetic field to navigate through the water/sediment column gradients in a behavior called magnetotaxis (Lefèvre and Bazylinski 2013). Among all studied MTB, a unique group of magnetotactic organisms has been well characterized: the multicellular magnetotactic prokaryotes (MMPs). These organisms are composed of 10 to 60 genetically identical bacterial cells that move as a unit and present a complete and obligatory multicellular life cycle (Kolinko et al. 2014).

Despite all information obtained from their genome and their high abundance in some marine environments, we still do not have an MMP isolated in pure culture. However, culture-independent techniques have allowed multiple MMPs to be characterized to the molecular and structural level, granting these organisms the *Candidatus* status: *Ca.*

*Magnetoglobus multicellularis*, *Ca. Magnetomorum litorale*, *Ca. Magnetanas tasingtaoensis*, *Ca. Magnetanas rongchenensis*, and *Ca. Magnetanas drummondensis*.

MMPs observed so far can present two morphotypes, spheric (sMMPs) or ellipsoidal (eMMPs), sMMPs being the most commonly observed in environmental samples (FIG. 1). These organisms can be found virtually in every saline environment where studies of MTB have been performed.

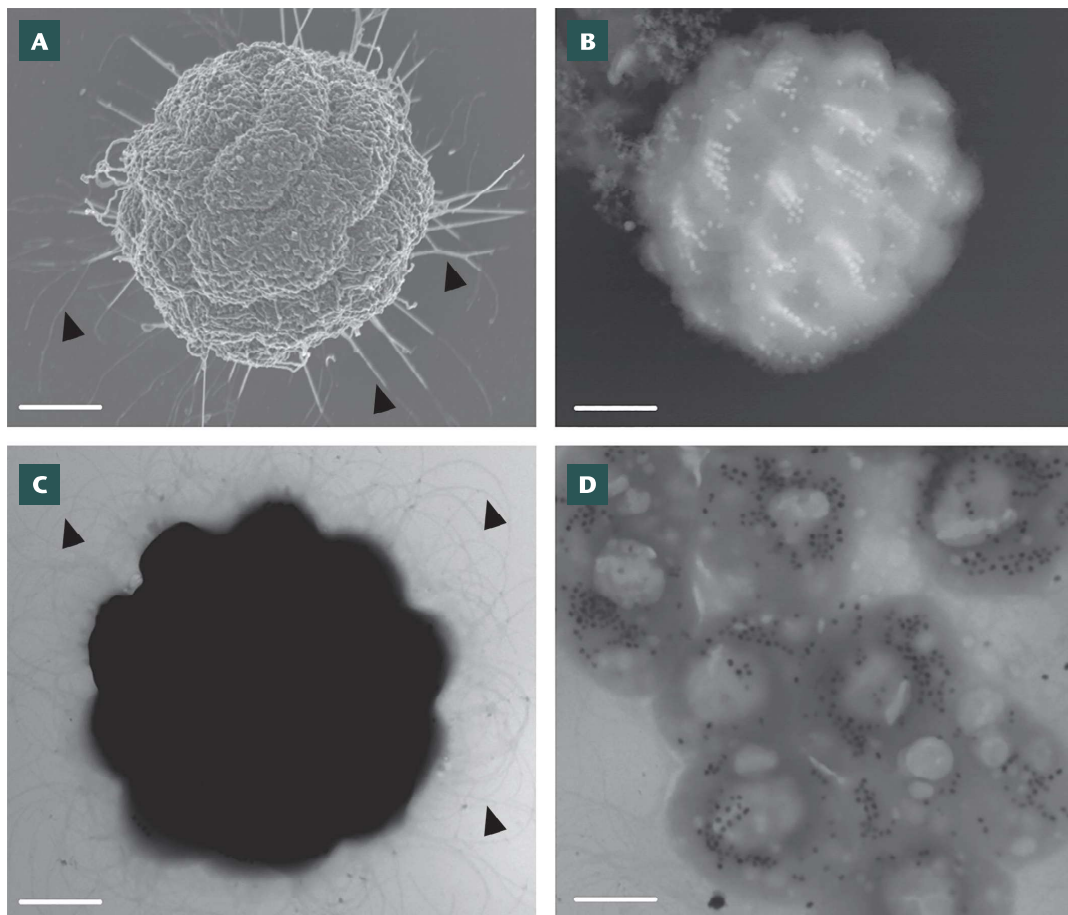
Phylogenetic analyses indicate that eMMPs and sMMPs belong to the same branch of the Desulfobacteraceae family, but are most likely representatives of different genera. Each MMP can produce hundreds of magnetite (Fe<sub>3</sub>O<sub>4</sub>) or greigite (Fe<sub>3</sub>S<sub>4</sub>) magnetosomes, with a couple of species being able to produce crystals of both minerals (Lins et al. 2007). These crystals can have an anisotropic structure (bullet-shaped or tooth-shaped) in the case of magnetite magnetosomes or an octahedral shape in the case of greigite crystals (Abreu et al. 2011).

As in MTB, the biomineralization process in MMPs is genetically controlled by a set of genes clustered in their genomes (Abreu et al. 2011) (see the last section of this chapter; Byrne and Amor 2023 this issue). The organization of magnetosomes and flagella in MMPs is crucial for an efficient coordination of their magnetically guided swimming. Magnetosomes are generally aligned as a continuous chain along the whole organism body from one cell to the other (FIG. 1B). Genomic analyses indicate the flagella position (Arrowheads in FIG. 1) and organization on the cell membrane are well controlled (Leão et al. 2017).

Enrichment techniques and single-cell correlative spectroscopy and microscopy techniques have been applied to better understand the physiology of MMPs and uncover their metabolic capabilities (Schaible et al. 2022). We believe these approaches will soon advance us closer to deciphering the biomineralization and unique life cycle mysteries of this unique prokaryotic organism.

1 Marine Science Institute  
The University of Texas at Austin  
Port Aransas, TX, USA  
E-mail: pedroleao@micro.ufrj.br

2 Aix-Marseille University, CNRS  
Commissariat à l'énergie atomique et aux énergies alternatives (CEA)  
UMR 7265 Institute of Biosciences and Biotechnologies of Aix-Marseille, CEA Cadarache  
13115 Saint-Paul-lez-Durance, France  
E-mail: christopher.lefevre@cea.fr

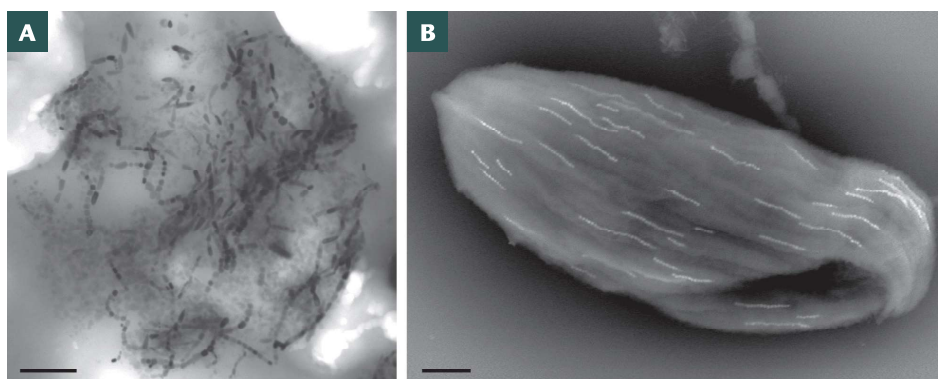


**FIGURE 1** Electron microscopy images of multicellular magnetotactic prokaryotes (MMPs) isolated from sediments of the Mediterranean Sea near Marseille, France. **(A)** Scanning electron microscopy (SEM) image of an MMP observed at low voltage (1.00 kV) to show the surface of the cells (black arrowheads point the flagella). **(B)** SEM image of an MMP observed at high voltage (15.00 kV), using a backscattered electron detector, showing discontinuous aligned magnetosome chains inside the cells (white structures). **(C)** Transmission electron microscopy

(TEM) image of an MMP showing the abundance of flagella on the cell surface (black arrowheads). Note that the magnetosomes inside the cells are not visible when the thick spherical structure is conserved during sample preparation. **(D)** TEM image of disaggregated cells of the MMP allows the observation of magnetosomes (here greigite magnetosomes) inside the cells (dark structures inside the cell). All scale bars represent 1  $\mu\text{m}$ . Arrowheads point to flagella on the organism's surface in **(A)** and **(C)**.

## MAGNETICALLY RESPONSIVE UNICELLULAR EUKARYOTES

Several magnetically responsive microeukaryotes (i.e., protists) have been described in marine and freshwater habitats. A decade after the discovery of the first MTB, the first magnetotactic microbial eukaryote was reported in brackish water sediments from a coastal mangrove swamp in Fortaleza, Brazil (Torres de Araujo et al. 1986). The difficulty in finding and collecting samples limited the study of these Euglenozoa-like protists to light and electron microscopy analyses. Populations of diverse magnetic unicellular eukaryotes were later observed in the chemocline of the seasonally chemically stratified, coastal Salt Pond, Massachusetts, USA (Bazylinski et al. 2000), in sediments of the Mediterranean Sea in France (Monteil et al. 2018), and in intertidal sediments of Huiquan Bay, China (Chen et al. 2021). Biflagellates, dinoflagellates, and ciliates were observed among magnetically concentrated microbial communities. Like MTB, they migrate and accumulate at the edge of water droplets in a magnetic field, but display



**FIGURE 2** **(A)** Transmission electron microscopy (TEM) image of a digestive vacuole containing magnetite particles of different shape found in a ciliate grazing MTB isolated from sediment of the Mediterranean Sea. **(B)** Scanning electron microscopy (SEM) image observed at high voltage (15.00 kV) using a backscattered electron detector of a magnetotactic protist containing symbiotic bacteria attached at its surface that produce magnetite particles. Scale bars represent 0.5  $\mu\text{m}$  in **(A)** and 1  $\mu\text{m}$  in **(B)**.



a behavior that could be associated with predation. In these single-celled eukaryotes, magnetite particles with morphologies and dimensions similar to those of MTB were visualized (FIG. 2A). The ingestion of MTB is responsible for the magnetic response of these protists, which are known to be bacterivorous organisms. Culture experiments also showed that magnetosomes could be ingested and dissolved within acidic vacuoles of predatory ciliates (Martins et al. 2007).

Recently, a magnetotactic protist belonging to Euglenozoa was observed in marine sediments worldwide (Monteil et al. 2019). Its magnetoreception was the result of a cooperation with ectosymbiotic bacteria with whom they live in a mutualistic symbiosis. Magnetoreception is, also in this situation, magnetite-based and originates from prokaryotes biomineralizing magnetosome chains. Unlike MTB-grazers, the sensing and geolocalization in this biological system benefit both organisms thanks to the long-term cooperation established with the host. Microscopy and genomic analyses indicate these ectosymbiotic bacteria are not magnetotactic like MTB in the sense that they do not move by means of their flagella and do not sense chemical gradients. Hundreds of these bacteria are aligned parallel to the host motility axis and magnetically orient it (FIG. 2B) (Chevrier et al. 2023).

In 2020, a new discovery reported a possible biomineralization-based magnetoreception in a unicellular eukaryote (Leão et al. 2020). Uncultured, single-celled eukaryotic flagellates from two Brazilian freshwater sites were observed harboring bullet-shaped magnetite magnetosomes aligned in complex aggregations of multiple chains within the cell. Light and transmission electron microscopy images of these magnetotactic microbes did not allow their identification and no genotyping or genome sequencing was performed. Because of the magnetosomes' size (two times longer than bacterial magnetosomes) and the absence of specific microcompartments typical of a bacterial cell or digestive vacuoles, observations support that the biomineralization is performed by the eukaryote itself.

So far, microbial magnetoreception seems to be restricted to aquatic microorganisms and to be systematically coupled to magnetotaxis, which includes biomineralization of magnetic particles, chemo-aerotaxis, and a motility response. Two other ecological strategies were shown to be associated indirectly with magnetoreception in microorganisms: predation of MTB and symbiosis with magnetic bacteria. The distribution of magnetotaxis among prokaryotes and unicellular eukaryotes inhabiting anoxic/microoxic habitats is an indication that this function represents a key adaptation to these habitats.

## **MAGNETORECEPTION IN EUKARYOTES**

Magnetoreception is the ability to sense magnetic fields. As presented earlier, some unicellular organisms are capable of using the geomagnetic field for navigation, combining this sensor with other responses. Magnetotactic microorganisms use a combination of sensory systems to navigate, magnetotaxis being just a complex mechanism that couples chemo-aerotaxis with magnetic orientation (Lefèvre and Bazylinski 2013). Magnetoreception appears to be a complex feature in eukaryotes too. For example, some young migratory birds inherit their migratory skills (Berthold 1999). However, even with this genetic component, they still need to link them with other senses to perform an effective migration. It is similar for magnetotactic organisms; having magnetosomes allows them to sense the magnetic field and transfer the magnetic moment to their cell body. However,

this stimulus needs to be coordinated with chemotactic receptors and flagella propulsion to deliver an effective magnetotactic behavior.

Migratory animals have developed a complex and elaborate system to detect, combine, and integrate a variety of signals in their nervous system. Only through this integration can they convert multiple signals into an efficient navigation system. Olfaction, hearing, and sight are some of the well characterized signals animals can collect from their environment to help them during navigation. Even though progress has been made, the mechanism involved in sensing the Earth's magnetic field in animals remains unknown. Some broad open questions are: (i) How do animals sense the geomagnetic field? (ii) How is this magnetic stimulus perceived by animals? and (iii) How does an organism use the perceived magnetic signal to navigate? In this section, we review some of the advances made in answering these questions in recent years and some of their still-open mysteries.

### ***How Do Animals Sense the Geomagnetic Field?***

Biological material is permeable to magnetic fields. This way, their sensors can be anywhere inside their bodies. Magnetic crystals found in a broad range of animal tissues raised the possibility that these structures participate as magnetic sensors. This hypothesis based on magnetic particle magnetoreception, however, is not the only one proposed. It was also hypothesized that electroreceptors (e.g., in sharks) or even radical pairs (e.g., in birds) (Hiscock et al. 2016) could be involved in large eukaryotes' magnetoreception. For the purpose of this article, however, we focus on the hypothesis concerning the participation of biomineralized particles.

### ***How is Magnetic Stimulus Perceived by Animals?***

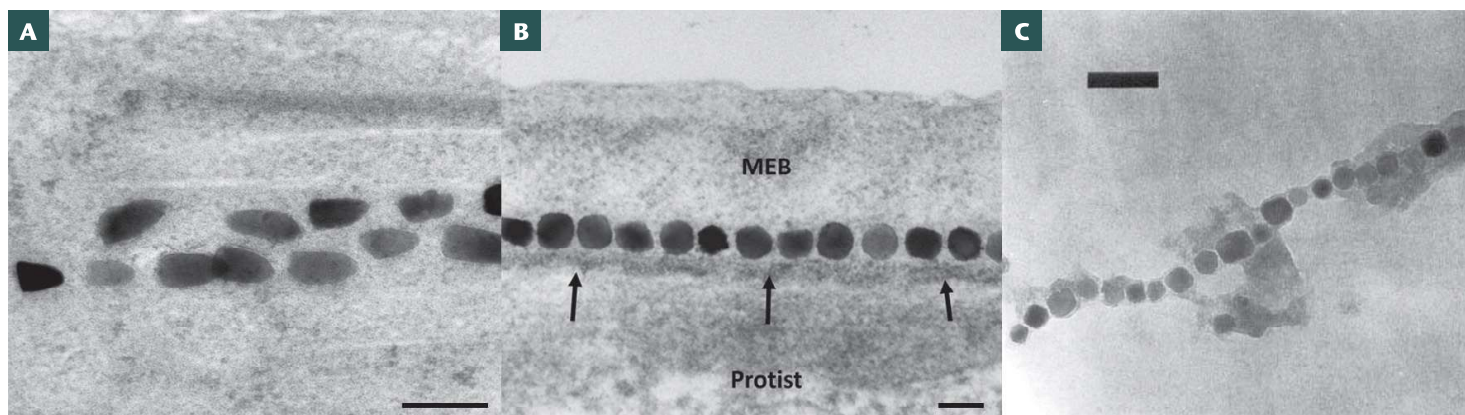
In MTB, the magnetic moment perceived by magnetosome chains is transferred to the cell body through mechanical torque as a result of magnetosomes being linked to the cell by specific magnetoskeleton proteins (Uebe and Schüler 2016). This discovery demonstrates how magnetic crystals work as an internal compass needle.

The discovery of magnetosomes led to the finding of magnetite and other iron oxides in a large range of animals (Winklhofer and Kirschvink 2010). However, the presence of magnetic minerals in animal tissues can also be linked to other physiological processes, such as the control of iron homeostasis in the organism (Wiltschko and Wiltschko 1972). The holy grail of magnetoreception studies in large eukaryotes has been to find these magnetic crystals inside the cell in a consistent and specific location that would link them to the organism's nervous system.

To date, structures found in association with the olfactory epithelium of fish (Bellinger et al. 2022) and the ophthalmic branch of the trigeminal nerve in birds (Fleissner et al. 2003) are the most promising links to magnetic particle magnetoreception. Nevertheless, a link between these structures and the nervous system of animals is still under debate.

### ***How Does an Organism Use the Perceived Magnetic Signal to Navigate?***

A strong argument in favor of the magnetic particle magnetoreception hypothesis is its straightforward physics (Wiltschko and Wiltschko 1972) and evidence of functionality in MTB. Turtles and fish also seem to use magnetic-



**FIGURE 3** Magnetic crystal organization in different magnetically responsive organisms. (A) Magnetosome chain inside a cell of an MMP. (B) Magnetosomes organized in chain inside a magnetic ectosymbiotic bacterium (MEB) attached to the surface of a magnetotactic protist. Black arrows indicate the junction between the MEB and the protist. (C) Cluster of magnetic particles extracted from ethmoid tissue of sockeye salmon. Scale bars represent 100 nm. IMAGE EDITED WITH PERMISSION FROM KIRSCHVINK (1989).

guided navigation in complete darkness, something that would be a problem for the other proposed hypothesis (Walker et al. 1997).

Without a clear link to the nervous system of animals, it is hard to understand the mechanism that allows them to interpret the magnetic stimulus. A few theories predict that the magnetic signal is responsible for controlling mechanosensitive ion channels (Winklhofer and Kirschvink 2010). Others propose that magnetic fields could move ferritin complexes, controlling the flux of ions in a channel (Wheeler et al. 2016).

Although magnetic particles have been found in many animals, it is important to highlight that no ultrastructural organization of these particles similar to the chains of magnetosomes found in MTB (FIG. 3) or a link of these structures to sensory tissues or systems in these organisms have been observed.

### EVOLUTION OF BIOMAGNETISM IN PROKARYOTES AND EUKARYOTES

Our knowledge of the ecology, diversity, and evolution of MTB has dramatically increased in recent years mainly due to the improvement of DNA sequencing and the methods to analyze and compare genes and genomes (Lefèvre and Bazylinski 2013; Lin et al. 2020). Magnetosome biomineralization in MTB requires the coordination of a complex set of interacting proteins with a large range of functions and domains (Uebe and Schüler 2016). The presence of a highly conserved gene set in all MTB indicates that magnetosomes emerged only once over the course of bacterial diversification (Lefèvre and Bazylinski 2013). While there is consensus about this fact, how the genetic basis for magnetosome formation was then transferred to the descendants and how the pathway diversified throughout evolution is controversial. MTB and non-MTB are found in the same taxonomical groups (e.g., phyla) (Lefèvre and Bazylinski 2013), but only MTB possess genes specifically associated with magnetosome chain biogenesis. To study the evolutionary history of magnetotaxis, two phylogenetic reconstructions of MTB are usually inferred. One is based on MTB-conserved proteins that are not involved in magnetosome formation and a second one built from magnetosome proteins shared by all MTB. Congruence between these two evolutionary

histories supports vertical inheritance of magnetosome genes: they would be transferred by descent, rather than by two bacterial cells exchanging genetic material, which is referred to as horizontal transfer (Lefèvre et al. 2013). In the case of vertical transfer, magnetosome genes would be inherited from a single common ancestor from which all MTB phyla would originate. However, this scenario is not parsimonious because it implies many evolutionary events leading to the loss of the magnetosome genes in non-MTB contained in the same taxonomical groups as MTB. The apparent congruence of these evolutionary reconstructions may be misleading in suggesting a sole vertical inheritance of the magnetosome genes. Because magnetosome genes are contained within a single gene cluster, one can assume that such a cluster is able to be transferred from one bacterium to another through horizontal gene transfers. Indeed, horizontal gene transfers have been evidenced between MTB of the same genus or species (Monteil et al. 2020). It was assumed that repeated horizontal gene transfers along with other genetic rearrangement of the entire gene set contributed to the similar evolution of magnetotaxis and MTB species. Because magnetosome genes of different MTB strains may support different evolutionary scenarios, it remains difficult to arbitrate between vertical and horizontal inheritance (Monteil et al. 2020).

Thus, only one prokaryotic origin has been formally demonstrated, and a possible independent emergence of eukaryotes must be investigated. Indeed, because eukaryotic and prokaryotic magnetoreception is linked to the biomineralization of magnetic particles, a common origin of the biomineralization in protists and bacteria is appealing. Moreover, microbial magnetoreception has often tentatively been related to that of macroorganisms. As a consequence, it was speculated that ancient prokaryotic or eukaryotic forms of magnetosomes or even endosymbiotic MTB could be the origin of magnetoreception in animals (Kirschvink et al. 2001). The possibility of a symbiosis between a magnetotactic bacterium that would be at the origin of magnetoreception remains very speculative, as there is no evidence of the presence of MTB in symbiosis with living or extinct animals. One study reported the presence of MTB within the marine bivalve *Thyasira cf. gouldi* (Dufour et al. 2014). This association is, however, likely more related to predation as the magnetotactic cells lose the integrity of their magnetosome chain and possibly their flagellum in their host. Moreover, the bivalves in that study appeared not to use MTB for magnetoreception.

Recently, magnetite particles were observed in the salmonid olfactory epithelium (Bellinger et al. 2022). A gene expression study (i.e., transcriptomic) of the salmon olfactory cells revealed the presence of proteins sharing low homology with proteins involved in magnetosome formation in MTB. This led to the hypothesis of ancient symbiotic



events leading to the transfer of magnetite biomineralization capacity from MTB to eukaryotes. Magnetosome proteins belong to widespread and functionally diverse protein superfamilies. Consequently, they share features with proteins that have diverse functions unrelated to biomineralization. It is thus not surprising to find distant homologous proteins in all domains of life (Monteil et al. 2022). Although we cannot rule out the possibility of a common origin of magnetite biomineralization between MTB and eukaryotes or from a secondary horizontal gene transfer of the whole magnetosome genes set, we cannot exclude that magnetic biomineralization emerged independently in eukaryotes and converged toward the same function. Thus, there is so far no evidence of a connection between MTB and magnetoreception in animals. We

believe that future research will contribute to deciphering some enigmas about the diversity of magnetoreception mechanisms and their emergence and evolution in micro- and macroorganisms.

## ACKNOWLEDGMENTS

PL acknowledges the support and guidance provided by Professor Ulysses Lins during all his research in the magnetotactic organisms field. CTL acknowledges support from the French national research agency: ANR project SymbioMagnet-21-CE02-0034-01. We thank R. Bolzoni for providing SEM images.

## REFERENCES

- Abreu F and 10 coauthors (2011) Common ancestry of iron oxide- and iron-sulfide-based biomineralization in magnetotactic bacteria. *The ISME Journal* 5: 1634-1640, doi: 10.1038/ismej.2011.35
- Bazylinski DA, Schlezinger DR, Howes BH, Frankel RB, Epstein SS (2000) Occurrence and distribution of diverse populations of magnetic protists in a chemically stratified coastal salt pond. *Chemical Geology* 169: 319-328, doi: 10.1016/S0009-2541(00)00211-4
- Bellinger MR and 5 coauthors (2022) Conservation of magnetite biomineralization genes in all domains of life and implications for magnetic sensing. *Proceedings of the National Academy of Sciences* 119: e2108655119, doi: 10.1073/pnas.2108655119
- Berthold P (1999) A comprehensive theory for the evolution, control and adaptability of avian migration. *Ostrich* 70: 1-11, doi: 10.1080/00306525.1999.9639744
- Byrne JM, Amor M (2023) Biomagnetism: insights into magnetic minerals produced by microorganisms. *Elements* 19: 208-214
- Chen S and 7 coauthors (2021) Observations on a magnetotactic bacteria-grazing ciliate in sediment from the intertidal zone of Huiquan Bay, China. *Journal of Oceanology and Limnology* 39: 2053-2062, doi: 10.1007/s00343-021-1011-3
- Chevrier DM and 16 coauthors (2023) Collective magnetotaxis of microbial holobionts is optimized by the three-dimensional organization and magnetic properties of ectosymbionts. *Proceedings of the National Academy of Sciences* 120: e2216975120, doi: 10.1073/pnas.2216975120
- Dufour SC and 5 coauthors (2014) Magnetosome-containing bacteria living as symbionts of bivalves. *The ISME Journal* 8: 2453-2462, doi: 10.1038/ismej.2014.93
- Fleissner G and 6 coauthors (2003) Ultrastructural analysis of a putative magnetoreceptor in the beak of homing pigeons. *Journal of Comparative Neurology* 458: 350-360, doi: 10.1002/cne.10579
- Hiscock HG and 7 coauthors (2016) The quantum needle of the avian magnetic compass. *Proceedings of the National Academy of Sciences* 113: 4634-4639, doi: 10.1073/pnas.1600341113
- Kirschvink JL (1989) Magnetite biomineralization and geomagnetic sensitivity in higher animals: an update and recommendations for future study. *BioElectroMagnetics* 10: 239-259, doi: 10.1002/bem.2250100304
- Kirschvink JL, Walker MM, Diebel CE (2001) Magnetite-based magnetoreception. *Current Opinion in Neurobiology* 11: 462-467, doi: 10.1016/S0959-4388(00)00235-X
- Kolinko S, Richter M, Glöckner F-O, Brachmann A, Schüler D (2014) Single-cell genomics reveals potential for magnetite and greigite biomineralization in an uncultivated multicellular magnetotactic prokaryote. *Environmental Microbiology Reports* 6: 524-531, doi: 10.1111/1758-2229.12198
- Leão P and 8 coauthors (2017) Ultrastructure of ellipsoidal magnetotactic multicellular prokaryotes depicts their complex assemblage and cellular polarity in the context of magnetotaxis. *Environmental Microbiology* 19: 2151-2163, doi: 10.1111/1462-2920.13677
- Leão P and 10 coauthors (2020) Magnetosome magnetite biomineralization in a flagellated protist: evidence for an early evolutionary origin for magnetoreception in eukaryotes. *Environmental Microbiology* 22: 1495-1506, doi: 10.1111/1462-2920.14711
- Lefèvre CT and 10 coauthors (2013) Monophyletic origin of magnetotaxis and the first magnetosomes. *Environmental Microbiology* 15: 2267-2274, doi: 10.1111/1462-2920.12097
- Lefèvre CT, Bazylinski DA (2013) Ecology, diversity, and evolution of magnetotactic bacteria. *Microbiology and Molecular Biology Reviews* 77: 497-526, doi: 10.1128/mbr.00021-13
- Lin W, Kirschvink JL, Paterson GA, Bazylinski DA, Pan Y (2020) On the origin of microbial magnetoreception. *National Science Review* 7: 472-479, doi: 10.1093/nsr/nwz065
- Lins U, Keim CN, Evans FF, Farina M, Buseck PR (2007) Magnetite (Fe<sub>3</sub>O<sub>4</sub>) and greigite (Fe<sub>3</sub>S<sub>4</sub>) crystals in multicellular magnetotactic prokaryotes. *Geomicrobiology Journal* 24: 43-50, doi: 10.1080/01490450601134317
- Martins JL and 5 coauthors (2007) Grazing protozoa and magnetosome dissolution in magnetotactic bacteria. *Environmental Microbiology* 9: 2775-2781, doi: 10.1111/j.1462-2920.2007.01389.x
- Monteil CL and 5 coauthors (2018) Accumulation and dissolution of magnetite crystals in a magnetically responsive ciliate. *Applied and Environmental Microbiology* 84: e02865-17, doi: 10.1128/AEM.02865-17
- Monteil CL and 15 coauthors (2019) Ectosymbiotic bacteria at the origin of magnetoreception in a marine protist. *Nature Microbiology* 4: 1088-1095, doi: 10.1038/s41564-019-0432-7
- Monteil CL and 8 coauthors (2020) Repeated horizontal gene transfers triggered parallel evolution of magnetotaxis in two evolutionary divergent lineages of magnetotactic bacteria. *The ISME Journal* 14: 1783-1794, doi: 10.1038/s41396-020-0647-x
- Monteil CL, Vallenet D, Schüler D, Lefèvre CT (2022) Magnetosome proteins belong to universal protein families involved in many cell processes. *Proceedings of the National Academy of Sciences* 119: e2208648119, doi: 10.1073/pnas.2208648119
- Schaible GA, Kohtz AJ, Cliff J, Hatzenpichler R (2022) Correlative SIP-FISH-Raman-SEM-NanoSIMS links identity, morphology, biochemistry, and physiology of environmental microbes. *ISME Communications* 2: 52, doi: 10.1038/s43705-022-00134-3
- Torres de Araujo FF, Pires MA, Frankel RB, Bicudo CEM (1986) Magnetite and magnetotaxis in algae. *Biophysical Journal* 50: 375-378, doi: 10.1016/s0006-3495(86)83471-3
- Uebe R, Schüler D (2016) Magnetosome biogenesis in magnetotactic bacteria. *Nature Reviews Microbiology* 14: 621-637, doi: 10.1038/nrmicro.2016.99
- Walker MM and 5 coauthors (1997) Structure and function of the vertebrate magnetic sense. *Nature* 390: 371-376, doi: 10.1038/37057
- Wheeler MA and 12 coauthors (2016) Genetically targeted magnetic control of the nervous system. *Nature Neuroscience* 19: 756-761, doi: 10.1038/nn.4265
- Wiltshcko W, Wiltshcko R (1972) Magnetic compass of European robins. *Science* 176: 62-64, doi: 10.1126/science.176.4030.62
- Winklhofer M, Kirschvink JL (2010) A quantitative assessment of torque-transducer models for magnetoreception. *Journal of the Royal Society Interface* 7: S273-S289, doi: 10.1098/rsif.2009.0435.focus ■