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## Magnetoreception in Microorganisms

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1 **Magnetoreception in microorganisms**

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23 **Magnetoreception is the sense whereby organisms geolocate and navigate in response to**  
24 **the Earth's magnetic field lines. For decades, magnetotactic bacteria have been the only**  
25 **known magnetoreceptive microorganisms. The magnetotactic behaviour of these aquatic**  
26 **prokaryotes is due to the biomineralization of magnetic crystals. While an old report**  
27 **alleged microbial algae with a similar behaviour, recent discoveries have demonstrated**  
28 **the existence of unicellular eukaryotes able to sense the geomagnetic field and revealed**  
29 **different mechanisms and strategies involved in such a sensing. Some ciliates can be**  
30 **magnetically guided after predation of magnetotactic bacteria, while some flagellates**  
31 **acquired this sense through symbiosis with magnetic bacteria. A report has even suggested**  
32 **that some magnetotactic protists could biomineralize magnetic crystals.**

33

### 34 **Sensing the Earth's magnetic field lines**

35 Microorganisms can sense environmental features and respond to their fluctuations through  
36 different systems of receptors dedicated to, for example, temperature, light, pressure, gravity,  
37 energy sources and all sorts of biogenic chemical signals [1–4]. The Earth's magnetic field is  
38 no exception and some microorganisms elaborated sensory structures or ecological strategies  
39 to exploit its variations. The Earth's core is a permanent magnet whose field vectors point the  
40 south magnetic pole away from the north magnetic at every location on the planet but at the  
41 equator [5]. The geomagnetic field lines resulting from horizontal and vertical components,  
42 every organism able to measure such vector may differentiate the deepness from the surface  
43 and the four cardinal directions. During the 11th century, humans learned how to artificially  
44 exploit the Earth's magnetic field for navigation with needle compasses [6], while many  
45 animals such as birds, fish and insects, naturally have this ability for long-distance migration  
46 [7–9]. Magnetoreception emerged in the microbial world too, in which this sense may represent  
47 a selective advantage for microorganisms living in spatially fluctuating niches like those of  
48 chemically stratified environments. Indeed, the field being locally unchanged, it limits  
49 environmental prospection for energy sources and electron acceptors to bidirectional transects  
50 instead of a volume [10]. This trait may thus compensate unstable disturbances of vertical  
51 chemical gradients and help microorganisms to move toward their optimal local niche. All  
52 magnetically sensitive microorganisms described to date associate this sense to a chemo-  
53 aerotaxis system to swim along chemical and oxygen gradients towards attractants or away  
54 repellents. This behaviour, called **magnetotaxis**, was until recently, observed in magnetotactic  
55 bacteria only. However, recent discoveries revealed that some unicellular eukaryotes in  
56 different phylogenetic groups are magnetotactic or at least become transiently

57 magnetoreceptive by different mechanisms and interactions [11,12]. Here, we propose to  
58 review the diversity and different strategies microbes have developed to obtain their magnetic  
59 sense.

60

### 61 **Bacterial magnetoreception and biomineralization of nanomagnets**

62 Magnetoreception in bacteria and vertebrates was clearly proven for both at the same period in  
63 the late 1970s [13–17]. For vertebrates, elucidating genetic, cellular and biophysical processes  
64 involved in magnetoreception remains a challenge in sensory biology for many decades [18,19].  
65 Several mechanisms are putatively involved in vertebrates magnetoreception, among which a  
66 magnetite-based magnetoreceptor, a light-driven electron transfer reaction in photoreceptors  
67 and an electromagnetic induction by electroreceptors [19]. In microorganisms however, only  
68 one mechanism is known: the **biomineralization** of permanent nanomagnets by bacteria within  
69 specific organelles called **magnetosomes** (Figure 1). The mechanistic and genetic basis of  
70 magnetic sensing in magnetotactic bacteria (MTB) is the best described so far and was  
71 extensively reviewed this last decade [20,21]. Most of our knowledge on magnetosome  
72 synthesis comes from genetic and biochemical studies performed on two model strains MSR-1  
73 and AMB-1 of the *Magnetospirillum* genus. Genomics and genetics identified one cluster of  
74 genes of variable size and organization responsible for magnetotaxis, within which an operon,  
75 namely the *mamAB* operon, that is essential for magnetosome formation in all MTB described  
76 so far [22,23]. Major progress has been made in the understanding of the genetic basis and  
77 biochemical mechanisms involved in magnetosome membrane biogenesis [24],  
78 biomineralization [25] and alignment [26]. The alignment in chains of several magnetosomes  
79 gives a magnetic moment to the cell along its motility axis, which ensures the parallel  
80 orientation with the Earth's magnetic field. Recent biodiversity studies, guided by the  
81 development of “omics” technologies, increased our knowledge on the diversity of these  
82 bacteria [27–29] and the mechanisms involved in their magnetotactic behaviour [30–32]. While  
83 the majority of the lineages described belong to several classes of Proteobacteria, MTB are also  
84 distributed in other phyla like the Nitrospirae and the Omnitrophica [33]. Metagenomic data  
85 also suggest that some bacteria within the Latescibacteria and Planctomycetes phyla could also  
86 form magnetosomes [27,29]. Magnetotactic species produce a diversity of chains with different  
87 crystalline structures or chemical composition (magnetite  $\text{Fe}_3\text{O}_4$  or greigite  $\text{Fe}_3\text{S}_4$ ) that seem to  
88 be clade-specific [34]. The processes that led to the **polyphyletic distribution** of  
89 magnetoreception in bacteria in such a wide range of phyla nourished a debate as soon as the  
90 first greigite producers were discovered [35]. The timing of magnetosome emergence and the

91 history of its diversification over bacteria evolution are a permanent matter of investigation that  
92 new genomes and MTB species regularly feed and will fully resolve [27,28,36–38]. The  
93 evolutionary steps that led to the emergence of such complex organelle itself and magnetic  
94 sensing are so far unknown. MTB evolved different magnetotactic behaviours according to the  
95 species [30] with different motility strategies [39] and specific dividing processes [40]. These  
96 behaviours represent a selective advantage for these bacteria that find more efficiently their  
97 habitat thanks to the inclination of the magnetic field lines [41]. Despite the diversity of the  
98 morphologies, motility behaviours, magnetosomes chains and genetic groups, the bacterial  
99 magnetic sensing is always associated to bacteria sharing the same niche [29]. This niche is  
100 located at the anoxic-microoxic interface of aquatic sediments where the equilibrium of  
101 environmental conditions, notably redox, is fragile [30,42]. This zone is the seat of important  
102 geochemical processes [42], to which some MTB species were shown to participate in [43].

103

#### 104 **Magnetically responsive protozoan grazers**

105 Benthic microbial communities are not only composed of prokaryotes, but also of microbial  
106 eukaryotes among which **protists** and fungi that share the same habitat and need to adapt to the  
107 same environmental pressures. After the discovery of the first MTB, arose the hypothesis that  
108 magnetotaxis could have evolved in protists thriving in anoxic/microoxic aquatic habitats. In  
109 the early years of MTB research, magnetotactic aggregates formed by tens of cells were  
110 discovered in a marine lagoon in Brazil [44]. Their multicellularity was rather supporting that  
111 these organisms were unlikely bacteria. In fact, those aggregates were the so-called  
112 multicellular magnetotactic prokaryotes (MMPs) that represent one of the most interesting and  
113 unusual examples of prokaryotic morphology (Figure 1D and E) [45,46]. Later, an Americano-  
114 Brazilian research network opened the way to a new field of research on magnetoreception by  
115 observing the first magnetotactic microbial eukaryote [47]. The difficulties to find and collect  
116 them have been a huge barrier to the characterization of their magnetoreception for years.  
117 Efforts to find them again failed and their study was still limited by the light and electron  
118 microscopy analyses carried out in the 80's.

119 Fifteen years later, populations of diverse magnetic unicellular eukaryotes were observed in the  
120 **chemocline** of the seasonally chemically stratified, coastal Salt Pond, Massachusetts, USA  
121 [48]. Biflagellates, dinoflagellates and ciliates were observed among magnetically concentrated  
122 microbial communities. A similar observation, from the same environment was reported later  
123 [49]. Like magnetotactic bacteria, they migrated and accumulated at the edge of a hanging water  
124 droplet in a magnetic field but displayed a different swimming compared to MTB. In these

125 single-celled eukaryotes, magnetite particles with morphologies and dimensions similar to  
126 those of magnetosome-producing bacteria were visualized. However, the origin of these  
127 particles was difficult to determine. Based on their observation, endosymbiosis could not be  
128 excluded as well as biomineralization by the protist itself, but ingestion of MTB was suggested  
129 to be responsible for the magnetic response of some protists, known to be bacterivorous  
130 organisms. As many aquatic protists, MTB grazers (i.e. protists that predate MTB) are  
131 facultative anaerobes capable of both aerobic and anaerobic growth, which should allow them  
132 to easily predate MTB. In Salt Pond, it was shown that the magnetically responsive protists  
133 were more abundant during the early and late season of stratification, when the chemocline  
134 narrows and MTB concentrate in a smaller volume [49], indicating a correlation between  
135 concentration of MTB and that of magnetically responsive protists. Moreover, when the  
136 magnetotactic protists were magnetically concentrated at the edge of a droplet where MTB  
137 aggregate, they appeared to exhibit a slow looping swimming motion that could be associated  
138 to a predatory behaviour [49].

139 By feeding a predatory ciliate with magnetically purified *Ca. Magnetoglobus multicellularis*, it  
140 has been shown that greigite magnetosomes could be dissolved within the acidic vacuoles of  
141 the ciliate [50]. In this study, it was not possible to state if this behaviour occurs in  
142 environmental conditions and if magnetoreception could arise from the interaction. Recently,  
143 this behaviour was investigated in natural populations of protists and MTB, and it was shown  
144 that ciliates affiliated to the genus *Uronema* (Stramenopiles-Alveolates-Rhizaria, SAR group)  
145 were able to ingest hundreds of MTB into acidic vacuoles to progressively become sensitive to  
146 the variations of the magnetic fields in the same way than MTB (Figure 2A and B) [11]. The  
147 magnetic response in MTB-grazers is certainly not encoded in the eukaryote genome, but this  
148 behaviour seems to facilitate movement of grazers towards the prey biomass. It is still unclear  
149 if a chemotaxis is also involved and if this interaction has been selected over the course of the  
150 protist evolution. However, the directed grazing towards these preys specifically and the  
151 magnetic response suggest that this interaction is widespread among marine and freshwater  
152 heterotrophic flagellates and ciliates (Figure 2). MTB-grazers seem to have evolved different  
153 strategies for the internalization of MTB and their magnetosome chains: (i) sequestration in  
154 food vacuoles (Figure 2A and B), (ii) accumulation in a specific location in the cell (Figure 2C  
155 and D), and (iii) an apparently random storage in the cell (Figure 2E) [11,48,50]. These  
156 magnetically responsive protists also appear to have evolved different strategies to deal with  
157 iron toxicity with (i) the egestion of magnetic inclusions where magnetosomes accumulated  
158 [48] and (ii) the progressive dissolution of magnetosomes until the colloidal iron would be

159 expelled from the protistan cell *via* the **cytoproct** [11,50,51]. Protists that feed on MTB have  
160 been proposed to play a significant role in iron cycling [11,48,49]. It was shown that digestion  
161 of colloidal iron in the food vacuoles of protists during grazing of particulate and colloidal  
162 matter could generate more bioavailable iron for other species, such as phytoplankton [52,53].  
163 Thus, MTB grazing could be involve in recycling particulate iron back to a bioavailable form  
164 in the environment through dissolution [54].

165

### 166 **Symbiotic origin of magnetoreception in protists**

167 Long neglected, **mutualistic symbiosis** and cooperation are today recognized as major  
168 diversification forces in the same way as competition for resources and natural selection have  
169 been for centuries [55]. These concepts even became central in our understanding of the  
170 mechanisms and strategies governing species interactions and adaptation in innumerable  
171 biological systems. Mutualistic symbioses between prokaryotes – macroscopic eukaryotes are  
172 the best examples. They have been particularly well documented for insects, plants or corals,  
173 for which studies have shown the importance of certain highly specialized algae, bacteria and  
174 fungi on host nutrition and reproduction [56–58]. These symbioses are also extremely diverse  
175 and abundant between unicellular eukaryotes and prokaryotes, even though less characterized  
176 [59]. Some of them are even the foundation of the evolutionary scenarios on organelle  
177 acquisition and **eukaryogenesis** [60]. Symbiotic associations between protists and bacteria or  
178 archaea are common in anoxic marine sediments [61]. Prokaryotic symbionts can be associated  
179 with their protist hosts as ectosymbionts (attached to the host surface) or as endosymbionts  
180 (located beneath the host cell membrane). These symbionts can expand the host niche by  
181 complementing host metabolism, improving its motility or adaptation to new conditions.

182 The recent discovery of magnetotactic **holobionts** changed our vision of magnetoreception in  
183 unicellular eukaryotes. A magnetotactic protist belonging to the Euglenozoa, Excavates, was  
184 observed in marine sediments worldwide [12,62]. Its magnetoreception was the result of a  
185 cooperation with ectosymbiotic bacteria with whom they live in a mutualistic symbiosis (Figure  
186 3) [12]. Again, magnetoreception is magnetite-based and originates from prokaryotes  
187 biomineralizing magnetosomes chains. Unlike MTB-grazers, the sensing and geolocalization  
188 in this biological system benefits to both organisms thanks to the long-term cooperation  
189 established with the host. Microscopy and genomic analyses indicate these ectosymbiotic  
190 bacteria are not magnetotactic like MTB in the sense they do not move by means of their own  
191 flagella and do not sense chemical gradients; they can be considered only as magnetic. With  
192 the protistan host, magnetic ectosymbiotic bacteria (MEB) form a microbial holobiont acting

193 as a supramicroorganism and an ecological unit. Hundreds of these MEB, all belonging to a  
194 single strain of the Deltaproteobacteria class, are aligned parallel to the host motility axis  
195 (Figure 3A and B) and magnetically orient it. Surprisingly, it was experimentally proven that  
196 this magnetic guidance was influenced by oxygen concentrations while genome sequencing  
197 showed that MEB could not sense chemical gradients. It is thus likely that holobiont  
198 magnetotaxis was collectively ensured thanks to the biflagellate chemotaxis. The partners'  
199 interdependency relies also on metabolic exchanges, among which some of them could be  
200 identified based on the host ultrastructure and MEB genome. Their **syntrophy** is based on the  
201 transfer of molecular hydrogen from the host to the MEB that use it to reduce sulphate. Protists  
202 are bacteria predators and ferment organic matter into energy thanks to mitochondrion-like  
203 organelles called **hydrogenosomes** [63]. This process generates ATP and by products like CO<sub>2</sub>,  
204 acetate and H<sub>2</sub> that is diffused through the membrane plasma. Other chemicals might be  
205 exchanged but need to be identified through isotope probing and comparative genomics. For  
206 example, genomic data indicate that acetate and CO<sub>2</sub> are likely used by the MEB as well [12].

207

### 208 **Magnetic biomineralization in protists?**

209 The search for biomineralizing magnetic microbial eukaryotes has become an endeavour for  
210 many researchers as soon as Torres de Ajaujo and coworkers reported in 1986 the magnetotactic  
211 algae with many magnetite particles organized in chains [47]. It was clear that the  
212 magnetoreception of these microorganisms was magnetite-based similarly to MTB. Although  
213 the chains appeared to be located in or near the cell wall, authors could not identify their  
214 organization relative to each other and from the flagellate motility axis. With the limitation of  
215 the imaging techniques and DNA typing at that time, many questions remained unanswered,  
216 making it hard to conclude about the origin of their magnetoreception. No ultrastructural feature  
217 could inform on the presence or the absence of ecto- or endo-symbiotic bacteria even though  
218 bullet-shaped magnetosomes looked like those of Deltaproteobacteria [34]. These flagellated  
219 protists, tentatively identified as *Anisonema platysomum* (Euglenophyceae, Euglenozoa,  
220 Excavata) based on morphological criteria, were not observed again in decades after their first  
221 isolation in a coastal mangrove swamp in northeastern Brazil.

222 In 2019, a new report revivals the hypothesis of a biomineralization-based magnetoreception in  
223 unicellular eukaryotes [64]. Uncultured single-celled eukaryotic flagellates from two different  
224 Brazilian freshwater sites were observed harbouring anisotropic bullet-shaped magnetite  
225 magnetosomes aligned in complex aggregations of multiple chains within the cell. Light and  
226 transmission electron microscopy (TEM) images of these magnetotactic microbes were not



227 decisive enough to allow their identification and no genotyping or genome sequencing was  
228 performed. Their size, morphology and the multiple flagella at the anterior pole of the cells  
229 attested that the protist belongs to another group of that previously observed 30 years before.  
230 Because of the magnetosomes size two times longer than bacterial magnetosomes and the  
231 absence of specific micro-compartments typical of a bacterial cell or digestive vacuoles,  
232 observations rather supported that the biomineralization is performed by the eukaryote itself.  
233 However, contrasted TEM cross sections are missing to validate the ultrastructure of the  
234 magnetotactic protist and the relative position of the magnetosomes chains. If such result was  
235 validated, magnetoreception could have arose from an ancient endosymbiosis event with an  
236 MTB, but also from a secondary lateral gene transfer of the whole magnetosome genes cluster.  
237 Even if these scenarios are those the most plausible and parsimonious, it is not to exclude that  
238 magnetic biomineralization emerged independently a second time in eukaryotes and converged  
239 toward the same function. Future research, such as the identification of the genetic determinants  
240 involved in magnetosomes formation, will help to validate that magnetosome magnetite  
241 biomineralization occurs in this protist.

242

### 243 **Concluding Remarks and Future Prospects**

244 The latest discoveries have unravelled a broader diversity of magnetoreceptive microorganisms  
245 in the Eukarya domain than previously thought. Advances in single-cell sorting and genomics  
246 are opening up a path to study their ultrastructural, phylogenetic and biological characterization.  
247 So far, microbial magnetoreception seems to be restricted to aquatic microorganisms and to be  
248 systematically coupled to magnetotaxis, which includes biomineralization of magnetic  
249 particles, chemo-aerotaxis and a motility response. But two other ecological strategies were  
250 shown to be associated indirectly with magnetoreception in microorganisms: predation of  
251 magnetotactic bacteria and symbiosis with magnetic bacteria (Figure 4). The distribution of this  
252 function among microorganisms inhabiting anoxic/microoxic habitats strengthens the idea that  
253 it represents a key adaptation to these habitats. Although our knowledge on the ecology,  
254 diversity and evolution of magnetoreceptive microorganisms have dramatically increased these  
255 recent years [29,37,65], many important questions remain unanswered and should be addressed  
256 in future work (see Outstanding Questions). Only one prokaryotic origin has been formally  
257 demonstrated, and a possible independent emergence in eukaryotes needs to be investigated.  
258 The discovery of magnetotactic protists specifically, paves the way to a new field of research  
259 at the interface of many disciplines. It is unclear yet in which extent this trait is widespread  
260 among benthic protists since the classical isolation protocols and methods still need to be

261 adapted to these organisms. Furthermore, all magnetoreceptive microorganisms identified to  
262 date are those coupling magnetoreception and geolocalization to navigation. But other  
263 biological systems showed that geolocalization may be used for a purpose other than navigation,  
264 as some immobile fungi that use gravity instead to sense verticality and direct the spread of  
265 spores [66]. Thus, beyond exploring the diversity of magnetotactic organisms, alternative  
266 protocols should be developed to isolate magnetoreceptive microorganisms that are not  
267 magnetotactic. Exploration of new habitats along with the application of new material and  
268 methods for the observation of magnetically responsive organisms will certainly answer this  
269 question and many others that the scientific community is currently enthusiastic about.

270 The discovery of microorganisms able of magnetoreception is also particularly appealing for  
271 some scientists that search for the origin of magnetoreception in macroorganisms like migratory  
272 birds or fish. Indeed, for non-specialists in evolutionary biology, it is easy to mistakenly think  
273 that modern lineages of microbial eukaryotes reflect ancestral forms of these. As a consequence,  
274 it was speculated that ancient prokaryotic or eukaryotic forms of magnetosomes or even  
275 endosymbiotic MTB could be at the origin of magnetoreception in animals [67,68]. The  
276 possibility of a symbiosis between a magnetotactic bacterium that would be at the origin of  
277 magnetoreception remains very speculative, as there is no evidence of the presence of MTB in  
278 symbiosis with such animal. For example, magnetite biomineralization mechanisms have been  
279 identified for some macroorganisms such as chitons or honeybees and would involve ferritin  
280 deposition [71,72], not magnetosome formation. Then, despite the report of the presence of  
281 magnetotactic symbionts [69], closely related to the free-living MTB strain SS-5 [70], within  
282 the marine bivalve *Thyasira cf. gouldi*, this association is likely more related to predation.  
283 Indeed, the magnetotactic cells in their host lose the integrity of their magnetosome chain and  
284 possibly their flagellum. Moreover, the bivalves appeared to not use magnetotactic bacteria for  
285 magnetoreception while bacteria do not seem to take any advantage to be in the host. Thus,  
286 there is no evidence of a connexion between magnetotactic bacteria and magnetoreception in  
287 animals so far. We believe that advanced methods in imaging and genomics will contribute in  
288 the future to decipher some of the enigma about the diversity of the magnetoreceptive  
289 mechanisms, its emergence and evolution in micro- and macroorganisms.

290

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296

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451

452 **Glossary**

453 **Biomining:** biological process by which eukaryotes and prokaryotes are able to  
454 produce minerals.

455 **Chemocline:** horizontal layer formed in aquatic habitats by a strong vertical chemistry gradient  
456 that marks the boundary between two contrasted chemical environments.

457 **Cytopyge:** special pore in the pellicle of ciliates used for exocytosis and membrane recycling.

458 **Eukaryogenesis:** evolutionary transition at the origin of the eukaryotic cell.

459 **Grazing:** feeding strategy that some protozoa evolved to feed on microorganisms.

460 **Hydrogenosomes:** double membrane-bounded organelles of mitochondrial ancestry found in  
461 some anaerobic eukaryotes. They are involved in catabolic processes that produce molecular  
462 hydrogen, acetate, carbon dioxide and ATP.

463 **Holobiont:** Assemblage of different species living in symbiosis that forms an ecological unit.

464 **Magnetosomes:** prokaryotic organelles composed of nano-sized, magnetic, iron-mineral  
465 crystals, enveloped by a biological membrane. Usually arranged in chains within the cell, they  
466 provide the cell with a permanent magnetic dipole and allow magnetic sensing.

467 **Magnetotaxis:** behaviour of some motile aquatic bacteria that align passively along Earth's  
468 magnetic field lines while they swim to facilitate their navigation towards their preferred  
469 habitat.

470 **Mutualistic symbiosis:** long-term relationship between different species living in symbiosis in  
471 which all partners benefit from the biological interaction.

472 **Protists:** unicellular eukaryotic microorganisms (cells containing a nucleus). They do not refer  
473 to a taxonomic unit and are polyphyletically distributed into the Eukarya domain.

474 **Protozoa:** heterotrophic unicellular eukaryotes that feed on organic matter such as other  
475 microorganisms.

476 **Polyphyletic distribution:** Distribution of a trait or organisms in different taxonomic groups  
477 that are not related by a direct common ancestor.

478 **Symbiosis:** defines a long-term physical coexistence of two or more species, in which at least  
479 one partner is dependent on the others, no matter what the effect of the interaction on the  
480 partner's fitness.

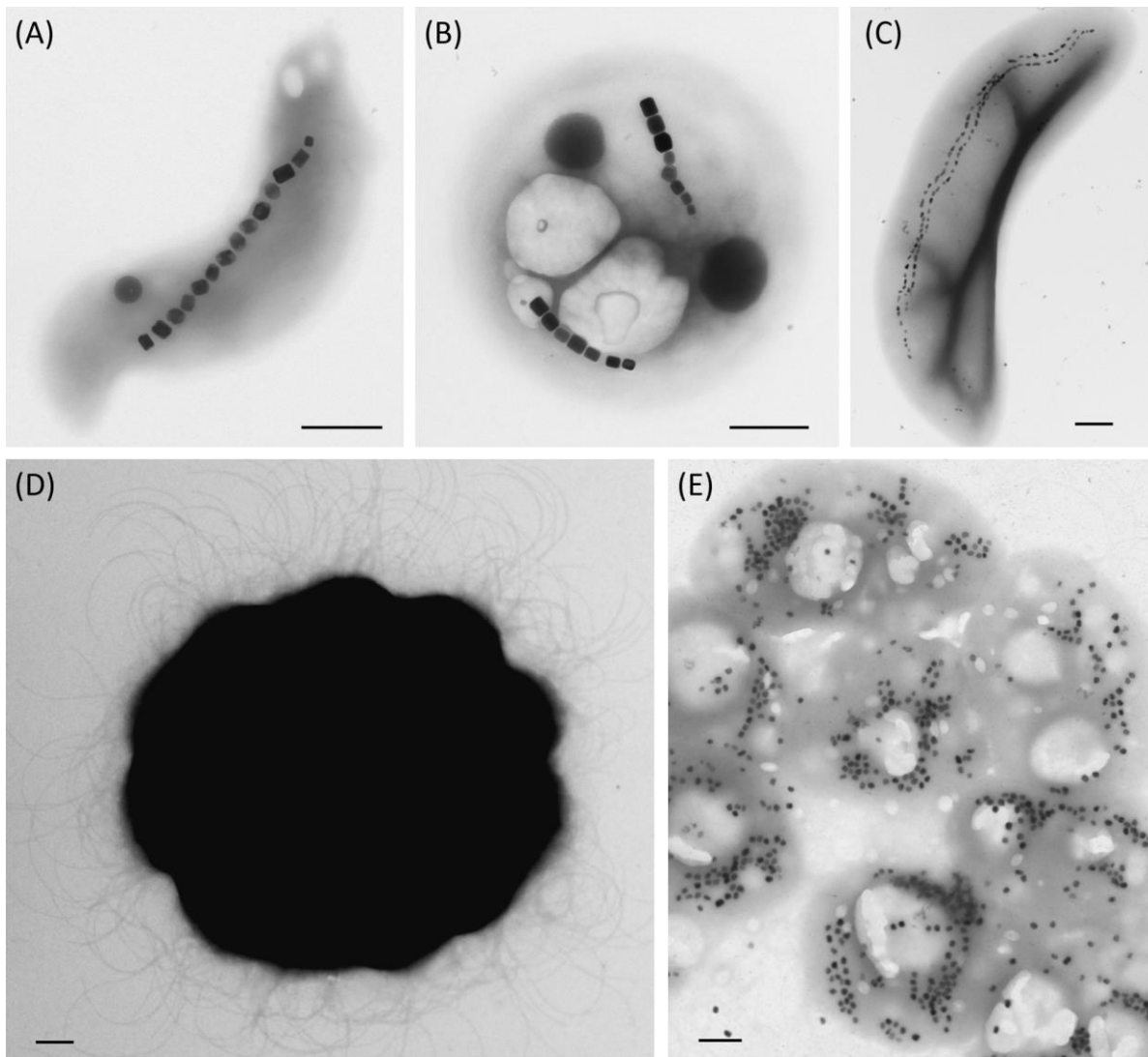
481 **Syntrophy:** trophic interdependency of two symbiotic species. Also referred as a mutualistic  
482 metabolism in which partner's metabolisms rely on the exchange of metabolic products of each  
483 other's.

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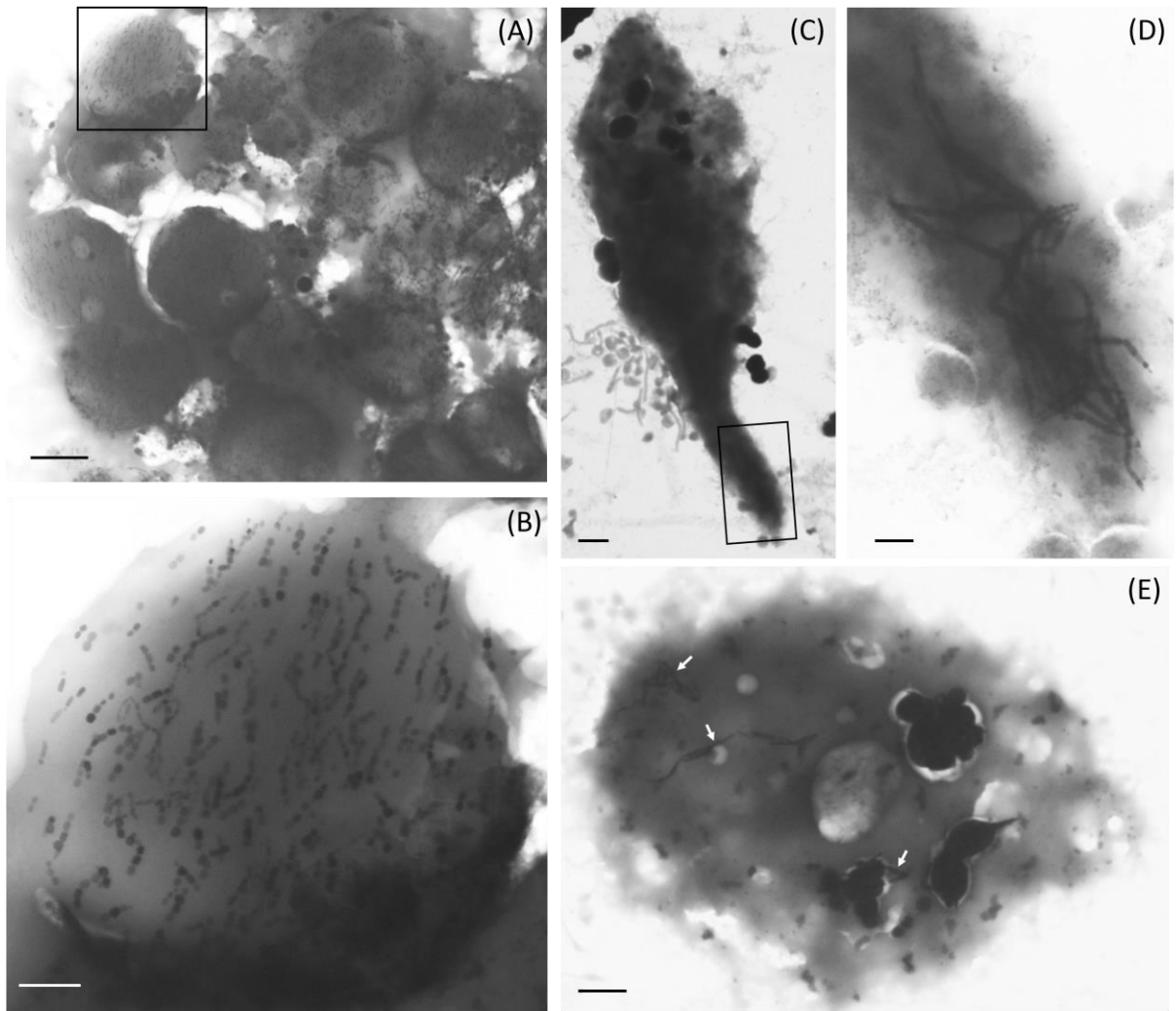
486 **Figures and figure legends**



487  
488 **Figure 1. Transmission electron microscope images of magnetotactic bacteria.**  
489 Magnetotactic spirillum (A), cocci (B) and curved rod (C) isolated from the freshwater Lake  
490 Pavin, France. Intact (D) and disaggregated (D) multicellular magnetotactic prokaryote (MMP)  
491 isolated from the Mediterranean Sea in Carry-le-Rouet, France. Magnetotactic cells in (A-C)  
492 produce elongated prismatic (A and B) or bullet-shaped (C) magnetite magnetosomes while the  
493 MMP (E) produce octahedral greigite magnetosomes. Scale bars represent 0.5  $\mu\text{m}$ .

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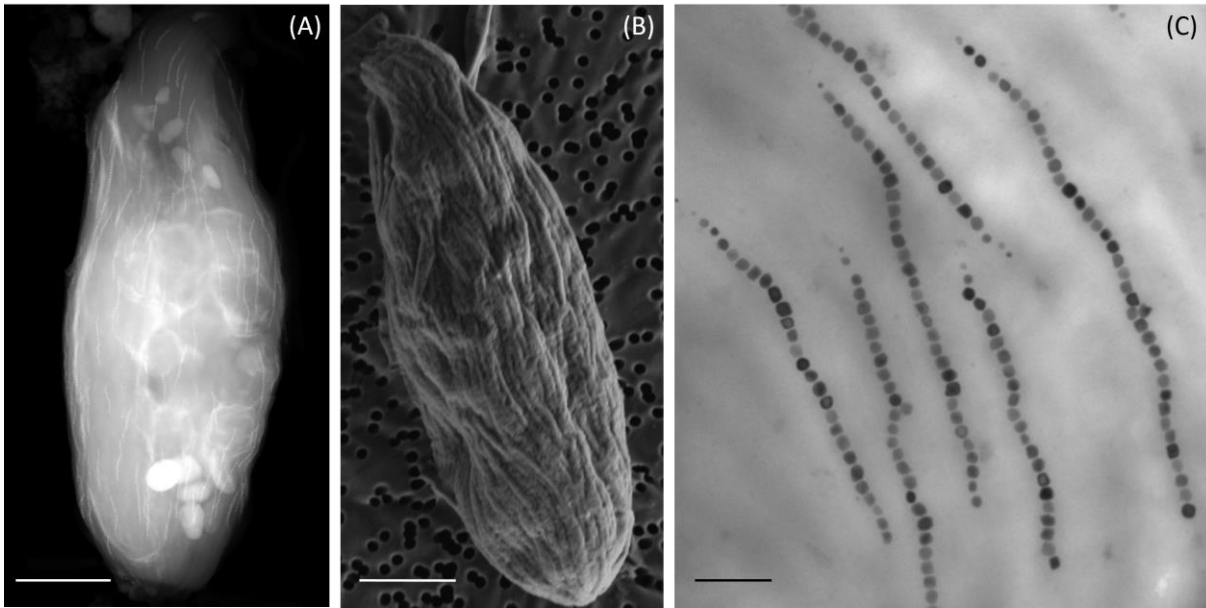
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497 **Figure 2. Transmission electron microscope images of magnetic ciliates that grazed**  
 498 **magnetotactic bacteria isolated from the Mediterranean Sea.** (A-B) Ciliate that sequesters  
 499 magnetosomes in digestive vacuoles. The black frame in (A) shows where the higher  
 500 magnification image in (B) was taken. (C-D) Ciliate that accumulates magnetosomes in a  
 501 specific location within its cytoplasm. The black frame in (C) shows where the higher  
 502 magnification image in (D) was taken. (E) Ciliate that randomly stores grazed magnetotactic  
 503 bacteria inside its cell. Scale bars represent 2  $\mu\text{m}$  (A, C and E) and 0.5  $\mu\text{m}$  (B and D).

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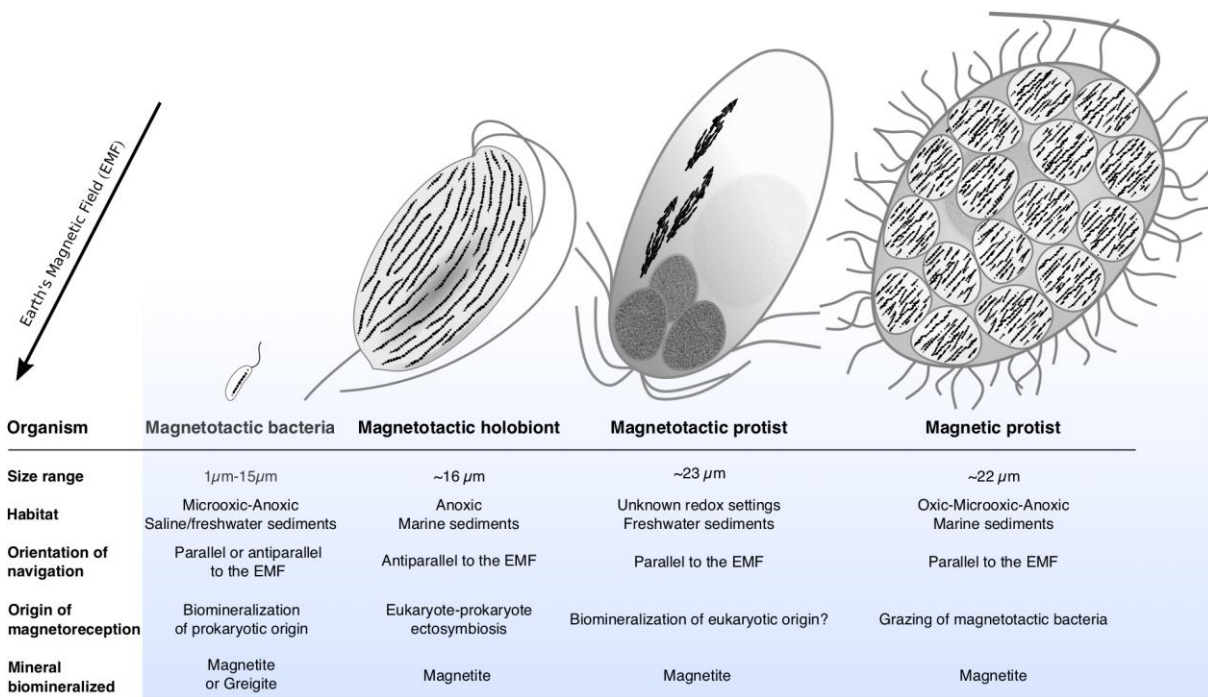
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**Figure 3. Electron microscope images of magnetotactic holobionts isolated from the Mediterranean Sea.** High angle annular dark field scanning transmission electron microscope (A) and scanning transmission electron microscope (B) images of single magnetotactic holobionts showing the presence of hundreds of bacteria surrounded a protistan cell. (C) Transmission electron microscope image of several magnetosome chains produced by magnetic ectosymbiotic bacteria allowing magnetoreception of the protist. Scale bars represent 2  $\mu\text{m}$  (A and B) and 0.5  $\mu\text{m}$  (C). (A and B) Image courtesy of N. Menguy and K. Benzerara, respectively.



514

515 **Figure 4. Schematic comparison of magnetoreceptive microorganisms morphologies and**  
 516 **magnetic behaviours.** Magnetosomes chains are represented in black. Organism's anterior-  
 517 posterior orientation is given relative to the Earth Magnetic Field (EMF) direction in the  
 518 Northern Hemisphere. These orientations are reverse for microorganisms of the Southern  
 519 Hemisphere.

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