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► **To cite this version:**

Caroline Monteil, Christopher T. Lefèvre. Magnetoreception in Microorganisms. Trends in Microbiology, 2019, 28 (4), pp.266-275. 10.1016/j.tim.2019.10.012 . cea-02378779

HAL Id: cea-02378779

<https://cea.hal.science/cea-02378779>

Submitted on 7 Nov 2020

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1 **Magnetoreception in microorganisms**

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Keywords : magnetoreception; biomineralization; magnetosomes; magnetotactic bacteria;
protists; holobionts; symbiosis; grazing

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 Fe_3O_4 or greigite Fe_3S_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 CO₂,
204 acetate and H₂ 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 CO₂ 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

291 **Acknowledgments**

292 We thank the French National Research Agency (ANR-16-TERC-0025-01 and ANR-18-CE31-
293 0003), the New Zealand Ministry for Business, Innovation and Employment (grant no.

294 LVLX1703) and all our collaborators and other researchers that contribute to make this field of
295 research so exciting and in perpetual progression.

296

297 **References**

- 298 1 Bryant, D.A. and Frigaard, N.-U. (2006) Prokaryotic photosynthesis and phototrophy
299 illuminated. *Trends Microbiol.* 14, 488–496
- 300 2 Walsby, A.E. (1994) Gas vesicles. *Microbiol. Rev.* 58, 94–144
- 301 3 Wadhams, G.H. and Armitage, J.P. (2004) Making sense of it all: bacterial chemotaxis.
302 *Nat. Rev. Mol. Cell Biol.* 5, 1024–1037
- 303 4 Shivaji, S. and Prakash, J.S.S. (2010) How do bacteria sense and respond to low
304 temperature? *Arch. Microbiol.* 192, 85–95
- 305 5 Guyodo, Y. and Valet, J.P. (1999) Global changes in intensity of the Earth's magnetic field
306 during the past 800 kyr. *Nature* 399, 249–252
- 307 6 Merrill, R.T. and McElhinny, M.W. (1983) *The Earth's Magnetic Field: Its History, Origin,*
308 *and Planetary Perspective*, Academic Press.
- 309 7 Wiltshcko, R. and Wiltshcko, W. (2012) Magnetoreception. *Adv. Exp. Med. Biol.* 739, 126–
310 141
- 311 8 Clites, B.L. and Pierce, J.T. (2017) Identifying Cellular and Molecular Mechanisms for
312 Magnetosensation. *Annu. Rev. Neurosci.* 40, 231–250
- 313 9 Begall, S. *et al.* (2014) Magnetoreception in Mammals. In *Advances in the Study of*
314 *Behavior, Vol 46* 46 (Naguib, M. *et al.*, eds), pp. 45–88, Elsevier Academic Press Inc
- 315 10 Klumpp, S. *et al.* (2019) Swimming with magnets: From biological organisms to synthetic
316 devices. *Phys. Rep.* 789, 1–54
- 317 11 Monteil, C.L. *et al.* (2018) Accumulation and Dissolution of Magnetite Crystals in a
318 Magnetically Responsive Ciliate. *Appl. Environ. Microbiol.* 84, pii: e02865-17
- 319 12 Monteil, C.L. *et al.* (2019) Ectosymbiotic bacteria at the origin of magnetoreception in a
320 marine protist. *Nat. Microbiol.* DOI: 10.1038/s41564-019-0432-7
- 321 13 Blakemore, R. (1975) Magnetotactic bacteria. *Science* 190, 377–379
- 322 14 Walcott, C. *et al.* (1979) Pigeons have magnets. *Science* 205, 1027–1029
- 323 15 Gould, J.L. *et al.* (1978) Bees have magnetic remanence. *Science* 201, 1026–1028
- 324 16 Frankel, R. *et al.* (1979) Magnetite in Freshwater Magnetotactic Bacteria. *Science* 203,
325 1355–1356
- 326 17 Bellini, S. (2009) On a unique behavior of freshwater bacteria. *Chin. J. Oceanol. Limnol.*
327 27, 3–5

- 328 18 Mouritsen, H. (2018) Long-distance navigation and magnetoreception in migratory
329 animals. *Nature* 558, 50–59
- 330 19 Nordmann, G.C. *et al.* (2017) Magnetoreception—A sense without a receptor. *PLOS Biol.*
331 15, e2003234
- 332 20 Uebe, R. and Schüler, D. (2016) Magnetosome biogenesis in magnetotactic bacteria. *Nat.*
333 *Rev. Microbiol.* 14, 621–637
- 334 21 Grant, C.R. *et al.* (2018) Organelle Formation in Bacteria and Archaea. *Annu. Rev. Cell*
335 *Dev. Biol.* 34, 217–238
- 336 22 Lohsse, A. *et al.* (2011) Functional analysis of the magnetosome island in *Magnetospirillum*
337 *gryphiswaldense*: the mamAB operon is sufficient for magnetite biomineralization. *PLoS*
338 *One* 6, e25561
- 339 23 Lefèvre, C.T. *et al.* (2013) Comparative genomic analysis of magnetotactic bacteria from
340 the Deltaproteobacteria provides new insights into magnetite and greigite magnetosome
341 genes required for magnetotaxis. *Environ. Microbiol.* 15, 2712–2735
- 342 24 Raschdorf, O. *et al.* (2016) Genetic and Ultrastructural Analysis Reveals the Key Players
343 and Initial Steps of Bacterial Magnetosome Membrane Biogenesis. *PLOS Genet.* 12,
344 e1006101
- 345 25 Hershey, D.M. *et al.* (2016) MamO Is a repurposed serine protease that promotes magnetite
346 biomineralization through direct transition metal binding in magnetotactic bacteria. *PLoS*
347 *Biol.* 14, e1002402
- 348 26 Toro-Nahuelpan, M. *et al.* (2019) MamY is a membrane-bound protein that aligns
349 magnetosomes and the motility axis of helical magnetotactic bacteria. *Nat. Microbiol.* DOI:
350 10.1038/s41564-019-0512-8
- 351 27 Lin, W. *et al.* (2018) Genomic expansion of magnetotactic bacteria reveals an early
352 common origin of magnetotaxis with lineage-specific evolution. *ISME J.* 12, 1508–1519
- 353 28 Lin, W. *et al.* (2017) Origin of microbial biomineralization and magnetotaxis during the
354 Archean. *Proc. Natl. Acad. Sci. U. S. A.* 114, 2171–2176
- 355 29 Lin, W. *et al.* (2017) Diversity and ecology of and biomineralization by magnetotactic
356 bacteria. *Environ. Microbiol. Rep.* 9, 345–356
- 357 30 Lefèvre, C.T. *et al.* (2014) Diversity of magneto-aerotactic behaviors and oxygen sensing
358 mechanisms in cultured magnetotactic bacteria. *Biophys. J.* 107, 527–538
- 359 31 González, L.M. *et al.* (2015) Sudden motility reversal indicates sensing of magnetic field
360 gradients in *Magnetospirillum magneticum* AMB-1 strain. *ISME J.* 9, 1399–1409

361 32 Popp, F. *et al.* (2014) Polarity of bacterial magnetotaxis is controlled by aerotaxis through
362 a common sensory pathway. *Nat. Commun.* 5, 5398

363 33 Kolinko, S. *et al.* (2016) Single-cell genomics of uncultivated deep-branching
364 magnetotactic bacteria reveals a conserved set of magnetosome genes. *Environ. Microbiol.*
365 18, 21–37

366 34 Pósfai, M. *et al.* (2013) Phylogenetic significance of composition and crystal morphology
367 of magnetosome minerals. *Front. Microbiol.* 4, 344

368 35 DeLong, E.F. *et al.* (1993) Multiple evolutionary origins of magnetotaxis in bacteria.
369 *Science* 259, 803–806

370 36 Lefèvre, C.T. *et al.* (2013) Monophyletic origin of magnetotaxis and the first
371 magnetosomes. *Environ. Microbiol.* 15, 2267–2274

372 37 Lefèvre, C.T. and Wu, L.F. (2013) Evolution of the bacterial organelle responsible for
373 magnetotaxis. *Trends Microbiol.* 21, 534–543

374 38 Monteil, C.L. *et al.* (2018) Genomic study of a novel magnetotactic Alphaproteobacteria
375 uncovers the multiple ancestry of magnetotaxis. *Environ. Microbiol.* 20, 4415–4430

376 39 Murat, D. *et al.* (2015) Opposite and coordinated rotation of amphitrichous flagella governs
377 oriented swimming and reversals in a magnetotactic spirillum. *J. Bacteriol.* 197, 3275–3282

378 40 Lefèvre, C.T. *et al.* (2015) Positioning the Flagellum at the Center of a Dividing Cell To
379 Combine Bacterial Division with Magnetic Polarity. *mBio* 6, e02286

380 41 Bennet, M. *et al.* (2014) Influence of Magnetic Fields on Magneto-Aerotaxis. *PLoS ONE*
381 9, e101150

382 42 Brune, A. *et al.* (2000) Life at the oxic-anoxic interface: microbial activities and
383 adaptations. *FEMS Microbiol. Rev.* 24, 691–710

384 43 Rivas-Lamelo, S. *et al.* (2017) Magnetotactic bacteria as a new model for P sequestration
385 in the ferruginous Lake Pavin. *Geochem. Perspect. Lett.* 5, 35–41

386 44 Esquivel, D. *et al.* (1983) Magnetotactic Microorganisms in the Rio-De-Janeiro Region.
387 *Biol. Cell* 47, 227–233

388 45 Abreu, F. *et al.* (2013) Cell adhesion, multicellular morphology, and magnetosome
389 distribution in the multicellular magnetotactic prokaryote Candidatus Magnetoglobus
390 multicellularis. *Microsc. Microanal. Off. J. Microsc. Soc. Am. Microbeam Anal. Soc.*
391 *Microsc. Soc. Can.* 3, 1–9

392 46 Qian, X.-X. *et al.* (2019) Juxtaposed membranes underpin cellular adhesion and display
393 unilateral cell division of multicellular magnetotactic prokaryotes. *Environ. Microbiol.*
394 DOI: 10.1111/1462-2920.14710

- 395 47 Torres de Araujo, F.F. *et al.* (1986) Magnetite and magnetotaxis in algae. *Biophys. J.* 50,
396 375–378
- 397 48 Bazyliński, D.A. *et al.* (2000) Occurrence and distribution of diverse populations of
398 magnetic protists in a chemically stratified coastal salt pond. *Chem. Geol.* 169, 319–328
- 399 49 Simmons, S.L. and Edwards, K.J. (2006) Geobiology of magnetotactic bacteria. In
400 *Magnetoreception and Magnetosomes in Bacteria* pp. 77–102, Springer, Berlin, Heidelberg
- 401 50 Martins, J.L. *et al.* (2007) Grazing protozoa and magnetosome dissolution in magnetotactic
402 bacteria. *Environ. Microbiol.* 9, 2775–2781
- 403 51 Allen, R. (1974) Food vacuole membrane growth with microtubule-associated membrane-
404 transport in *Paramecium*. *J. Cell Biol.* 63, 904–922
- 405 52 Barbeau, K. *et al.* (1996) Role of protozoan grazing in relieving iron limitation of
406 phytoplankton. *Nature* 380, 380061a0
- 407 53 Pernthaler, J. (2005) Predation on prokaryotes in the water column and its ecological
408 implications. *Nat. Rev. Microbiol.* 3, 537–546
- 409 54 Sherr, E.B. and Sherr, B.F. (2002) Significance of predation by protists in aquatic microbial
410 food webs. *Antonie Van Leeuwenhoek* 81, 293–308
- 411 55 Margulis, L. and Fester, R. (1991) *Symbiosis as a Source of Evolutionary Innovation:
412 Speciation and Morphogenesis*, MIT Press.
- 413 56 Rowan, R. and Knowlton, N. (1995) Intraspecific diversity and ecological zonation in coral
414 algal symbiosis. *Proc. Natl. Acad. Sci. U. S. A.* 92, 2850–2853
- 415 57 Engel, P. and Moran, N.A. (2013) The gut microbiota of insects - diversity in structure and
416 function. *Fems Microbiol. Rev.* 37, 699–735
- 417 58 Vandenkoornhuyse, P. *et al.* (2015) The importance of the microbiome of the plant
418 holobiont. *New Phytol.* 206, 1196–1206
- 419 59 López-García, P. *et al.* (2017) Symbiosis in eukaryotic evolution. *J. Theor. Biol.* 434, 20–
420 33
- 421 60 López-García, P. and Moreira, D. (2015) Open questions on the origin of eukaryotes.
422 *Trends Ecol. Evol.* 30, 697–708
- 423 61 Bernhard, J.M. *et al.* (2000) The Santa Barbara Basin is a symbiosis oasis. *Nature* 403, 77–
424 80
- 425 62 Yubuki, N. and Leander, B.S. (2018) Diversity and Evolutionary History of the
426 Symbiontida (Euglenozoa). *Front. Ecol. Evol.* 6, 100. doi: 10.3389/fevo.2018.00100
- 427 63 Müller, M. *et al.* (2012) Biochemistry and evolution of anaerobic energy metabolism in
428 eukaryotes. *Microbiol. Mol. Biol. Rev. MMBR* 76, 444–495

429 64 Leão, P. *et al.* Magnetosome magnetite biomineralization in a flagellated protist: evidence
430 for an early evolutionary origin for magnetoreception in eukaryotes. *Environ. Microbiol.*
431 doi: 10.1111/1462-2920.14711

432 65 Lefèvre, C.T. and Bazylinski, D.A. (2013) Ecology, diversity, and evolution of
433 magnetotactic bacteria. *Microbiol Mol Biol Rev* 77, 497–526

434 66 Nguyen, T.A. *et al.* (2018) Evolutionary novelty in gravity sensing through horizontal gene
435 transfer and high-order protein assembly. *PLOS Biol.* 16, e2004920

436 67 Kirschvink, J.L. *et al.* (2001) Magnetite-based magnetoreception. *Curr. Opin. Neurobiol.*
437 11, 462–467

438 68 Natan, E. and Vortman, Y. (2017) The symbiotic magnetic-sensing hypothesis: do
439 Magnetotactic Bacteria underlie the magnetic sensing capability of animals? *Mov. Ecol.* 5,
440 22. doi: 10.1186/s40462-017-0113-1

441 69 Dufour, S.C. *et al.* (2014) Magnetosome-containing bacteria living as symbionts of
442 bivalves. *ISME J.* 8, 2453–2462

443 70 Lefèvre, C.T. *et al.* (2012) Novel magnetite-producing magnetotactic bacteria belonging to
444 the Gammaproteobacteria. *ISME J.* 6, 440–450

445 71 Shaw, J.A. *et al.* (2009) Ultrastructure of the epithelial cells associated with tooth
446 biomineralization in the chiton *Acanthopleura hirtosa*. *Microsc Microanal.* 15, 154–65

447 72 Hsu, C.Y. and Chan, Y.P. (2011) Identification and localization of proteins associated with
448 biomineralization in the iron deposition vesicles of honeybees (*Apis mellifera*). *PLoS One.*
449 6, e19088

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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.

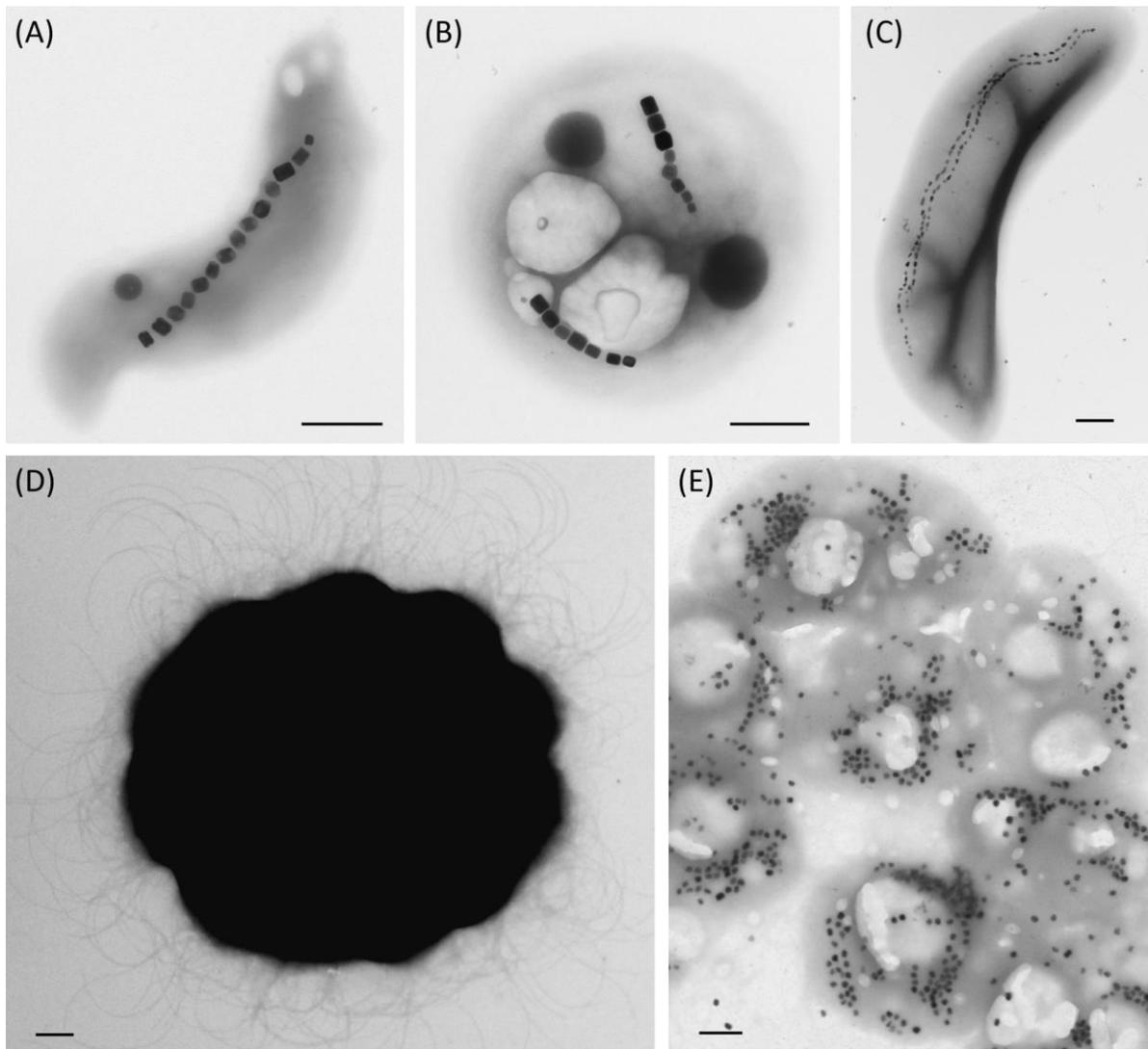
478 **Symbiosis:** defines a long-term physical coexistence of two or more species, in which at least
479 one partner is dependent on the others, no matter what the effect of the interaction on the
480 partner's fitness.

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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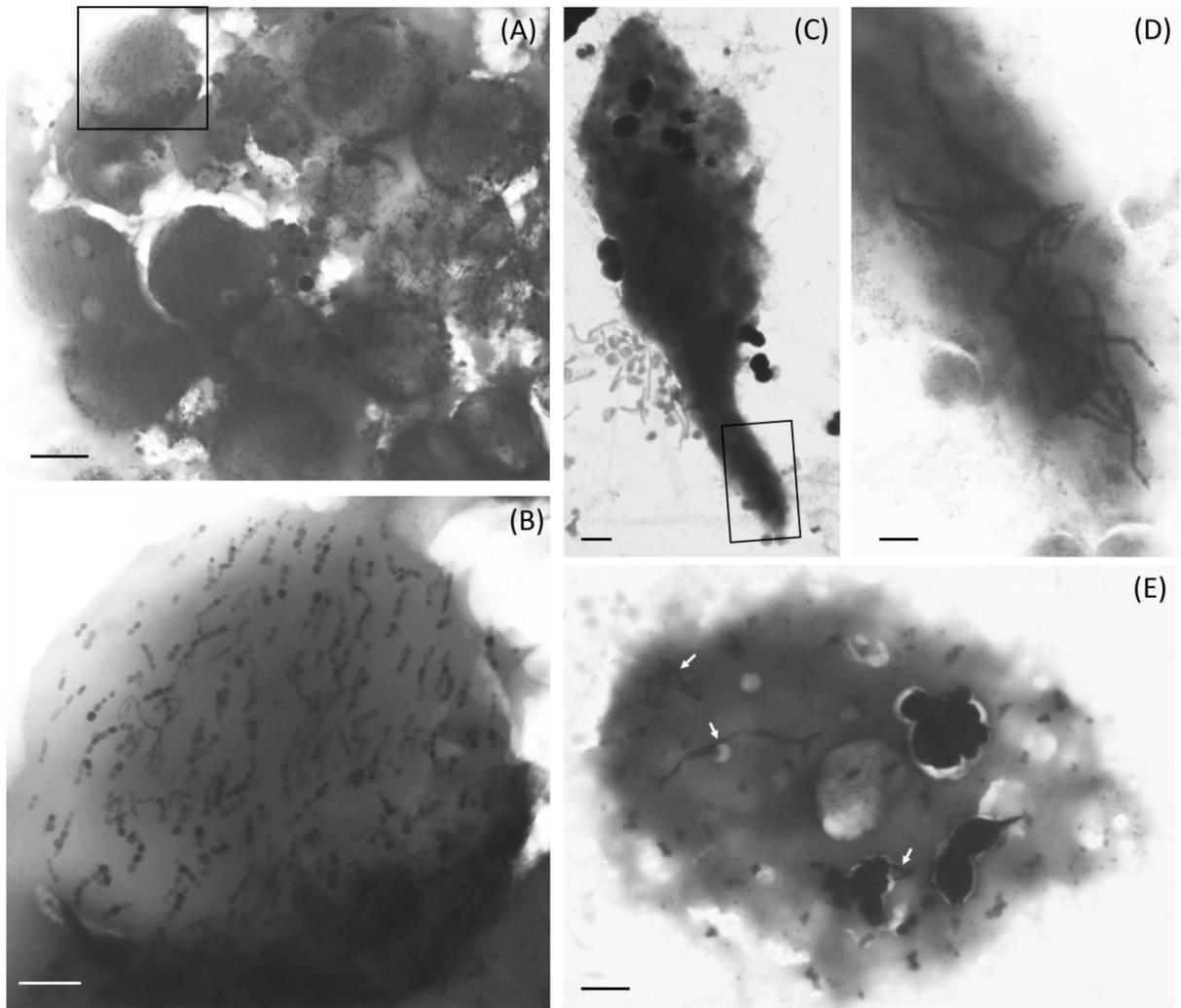
486 **Figures and figure legends**



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 μm.

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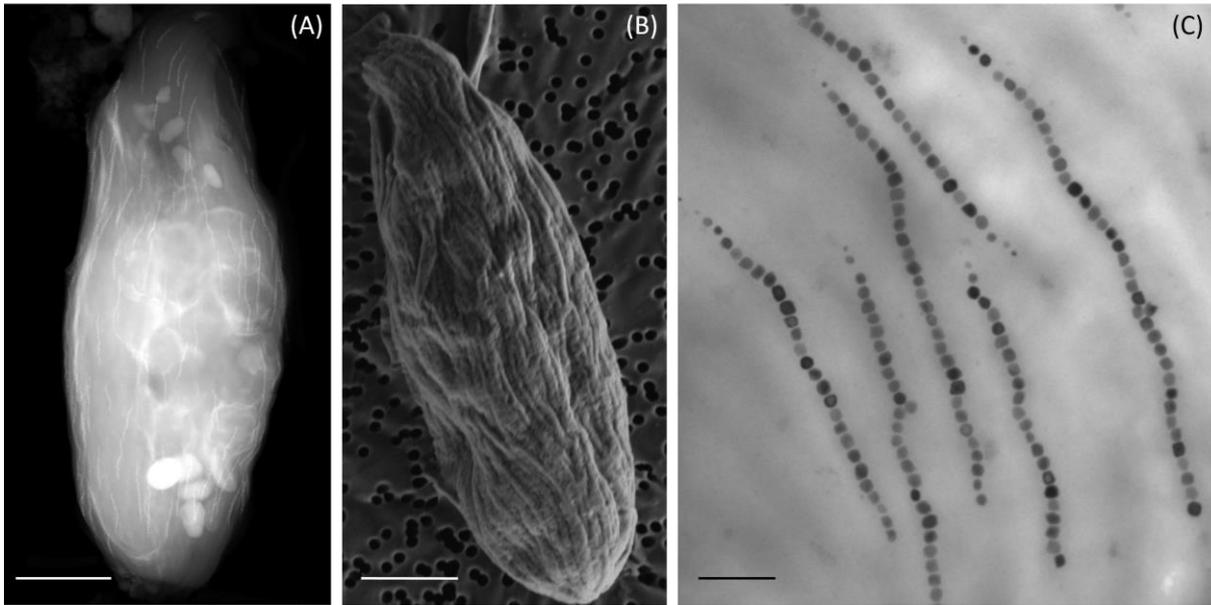
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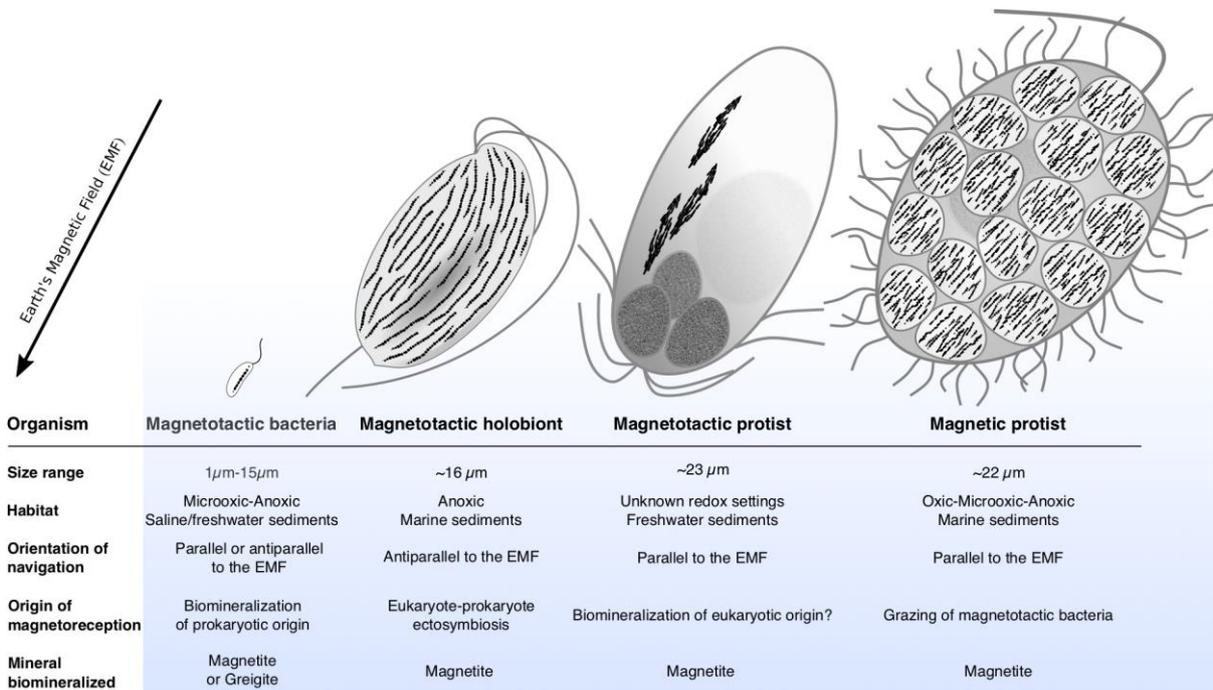
497 **Figure 2. Transmission electron microscope images of magnetic ciliates that grazed**
 498 **magnetotactic bacteria isolated from the Mediterranean Sea.** (A-B) Ciliate that sequesters
 499 magnetosomes in digestive vacuoles. The black frame in (A) shows where the higher
 500 magnification image 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 μm (A, C and E) and 0.5 μm (B and D).

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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 μm (A and B) and 0.5 μm (C). (A and B) Image courtesy of N. Menguy and K. Benzerara, respectively.



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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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