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1           **Key signatures of magnetofossils elucidated by mutant**  
2           **magnetotactic bacteria and micromagnetic calculations**

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17 **Key points:**

- 18 • Sediments containing fossilized magnetotactic bacteria bear magnetic signatures  
19     apparently associated with different sources of magnetite particles
  
- 20 • Intact and fold-collapsed single-stranded and multi-stranded magnetosome chains can  
21     explain all observed signatures of fossilized magnetotactic bacteria
  
- 22 • We provide criteria for the discrimination of distinct populations of ancient  
23     magnetotactic bacteria

24 **Abstract**

25 Magnetotactic bacteria (MTB) produce single- or multi-stranded chains of magnetic  
26 nanoparticles that contribute to the magnetization of sediments and rocks. Their magnetic  
27 fingerprint can be detected in ancient geological samples and serve as a unique  
28 biosignature of microbial life. However, some fossilized assemblages bear contradictory  
29 signatures pointing to magnetic components that have distinct origin(s). Here, using  
30 micromagnetic simulations and mutant MTB producing looped magnetosome chains, we  
31 demonstrate that the magnetofossil biosignature is produced by a combination of single-  
32 and multi-stranded chains, and that diagenetically-induced chain collapse, if occurring,  
33 must preserve the strong uniaxial anisotropy of native chains. This anisotropy is the key  
34 factor for distinguishing magnetofossils from other populations of natural magnetite  
35 particles, including those with similar individual crystal characteristics. Furthermore, the  
36 detailed properties of magnetofossil signatures depends on the proportion of equant and  
37 elongated magnetosomes, as well as on the relative abundances of single- and multi-  
38 stranded chains. This work has important paleoclimatic, paleontological and phylogenetic  
39 implications, as it provides a novel tool to differentiate distinct MTB lineages according  
40 to their chain and magnetosome morphologies, which will enable the tracking of the  
41 evolution of some of the most ancient biomineralizing organisms in a time-resolved  
42 manner. It also enables a more accurate discrimination of different sources of magnetite  
43 particles, which is pivotal for gaining better environmental and relative paleointensity  
44 reconstructions from sedimentary records.

45 **Plain language summary**

46 Magnetotactic bacteria (MTB) produce chains of magnetic nanoparticles that contribute  
47 to the magnetization of sedimentary rocks. Fossilized chains can be detected in ancient  
48 geological samples using magnetic measurements. They provide unique evidence for  
49 microbial life. However, remains of fossil MTB possess ambiguous magnetic properties  
50 that make their detection problematic. Here, we demonstrate, with the help of numerical  
51 simulations and a modified MTB producing looped chains, that the magnetic properties  
52 of MTB-rich sediments can be explained by a combination of chains made of single and  
53 multiple strands, and that chain collapse in the sediment, if occurring, likely preserves  
54 key magnetic properties, enabling the identification of fossil MTB. These properties  
55 depend also on the proportion of equidimensional and elongated magnetosomes, as well  
56 as on the relative abundances of single- and multi-stranded chains. This work has  
57 important implications, as it provides a novel tool to differentiate distinct MTB types  
58 according to their chain and magnetosome morphologies, enabling the tracking of the  
59 evolution of some of the most ancient mineral-producing organisms. It also enables a  
60 more accurate discrimination of different sources of magnetite particles, which helps  
61 gaining better environmental and relative paleointensity reconstructions from  
62 sedimentary records.

## 63 **1. Introduction**

64 Magnetite ( $\text{Fe}_3\text{O}_4$ ) is a ubiquitous iron oxide found in sediments and sedimentary  
65 rocks. It is a major carrier of sediments and rock magnetization used for numerous  
66 applications in Earth sciences including paleomagnetic, paleoclimate,  
67 paleoenvironmental, paleogeographic and paleontological reconstructions (e.g., Evans  
68 and Heller, 2003; Tauxe et al., 2010; Egli et al., 2013). In addition to lithogenic  
69 magnetite-bearing minerals (e.g., Chang et al., 2016), sediments contain secondary  
70 magnetite crystals formed in situ through diagenetic processes (e.g., Oldfield, 2007;  
71 Franke et al., 2007), but are also produced by bacteria participating in the sedimentary  
72 iron cycle (e.g., Lovely et al., 1987; Fortin and Langley, 2005; Miot et al., 2009).

73 Magnetotactic bacteria (MTB) are the only known microorganisms that produce intra-  
74 cellular nanoparticles of magnetite in organelles called magnetosomes under a genetically  
75 controlled pathway (Uebe and Schüler, 2016). They represent some of the most ancient  
76 biomineralizing organisms, with a proposed origin of  $\sim 3$  Ga (Lin et al., 2017). They are  
77 markers of oxic-anoxic transition zones in aquatic and sedimentary environments (Flies  
78 et al., 2005; Simmons et al., 2004), making them useful paleoenvironmental indicators  
79 (Hesse, 1994; Roberts et al., 2011; Usui et al., 2017; Chang et al., 2018; Wagner et al.,  
80 2021). Magnetosomes are assembled in chains, and provide the bacteria with a permanent  
81 magnetic dipole for navigation purposes (McCausland and Komeili, 2020). When MTB  
82 cells die, their magnetite chains can be trapped into sediments and subsequently  
83 fossilized (Petersen et al., 1986; Kopp & Kirschvink, 2008). MTB fossils (hereafter  
84 referred to as magnetofossils) can be preserved over geological times and contribute to  
85 sedimentary paleomagnetic and environmental records (Roberts et al., 2012; Larrasoña

86 et al., 2014; Ouyang et al., 2014). Their unambiguous identification and discrimination  
87 from abiotic magnetite would thus provide strong constraints on the evolution of life,  
88 biomineralization processes, and environmental conditions over geological times.

89 Arrangement of single domain (SD) magnetite crystals in linear chains combines two  
90 robust magnetofossil identification criteria, size and arrangement (Kopp and Kirschvink,  
91 2008), which are key parameters for a unique magnetic signature among all sources of  
92 natural magnetic minerals. Other types of secondary magnetite particles tend to have a  
93 wide size distribution exceeding the SD stability range (e.g., Gibbs-Eggar et al., 1999;  
94 Faivre et al., 2004; Liu et al., 2005). Most importantly, the special conditions required to  
95 form isolated, non-branched strings of abiogenic SD particles (e.g., Ruder et al., 2012)  
96 are unlikely to occur frequently in natural sediments. Because the magnetic extraction  
97 procedure required to prepare sufficiently concentrated samples for statistically  
98 significant TEM observations destroys the native arrangement of SD magnetite crystals  
99 in the sediment matrix, the in-situ identification of chain structures is only possible  
100 through indirect methods based on magnetic measurements of the bulk sediment.  
101 Unfortunately, the identification of magnetofossil signatures with magnetic methods is  
102 not always unique (e.g., Roberts et al., 2019). An additional complication arises from the  
103 fact that the lack of chain structures (e.g., Weiss et al., 2004) does not necessarily exclude  
104 a biological origin of SD magnetite particles, since chain collapses that erase the original  
105 magnetic fingerprints might occur during early diagenesis.

106 First-order reversal curve (FORC) diagrams (Egli, 2021), which rely on the measure-  
107 ment of partial hysteresis curves, can be used to discriminate isolated SD magnetite parti-  
108 cles and magnetosome chains from other structures, such as SD particle clusters and

109 larger lithogenic (titano-)magnetite crystals containing magnetic vortices (VO) or  
110 multiple magnetic domains (MD) (Roberts et al., 2017; Lascu et al., 2018), through a  
111 sharp signature called the central ridge (Egli et al., 2010; Roberts et al., 2012; Heslop et  
112 al., 2014a). Principal component analyses (PCA) of FORC diagrams obtained from  
113 magnetofossil-rich sediments (Lascu et al., 2015) and selective FORC measurements of  
114 secondary  $\lesssim 300$  nm magnetite particles through selective chemical leaching (Ludwig et  
115 al., 2013) contain signatures of VO or strongly interacting SD particle clusters with a  
116 large vertical dispersion around the central ridge, which contribute to 35-65% of the total  
117 magnetization (Table 1). FORC diagrams containing these features can be explained by  
118 mixtures of (i) well-dispersed uniaxial, non-interacting SD particles, or linear chains of  
119 such particles, contributing to the central ridge (collectively referred to as UNISD in the  
120 following), and (ii) non-SD or clustered SD particles contributing to the remaining parts  
121 of the FORC distribution. The associated magnetic hysteresis parameters  $M_{rs}/M_s$  and  
122  $B_{cr}/B_c$  (Dunlop, 2002) are close to the theoretical limit for non-interacting SD particles  
123 and intact magnetosome chains (Table 1). In particular, hysteresis squareness (the ratio  
124  $M_{rs}/M_s$  of remanent and saturation magnetizations) values  $\gtrsim 0.44$  are unrealistically large  
125 for samples containing non-SD or strongly interacting SD particles associable with 35-  
126 65% non-central ridge FORC contributions (Ludwig et al., 2013) (Figure 1).

127 The UNISD signature of magnetofossil-rich sediments is usually characterized by two  
128 narrow coercivity distributions (called biogenic soft, BS, and biogenic hard, BH), which  
129 are particularly evident in SD-selective magnetic responses such as the central ridge in  
130 FORC diagrams and the AF demagnetization of an anhysteretic remanent magnetization  
131 (ARM) (Egli, 2004a; Egli et al., 2010; Heslop et al., 2014a). The peculiar narrowness of

132 these coercivity distributions is determined by the uniaxial magnetic anisotropy of the  
133 chain structure, which, together with the shape anisotropy of equidimensional (BS) and  
134 elongated (BH) magnetosomes, yields median coercivities of ~30-50 mT and ~65-80 mT,  
135 respectively, for these two components.

136 The mixed FORC properties of magnetofossil endmembers have been explained with  
137 a form of chain collapse by which the linear magnetosome arrangement becomes increa-  
138 singly randomized after MTB death, leading to the formation of fractal-like magnetosome  
139 clusters (Harrison and Lascu, 2014; Chang et al., 2019). Isolated magnetosome chains  
140 collapse if bent beyond their elastic limit, due to the magnetostatic attraction between the  
141 opposed magnetic poles at their extremities (Shcherbakov et al., 1997; Kiani et al., 2015).  
142 Bending forces might be produced by mechanical interactions with sediment particles  
143 during mixing in the bioturbated layer, and during compaction. Chains might also be  
144 stabilized by electrostatic adhesion onto larger sediment particles, such as clay platelets  
145 (Galindo-Gonzalez et al., 2009). The lack of direct in situ observation of magnetofossil  
146 structures, the mixed character of the magnetic signature of magnetofossil-rich sediments,  
147 and the sometimes-poor definition of characteristic coercivity components, leave margins  
148 for contrasting interpretations of some geological materials. Most notable examples  
149 include the controversial biogenic origin of magnetite nanoparticles in the Martian  
150 meteorite ALH84001 (Thomas-Keprta et al., 2000; Golden et al., 2004; Weiss et al.,  
151 2004), and the origin of the sudden rise of SD magnetite concentration during the  
152 Paleocene-Eocene thermal maximum (Kent et al., 2003; Kopp et al., 2007; Wang et al.,  
153 2013; Wagner et al., 2021).

154        Extracted magnetosomes obtained from MTB cultures after cell lysis tend to form  
155 large clumps with an excessively low hysteresis squareness (Kobayashi et al., 2006; Li et  
156 al., 2012) (Table 1, Figure 1). This is also true for the hysteresis squareness of smaller  
157 magnetosome clusters produced by MTB whose genes responsible for chain assembly  
158 have been deleted, namely the  $\Delta mamJ$  MSR-1 strain in Katzmann et al. (2013) (see  
159 sections below), which might serve as analogue for the full collapse of isolated chains.  
160 Finally, the random-walk-based magnetosome assemblage algorithm of Harrison and  
161 Lascau (2014) produce a range of magnetic properties (Chang et al., 2019) comprised  
162 between the endmembers corresponding to linear chains and fractal-like particle clusters,  
163 respectively, depending on the assumed degree of randomness (Figure 1). In these  
164 simulations, FORC diagrams containing non-UNISD contributions comparable with  
165 those of magnetofossil endmembers are associated with hysteresis squareness values of  
166  $\sim 0.4$  or lower. Pedogenic magnetite, the only well-characterized natural example of non-  
167 biogenic secondary magnetite particles (Dearing et al., 2001), also features mixed UNISD  
168 and non-UNISD FORC properties (Table 1); however, in this case, the hysteresis  
169 squareness of  $\sim 0.2$  is compatible with the FORC signature. Thus, current interpretations  
170 of magnetofossil signatures appear to miss structures possessing the correct combination  
171 of UNISD and non-UNISD magnetic properties.

172        Excluding disordered clusters, which do not possess the correct magnetic signature,  
173 and the already investigated chain axis randomization, possible candidates for missing  
174 magnetofossil morphologies include native multistranded chains of magnetosomes  
175 produced by some MTB (Amor et al., 2020) and mechanically meaningful minimum-  
176 energy structures obtained from the collapse of isolated chains, such as rings and double

177 strands resulting from the fold-collapse of single-stranded chains that have been bent  
178 beyond the elastic limit (von Dobeneck et al., 1987; Philipse and Maas 2002; Kiani et al.,  
179 2018). Single- and multi-stranded chains in MTB and in the derived intact magnetofossils  
180 (Figure 2a,b) are in a native SD state that maximizes the total magnetic moment, with the  
181 magnetization of all magnetosomes being parallel to the chain axis (Hanzlik et al., 2002).  
182 This is the only possible zero-field magnetic configuration for single-stranded chains, but  
183 not for multiple strands, in which intermediate states with lower magnetic moments can  
184 be nucleated with the application of strong external fields (Hanzlik et al., 2002).  
185 Intermediate remanent states are formed when the magnetic moment of one strand is  
186 reversed with respect to the others, or when the magnetic moments of individual crystals  
187 form complex patterns (Varón et al., 2013). On the other hand, structures arising from  
188 chain collapse (Figure 2c,d), are expected to possess native flux-closure (FC)  
189 configurations characterized by a small net magnetic moment, as observed for instance in  
190 nanoparticle rings (Dunin-Borkowski et al., 2004; Takeno et al., 2014). These  
191 configurations minimize the magnetostatic energy by suppressing the external stray field  
192 of SD-like magnetic states. The low magnetic moment of collapsed structures makes  
193 them a poor sedimentary recorder of the Earth magnetic field, contrary to intact  
194 magnetosome chains, so that the fate of fossil magnetosome chains during diagenesis is  
195 expected to have important implications for the paleomagnetism of magnetofossil-rich  
196 sediments.

197 FORC measurements are sensitive to transitions between high-moment (SD-like) and  
198 low-moment (FC-like) magnetic configurations and their in-field stability ranges (Egli,  
199 2021). In particular, hysteresis squareness values close to 0.5, typical of randomly

200 oriented UNISD particles, depend on the room-temperature zero-field stability of high-  
201 moment states. This stability, which enables MTB to navigate along the Earth magnetic  
202 field, has been demonstrated experimentally for native single- and multistranded chains  
203 (Hanzlik et al., 2002; Pan et al., 2005), but no information is available for collapsed  
204 structures.

205 Here, we demonstrate that the unresolved magnetic signature of magnetofossils (i.e.,  
206 FORC signatures typical of magnetostatic interactions and FC, which do not lower the  
207 hysteresis squareness typical of UNISD particles) can be explained by the predominant  
208 contribution of intact or elastically deformed single- or multi-stranded magnetosome  
209 chains (non-collapsed). Contributions from fold-collapsed chains are also possible. Nu-  
210 cleation and annihilation of FC magnetic states explains non-UNISD signatures in FORC  
211 diagrams of magnetofossil-bearing sediments, while the strong uniaxial anisotropy of  
212 intact and fold-collapsed chains ensures that they still possess a UNISD-like hysteresis  
213 squareness of  $\sim 0.5$ . Our claim is supported by micromagnetic simulations of native  
214 single- and double-stranded chains and fold-collapsed chains. Unfortunately, MTB  
215 producing multi-stranded chains are not available for culture in the laboratory; however,  
216 the validity of our micromagnetic calculations has been tested by comparing the magnetic  
217 signature of intact chains with some structures that may be produced by the spontaneous  
218 collapse of isolated chains. For this purpose, we produced a mutant of the magnetotactic  
219 bacterium *Magnetospirillum magneticum* strain AMB-1 synthesizing looped structures  
220 similar to the rings described by Kiani et al. (2018) and to some structures obtained after  
221 dissolution of cultured cells of the same strain (Philipse and Maas, 2002). Looped chains  
222 might form in sediment after cell disruption, but before stabilizing structures such as

223 magnetosome membranes and the connecting cytoskeletal filament (Komeili et al., 2006)  
224 are dissolved, owing to the larger elastic response of membrane-filled gaps (Shcherbakov  
225 et al., 1997). Fold-collapsed chains, on the other hand, might form after dissolution of all  
226 biological structures, as a consequence of the much lower elastic limit associated with  
227 contacting magnetosomes (Shcherbakov et al., 1997).

228 From magnetic measurements and off-axis electron holography characterizations, we  
229 show that the looped chains produced by the AMB-1 mutant generate FC magnetic signa-  
230 tures similar to those obtained with our micromagnetic simulations of single- and multi-  
231 stranded chains, while lacking the hysteresis squareness of the simulations and of natural  
232 magnetofossil signatures. This demonstrates that the unique magnetic fingerprints of  
233 magnetofossils originate from strongly uniaxial magnetosome arrangements, rather than  
234 clusters, rings, and other forms of looped chains lacking a uniaxial shape. This work  
235 resolves longstanding and ongoing controversies about the interpretation of sedimentary  
236 sources of SD magnetite, establishing a theoretical and experimental framework that  
237 explains the magnetofossil signature and provides insights into the diversity of ancient  
238 MTB populations. A glossary of specialized terms used to describe magnetic  
239 measurements and micromagnetic modeling results is provided in the Supporting  
240 Information.

## 241 **2. Material and methods**

### 242 **2.1. Micromagnetic modeling**

243 To determine whether native multi-stranded and fold-collapsed magnetosome chains  
244 could explain the observed magnetofossil signatures, we modeled their FORC properties.

245 Micromagnetic models of high-resolution FORC measurements have been calculated for  
246 selected magnetosome morphologies and chain configurations representative of intact or  
247 elastically deformed chains, and of fold-collapsed chains. The magnetic properties of the  
248 simulated structures are determined mainly by two factors: the anisotropy of individual  
249 magnetosomes, which is controlled by their shape and crystal orientation, and in-chain  
250 magnetostatic interactions, which are controlled mainly by the chain geometry (Berndt et  
251 al., 2020). Magnetosome shapes can be classified as equant (cuboctahedral, octahedral),  
252 elongated (prismatic, elongated octahedral), and highly elongated (tooth- and bullet-sha-  
253 ped) (Amor et al., 2020). These categories form well-defined clusters of crystal sizes and  
254 shapes within the SD stability range of magnetite (Muxworthy and Williams, 2006;  
255 Newell, 2009) (Figure S1).

256 The geometry of intact single-stranded chains is controlled by the gaps between  
257 magnetosomes, the size decrease of immature crystals towards the chain extremities  
258 (tapering), and chain bending within the elastic limit. Magnetosomes in native multi-  
259 stranded chains are staggered: each magnetosome in one strand faces the gap between  
260 two magnetosomes of a nearby strand (Figure 2a,b). This arrangement favors the  
261 formation of strand bundles with a consistent magnetic polarity, eliminating repulsive  
262 forces (Hanzlik et al., 2002; Ruder et al., 2012). Contrastingly, magnetosomes in fold-  
263 collapsed chains are arranged side-to-side, and size tapering occurs only at one end, the  
264 other end being the kink point of the native chain (Figure 2d). The side-to-side  
265 magnetosome arrangement maximizes lateral attractive forces between strands with  
266 opposite magnetic polarities (Varón et al., 2013), as they result from fold-collapse. Fold-

267 collapsed chains can be observed inside freeze-dried cells (e.g., Figure 2b in Lins and  
268 Farina, 2004), where collapse is likely induced by cell shrinking.

269 The full variability of natural chain structures can be only partially reproduced  
270 because geometric parameters must be extrapolated from few observations. Therefore, we  
271 selected combinations of two magnetosome morphologies (cuboctahedral and prismatic),  
272 and three chain geometries (single-stranded, native double-stranded, and double-stranded  
273 from collapse by folding), as representative examples of magnetic endmembers dictated  
274 by the magnetosome aspect ratio (equant vs. elongated), and the existence of flux-closure  
275 configurations (single- vs. double-stranded). We generated  $\sim 10^5$  synthetic chains with  
276 random orientations and realistic geometries for each of the six categories obtained by  
277 combining the above-mentioned magnetosome morphologies and chain configurations  
278 (see Supporting Information for details).

279 Micromagnetic modeling has been performed in two steps using an energy  
280 minimization method. First, randomly oriented synthetic chains have been generated for  
281 each of the six configurations. Magnetosome-specific control parameters include size,  
282 shape, and crystal axes orientation, based on realistic distributions obtained from the  
283 literature (Figure S1). Chain-specific control parameters include magnetosome gaps,  
284 number of crystals, size tapering towards the extremities, and chain bending within the  
285 elastic limit. The geometry of double-stranded chains is additionally controlled by the lag  
286 of one strand with respect to the other, and by twisting of the two strands about a  
287 common axis (Figure 2a). The distributions of these parameters (Table S1) have been  
288 empirically chosen to match images reported in the literature. Representative examples of  
289 synthetic double-stranded chains are shown in Figures S2-S5. Next, FORC measurements

290 between  $\pm 0.3$  T have been simulated in 1 mT steps using a micromagnetic model of the  
291 chain magnetization. These calculations are based on the local minimization of the total  
292 energy determined by the magnetocrystalline and shape anisotropy of individual crystals,  
293 the Zeeman energy in the applied field, and the energy of magnetostatic interactions  
294 between pairs of crystals (see the Supporting Information for details). Because FORC  
295 measurements consists of a series of field sweeps starting at positive saturation, where  
296 there is only one local energy minimum (LEM), the evolution of LEM states is uniquely  
297 determined.

298 Like in Harrison and Lascu (2014), we assumed that individual crystals are homoge-  
299 neously magnetized, but we calculated magnetostatic interactions for the actual magneto-  
300 some shape, instead of using a point dipole approximation. The homogeneous magneti-  
301 zation approximation, which is needed to speed up calculations and cover the whole para-  
302 meter space with a sufficiently large number of high-resolution FORC simulations, holds  
303 reasonably well in all applied fields, including those immediately preceding transitions  
304 between magnetic states, for magnetosome sizes up to  $\sim 50$  nm, as seen by comparison  
305 with full micromagnetic models (Berndt et al., 2020). At larger sizes, the validity of this  
306 approximation declines progressively, as helical configurations start to nucleate inside the  
307 end magnetosomes. Nevertheless, the coercivities of remanence calculated by Berndt et  
308 al. (2020) for single-stranded chains of equidimensional and elongated magnetosomes are  
309 compatible with the coercivity distributions obtained from our simulations, so that the  
310 uncertainty introduced by our approximation is not expected to exceed the uncertainties  
311 associated with a poor knowledge of the real distribution of model parameters. Simulated  
312 FORC measurements (Figure S6) have been further processed with VARIFORC (Egli,

313 2013), using minimal smoothing parameters ( $s = 1$  over the central ridge, and  $s = 4$ ,  
314  $\lambda = 0.08$  over the remaining parts of the FORC diagram) to eliminate statistical noise.

315 The role of chain geometry for the stabilization of the remanent magnetization of high-  
316 moment states, which is essential for obtaining elevated hysteresis squareness values, has  
317 been investigated by calculating the energy barrier that must be overcome for a thermally  
318 activated transition to a different state at room temperature. For this purpose, we  
319 considered four prototypical arrangements of identical, equidimensional magnetosomes  
320 with no intrinsic anisotropy: (1) single-stranded chains, (2) native double-stranded chains,  
321 (3) fold-collapsed chains, and (4) circular rings. Optimal transition paths between LEM  
322 states have been calculated with the nudge-elastic-band and action minimization  
323 technique of Fabian and Shcherbakov (2018), upon identifying the magnetic moments of  
324 individual magnetosomes with the magnetic moments of elemental cells used in full  
325 micromagnetic simulations (see the Supporting Information for details).

326 The choice of an adequate initial path is crucial for obtaining a globally optimized  
327 transition between states. Single-stranded chains of  $>4$  crystals are known to reverse their  
328 remanent magnetization by nucleation of a reversed domain at one end (Hendriksen et al.,  
329 1994; Newell, 2009) and subsequent propagation of this domain to the other end. In this  
330 case, an adequate initial approximation of the reversing path is generated from an initial  
331 two-domain structure obtained by forcing the magnetic moment of the middle magneto-  
332 some to a direction perpendicular to the chain axis. This configuration is then relaxed  
333 while the strength of dipolar interactions in one of the two domains is slightly weakened  
334 to favor its denucleation (Figure S7a). The high-moment configuration of large rings  
335 consists of two domains separated by perpendicular magnetic moments pointing to the

336 same direction (Figure S7b). The transition to a zero-moment FC state with clockwise or  
337 counterclockwise magnetic moment arrangement is simulated in the same manner as for  
338 linear chains by denucleating one of the two domains. Finally, the transition path of  
339 double-stranded chains from the high-moment state, where the two strands are  
340 magnetized in the same direction, to the low-moment state, where the two strands have  
341 opposed magnetizations, requires the nucleation of a reversed domain at the extremity of  
342 one strand (Figure S7c). The nucleated domain creates an energetically favored FC  
343 configuration with the other strand, so that the transition to a complete FC state is  
344 obtained by growing the reverse domain until it reaches the other chain extremity.

## 345 **2.2. Deletion plasmid construction and generation of the $\Delta mamJ\Delta limJ\Delta MIS$ AMB-1** 346 **mutant strain**

347 To obtain a term of comparison for possible collapsed chain configurations and valida-  
348 tion of our micromagnetic modeling, we generated a mutant AMB-1 strain with looped  
349 magnetosome chains (Figure 3). Magnetosome formation in MTB requires genes  
350 contained in a specific portion of the genome called the magnetosome island (MAI)  
351 (Murat et al., 2010). The AMB-1 genome also contains a small version of the  
352 magnetosome island called the magnetotaxis islet (MIS) (Rioux et al., 2010). The MIS  
353 contains several genes, some of which perform redundant functions with their homologs  
354 in the MAI (Abreu et al., 2014). Previous work in *Magnetospirillum gryphiswaldense*  
355 strain MSR-1, a close relative of AMB-1, showed that the loss of the MAI gene *mamJ*  
356 results in collapse and aggregation of magnetosome chains (Scheffel et al., 2006).  
357 Surprisingly, the deletion of *mamJ* and its other MAI homolog *limJ* in AMB-1 does not  
358 produce collapsed chains and instead results in minor disruptions to the continuity of the

359 chain (Draper et al., 2011). We reasoned that redundant functions within the MIS might  
360 account for the dramatic differences between *mamJ* mutants in AMB-1 and MSR-1.  
361 Thus, a mutant strain ( $\Delta mamJ\Delta limJ\Delta MIS$ ) was produced by deleting the entire MIS and  
362 two MAI genes (*mamJ* and *limJ*) from AMB-1 genome. Detailed procedures for plasmid  
363 construction and AMB-1 transformation are provided in the Supporting Information.

### 364 **2.3. Bacterial cultures**

365 *Magnetospirillum magneticum* strain AMB-1 (ATCC700264) and the mutant AMB-1  
366 strain described in Section 2.2 were cultivated following ATCC recommendations in 500-  
367 mL screw-caped bottles until end of the exponential phase. Bottles were filled with 300  
368 mL of growth medium and placed in a glove box with controlled atmosphere (10% O<sub>2</sub>,  
369 90% N<sub>2</sub>) at 30°C after inoculation (1/100). The sole iron source in bacterial growth  
370 medium was Fe(III)-citrate added at 150 μM.

### 371 **2.4. Transmission electron microscopy**

372 Wild type and mutant AMB-1 cells were deposited on copper grids coated with a  
373 Formvar and carbon films and characterized with a FEI Tecnai 12 transmission electron  
374 microscope operating at 120 kV.

### 375 **2.5. Native magnetic moment measurements**

376 Magnetic characterizations of the mutant AMB-1 strain suggest that its looped  
377 magnetosome chain configurations possess a low net magnetic moment (see section 3.3).  
378 We thus investigated the native magnetic state of wild-type and mutant AMB-1 strains at  
379 the population level by comparing the magnetization of two different preparations of  
380 aqueous cell suspensions in a maximum external field of 2 mT, using a vibrating-sample

381 magnetometer (VSM). The external field is sufficiently large to partially align the cells,  
382 but not large enough to alter their native magnetic configuration. In this case, the  
383 magnetization of the suspension is expected to be proportional to the mean strength of the  
384 magnetic moments of individual cells. The first preparation contains cells directly taken  
385 from the culture and is used to assess the native magnetic moments. In the second  
386 preparation, the suspension is previously exposed to a 200 mT field. This field is strong  
387 enough to reset the native magnetic states, replacing them with a saturation remanent  
388 state that corresponds to the maximum magnetic moment that can be maintained in a null  
389 field. Cell suspensions for these experiments were prepared by centrifugation of AMB-1  
390 cultures (8000 rpm, 10 min), and subsequent suspension in 10 mL of phosphate buffer  
391 (PBS). 100  $\mu$ L of cell suspension were transferred in plastic vials (diameter of 4 mm) and  
392 placed in a Lakeshore Micro-Mag 3900 VSM for acquisition of remanent magnetizations  
393 at room temperature.

## 394 **2.6. Off-axis electron holography**

395 VSM characterizations of mutant AMB-1 demonstrated a vanishingly small native  
396 magnetic moment of the bacteria, which can be explained by the looped chain structures  
397 being in a FC state. To further confirm this hypothesis, we mapped the magnetic flux in  
398 the looped chains at the single-crystal level with off-axis electron holography. Electron  
399 holography is an interferometric method that correlates morphological and local magnetic  
400 characterizations of magnetic materials. It allows quantitative mapping of the in-plane  
401 flux inside the magnetite chains produced by AMB-1 at the nanometer scale. Both wild-  
402 type and mutant AMB-1 strains were cultivated in 10-mL glass tubes following the  
403 protocol described above. Cells were centrifuged (8000 rpm, 10 min) and suspended in

404 100  $\mu$ L of phosphate buffer (PBS). They were then deposited on copper grids coated with  
405 an ultra-thin carbon membrane. Off-axis electron holography was carried out using a  
406 Hitachi HF3300C microscope operated at 300 kV and equipped with a cold field  
407 emission gun and a spherical aberration corrector (CEOS B-Corr). Electron holography  
408 experiments were performed in a specific corrected Lorentz mode, allowing a spatial  
409 resolution down to 0.5 nm in a magnetic field-free sample environment (Snoeck et al.,  
410 2014). All holograms were recorded in a 2-biprism configuration to avoid artifacts linked  
411 to Fresnel fringes and to set separately the interference area size and the fringe spacing  
412 (Harada et al., 2004). The fringe spacing is equal to 1 nm (7 pixels) allowing for a spatial  
413 resolution of 1.5 nm for the treated magnetic phase images. The exposure time was set to  
414 1 nm using dynamic automation acquisition for removing instabilities and applying the  
415 fringe  $\pi$ -shift method (Gatel et al., 2018; Volkov et al., 2013). Phase and amplitude  
416 images were extracted from the holograms by using homemade software based on fast-  
417 Fourier transform approach. The magnetic and electrostatic contributions have been  
418 separated by acquiring two holograms for which the sample has been switched upside  
419 down (flipped 180°): the magnetic contribution was obtained by evaluating the difference  
420 of the phase images from the two holograms divided by two.

## 421 **2.7. FORC measurements**

422 The magnetic properties of the wild-type and mutant AMB-1 strains were characterized  
423 with high-resolution FORC analyses using a VSM. AMB-1 cultures were recovered by  
424 centrifugation (8 000 rpm, 10 min). Bacterial pellets were transferred in a 1.5-mL Eppen-  
425 dorf tube and dried at room temperature under anoxic conditions in a glove box ( $[O_2] <$   
426 1ppm) to prevent magnetite oxidation. Samples were stored under anoxic conditions until

427 being measured with a Lakeshore 8600 VSM. High-resolution FORC measurements were  
428 performed in steps of 0.3 mT with a stepwise approach to the reversal field to avoid over-  
429 shooting artifacts (Wagner et al., 2021), and a pause of 1 s at reversal. Measurements  
430 have been processed with VARIFORC (Egli, 2013) using a minimum smoothing factor  
431  $s = 2$  across the central ridge, and  $s = 4$ ,  $\lambda = 0.14$  over the remaining parts of the FORC  
432 diagram.

### 433 **3. Results**

#### 434 **3.1 Chain geometry and magnetic states**

435 The existence of one or more than one pair of magnetic states, and the stability of  
436 these states against thermal relaxation and applied fields, depends on the interplay  
437 between the magnetic anisotropy of individual crystals and the magnetostatic interactions  
438 between them. The stabilizing or destabilizing effect of magnetostatic interactions  
439 depends in turn on the chain geometry. Because magnetosome elongation is the main  
440 factor controlling the magnetic anisotropy of individual crystals, and because elongation,  
441 if present, is parallel to the chain axis and has a stabilizing effect, the minimum stability  
442 granted by the chain geometry is best investigated assuming equidimensional  
443 magnetosomes with no magnetocrystalline anisotropy and purely dipolar interactions, as  
444 in Hendriksen et al. (1994). In this case, single-stranded chains possess only one pair of  
445 remanent states with all magnetic moments parallel or antiparallel to the chain axis  
446 (Figure 4a). For chains with  $>4$  magnetosomes, thermally activated transitions between  
447 these two states occur by nucleating a domain with reversed magnetization at one end of  
448 the chain (Figure 4b). The two domains with opposed axial moments are separated by a  
449 transition region of  $\sim 3$  crystals with magnetic moments that deviate from the chain axis.

450 Once the two domains are formed, the transition is completed by moving the transition  
451 region towards the other end of the chain, until the original domain is denucleated (Movie  
452 S1). The energy barrier that needs to be overcome for this transition is  $\Delta E = \beta_0 k_B T$ ,  
453 where  $k_B$  is the Boltzmann constant,  $T$  the absolute temperature, and  $\beta_0$  the so-called  
454 Boltzmann factor. At room temperature ( $T = 293$  K),  $\beta_0 \approx 836$  for  $N = 15$  magnetite  
455 magnetosomes with a diameter of 50 nm separated by 5 nm gaps. The energy barrier  
456 depends only weakly on the number of magnetosomes if  $N > 6$  (Table 2). For  
457 comparison, the stability threshold predicted by the Néel-Arrhenius law  $\tau = \tau_0 \exp(\beta_0)$ ,  
458 where  $\tau$  is the time constant of the spontaneous magnetization decay and  $\tau_0 \approx 0.1$ -1 ns  
459 (Moskowitz et al., 1997), is  $\beta_0 \approx 59$  for geologic time scales ( $\tau = 1$  Ga),  $\sim 32$  for the  
460 typical lifespan of a cell ( $\tau \approx 1$  day), and  $\sim 25$  for the typical time required to measure a  
461 single FORC ( $\tau \approx 1$  min). This yields a lower stability threshold of  $\sim 17$  nm for  $\tau \approx 1$  min.  
462 For comparison, Newell (2009) obtained a threshold of  $\sim 15$  nm for the same chain  
463 geometry and  $N = 6$ , using a purely analytical approach and upon including the magneto-  
464 crystalline anisotropy of magnetosomes with  $\langle 111 \rangle$  axes parallel to the chain axis. The  
465 latter adds stability to the magnetic moments, explaining the slightly smaller threshold.

466 The large energy barrier generated by axial magnetostatic interactions ensures that  
467 field-induced transitions between the two stable states of single-stranded chains occur in  
468 proximity of the theoretical switching fields predicted by micromagnetic models that  
469 neglect thermal activations, such as the one used here and those of Harrison and Lascu  
470 (2014) and Berndt et al. (2020). Nevertheless, thermal activations are still sufficiently  
471 large to produce a measurable vertical offset of the central ridge (Egli, 2013, 2021), due  
472 to the intrinsic time asymmetry of the FORC measurement protocol (Berndt et al., 2018).

473 The central ridge offset of high-resolution FORC measurements of magnetofossil-rich  
474 sediments, which is of the order of 0.3-0.5 mT (Egli et al., 2010; Ludwig et al., 2013;  
475 Wagner et al., 2021), can be explained by a Stoner-Wohlfarth model of thermally  
476 activated UNISD particles (Lanci and Kent 2018; Berndt et al., 2018) with  $\beta_0 \approx 400-600$ .

477 The high-moment remanent state of magnetosome rings, obtained by decreasing the  
478 applied field from saturation to zero, is similar to the “onion state” of toroidal magnetite  
479 nanoparticles described by Lewis et al. (2020), in which the magnetic flux enters the ring  
480 from one side, flows past the central hole, and exits on the other side (Figure 4c). In the  
481 limit case of large rings, the “onion state” is equivalent to two magnetic domains with  
482 clockwise and counterclockwise fluxes tangential to the circumference, separated by two  
483 transition zones similar to that of a single-stranded chain with two domains (Figure 4b).  
484 Deviations from the tangential magnetization in the transition zones point to the in-plane  
485 component of the field used to impart a saturation remanence. Unlike the case of single-  
486 stranded chains, where most of the energy barrier is associated with the nucleation of a  
487 new domain, transitions to a zero-moment FC state (Figure 4d) occur with little  
488 additional energy by moving one of the two domain boundaries until it merges with the  
489 other boundary, leaving a single domain with circular magnetization (Movie S2). The  
490 energy barrier of this transition is  $\beta_0 \approx 27$  for a ring made of 20 magnetosomes with 5 nm  
491 gaps. The FC state is much more stable, as seen from the energy required for the opposed  
492 transition ( $\beta_0 \approx 1632$ ). In practice, the saturation remanence of  $N = 20$  rings will decay  
493 exponentially to zero (which is the net magnetization of the FC states) in  $\sim 9$  minutes. The  
494 saturation remanence of smaller rings is better stabilized (e.g.,  $\beta_0 \approx 55$  for  $N = 16$ ), but  
495 still much less than single-stranded chains with the same number of magnetosomes.

496 The high-moment remanent state of double-stranded chains is similar to that of single  
497 stranded chains, with the two strands possessing nearly axial moments with same polarity  
498 (Thomas et al., 2008) (Figure 4e). The magnetic moments of the end magnetosomes are  
499 not completely aligned with the chain axis, due to the reduced axial magnetostatic  
500 coupling and the stray field concentration at the chain extremities. Transitions to the low-  
501 moment remanent state, where the two strands with opposed polarities form a closed flux  
502 loop (Figure 4f), occur by nucleating a reverse domain in one of the two strands. An  
503 example can be seen in Figure 10 of Simpson et al. (2005), where two antiparallel  
504 domains in one strand are stabilized by a kink. The transition is then accomplished by  
505 extending the reverse domain until the original domain is fully denucleated (Movies S3-  
506 4). Native double-stranded chains with staggered magnetosomes (Figure 2a,b), and  
507 double-stranded chains with facing magnetosomes resulting from fold-collapse (Figure  
508 2d), undergo the same type of transitions between high- and low-moment states;  
509 however, the high-moment state of the native double-stranded chains is more stable than  
510 that of fold-collapsed chains (e.g.,  $\beta_0 \approx 751$  vs. 242 for  $N = 2 \times 11$ , Table 2), due to the  
511 staggered magnetosome arrangement (Hanzlik et al., 2002; Ruder et al., 2012). In both  
512 cases, high-moment states are stable over geologic times. The energy barriers that need to  
513 be overcome for the reversed transitions, from low- to high-moment states, are slightly  
514 larger than those of single-stranded chains.

### 515 **3.2 Micromagnetic FORC models**

516 Simulated FORC diagrams of single-stranded chains (Figure 5a,d) possess all the  
517 expected characteristics UNISD particles (Newell, 2005), also seen in cultured MTB (Li  
518 et al., 2012; Jovane et al., 2012; Wang et al., 2013, 2015). These characteristics include

519 (1) a sharp central ridge along  $B_u \approx 0$ , which is produced by the collective switching of all  
520 magnetic moments within individual chains, (2) lack of contributions over the upper qua-  
521 drant, and (3) a distribution of positive and negative amplitudes in the lower quadrant,  
522 nearly antisymmetric with respect to the  $B_c = -B_c$  diagonal, produced by the reversible  
523 rotation of the magnetic moments in the applied field (Egli, 2021). FORC measurements  
524 define three coercivity distributions (Egli, 2021) associated with (1) irreversible magneti-  
525 zation changes along the lower branch of the hysteresis loop ( $f_{\text{hys}}$ ), (2) the remanent  
526 magnetization of a so-called DC or backfield demagnetization curve ( $f_{\text{dcd}}$ ), and (3) the  
527 central ridge ( $f_{\text{cr}}$ ). In our simulations of single-stranded chains, all three distributions have  
528 identical, Gaussian-like shapes dictated by the in-field ( $f_{\text{irr}}$ ,  $f_{\text{cr}}$ ) and zero-field ( $f_{\text{dcd}}$ )  
529 magnetic moment changes associated with transitions from negative to positive high-  
530 moment states. The coercivity distributions are slightly narrower and biased towards  
531  $\sim 30\%$  higher fields with respect to the biogenic components BS and BH commonly found  
532 in magnetofossil-rich sediments (Chen et al., 2014; Egli, 2004a; Heslop et al., 2014a).  
533 This difference can be explained in part by the fact that micromagnetic calculations were  
534 based on stoichiometric magnetite, while real magnetofossils are often partially or  
535 completely maghemitized (Vali et al., 1987; Housen and Moskowitz, 2006). The  
536 maghemite endmember ( $\gamma\text{-Fe}_2\text{O}_3$ ) has a  $\sim 20\%$  lower spontaneous magnetization, and a  
537 similar reduction in coercivity is therefore expected. Furthermore, the magnetosome gap  
538 in real magnetofossils might be larger than assumed in our calculations, producing a  
539 further reduction of the switching field (Berndt et al., 2020).

540 Simulated FORC diagrams of double-stranded chain configurations feature typical  
541 flux-closure signatures (Figure 5b,c,e,f) as described in Egli (2021). These features are

542 fully developed only in fold-collapsed chains of equidimensional magnetosomes,  
543 resulting in a constricted hysteresis loop (Figure S6e) and clearly identifiable pairs of  
544 positive and negative lobes surrounding the central ridge (Figure 5c). These lobes are  
545 generated by transitions between high- and low-moment states with different in-field  
546 stability ranges (see Egli, 2021, and Figure 57 therein for a detailed explanation). The  
547 central ridge, on the other hand, is associated exclusively with the denucleation of FC  
548 configurations. Magneto-some elongation and staggering in native double-stranded  
549 chains add stability to the high-moment state, as seen by the partial suppression of the  
550 negative lobes around the central ridge (Figure 5b,e,f). The only natural example of  
551 FORC signature produced by multi-stranded chains is that of a concentrate of wild-type  
552 *M. bavaricum* cells extracted from a pond sediment (Roberts et al., 2012). This sample  
553 features positive contributions in the upper quadrant of the FORC diagram which might  
554 be attributed to the denucleation of FC states.

555 Contrary to the AMB-1 mutant (see below) and other examples of magnetic systems  
556 featuring this type of FORC signature, such as single-vortex (SV) particles (Dumas et al.,  
557 2007; Katzmann et al., 2013; Roberts et al., 2017), the hysteresis squareness of our mo-  
558 delled double-stranded chains is only slightly lowered with respect to the uniaxial SD  
559 case ( $M_{rs}/M_s = 0.471$ , Table 1, Figure 1), and fully compatible with magnetofossil  
560 signatures (Ludwig et al., 2013). Squareness values close to 0.5 for all simulated double-  
561 stranded and fold-collapsed chains means that they possess stable SD states in zero field,  
562 as observed on native chains (Li et al., 2015), and unlike the looped chains of the AMB-1  
563 mutant. Stable high-moment states in zero field require the hysteresis loop to be fully

564 reversible until the applied field reverses sign, which means that the FORC function is  
565 fully comprised within the so-called memory region (dashed lines in Figure 5).

566 The central ridge coercivity distributions of double-stranded chains are almost  
567 identical to those of single-stranded chains made of the same type of magnetosomes. This  
568 is expected from the similar stability of high-moment states in single-stranded chains and  
569 of FC states in double-stranded chains (Table 2). Non-central ridge coercivity  
570 distributions, on the other hand, contain additional low-field contributions related to the  
571 nucleation of FC states. In the case of equant magnetosomes, these contributions produce  
572 a second peak (fold-collapsed chains) or a shoulder (native chains) at  $B_c \approx 15$  mT. In the  
573 case of prismatic magnetosomes, coercivity distributions remain unimodal but become  
574 wider, and the peak position is lowered by  $\sim 10$  mT with respect to the central ridge. Non-  
575 central ridge coercivity distributions of native double-stranded chains are remarkably  
576 similar to the biogenic coercivity components BS and BH (Figure 5b,e).

### 577 **3.3 Mutant AMB-1 strain with looped chains**

578 Unlike the  $\Delta mamJ$  MSR-1 mutant, which produces agglomerated clusters of magneto-  
579 somes, the phenotype of our AMB-1 mutant contains looped magnetosome chains with  
580 necklace structures located either at one of the poles or at the center of the cell (Figure 3).  
581 Magnetosomes in the mutant strain fall mostly within the stable SD size range of single-  
582 stranded chains (Muxworthy and Williams, 2006; Newell, 2009). The magnetic behavior  
583 of bacteria was assessed using the magnetic coefficient ( $C_{mag}$ ), which relies on the  
584 differential measurement of a culture's optical density when a magnet is oriented either  
585 vertically or horizontally close to the cell suspension.  $C_{mag}$  is defined as the ratio of the  
586 maximum and minimum optical density measured and quantifies the capacity of bacteria

587 to orientate along an external magnetic field (Schüler et al., 1995).  $C_{\text{mag}}$  values at the end  
588 of bacterial growth were  $1.82 \pm 0.09$  and  $1.09 \pm 0.01$  for wild-type and mutant AMB-1  
589 (three replicates for each strain), respectively, demonstrating a very limited orientation  
590 capability for the mutant strain.

### 591 **3.4 Native magnetic states of wild-type and mutant AMB-1 cells**

592 MTB cells containing ideal magnetite chains possess already a saturation moment.  
593 Exposing them to large fields will thus not change the magnetization of a cell suspension.  
594 In practice, a ~40% increase is observed for the wild-type AMB-1 after applying a 200  
595 mT field (Figure 6a). This increase can be explained by the growth of aligned chain  
596 fragments with opposite native polarities within the same cell (Le Nagard et al., 2019). In  
597 this case, the application of a strong external field imparts the same polarity to all  
598 fragments, increasing the cell's total magnetic moment. A drastically different behavior is  
599 observed with the AMB-1 mutant, where the application of a 200 mT field produces an  
600 18-fold magnetization increase (Figure 6d). Along with the magnetic behavior assays  
601 ( $C_{\text{mag}}$ ), this result indicates a vanishingly small native magnetic moment of the AMB-1  
602 mutant, which is compatible with a FC configuration of its looped chains. Overall, these  
603 results show that virtually all mutant cells contain looped magnetosome chains.

### 604 **3.5 Electron holography**

605 Mapping of the magnetic flux in magnetosome chains produced by wild-type AMB-1  
606 (Figure 6b,c) indicates that the magnetic moments of individual magnetosomes are nearly  
607 parallel to the chain axis, as previously observed (Dunin-Borkowski et al., 1998). In con-  
608 trast, necklace structures of the mutant strain display a closed magnetic flux (Figure 6e,f).  
609 This configuration has a zero-net magnetic moment, up to small fluctuations due to

610 asymmetries (e.g., larger crystals on one side of the structure), confirming the origin of  
611 the vanishing native magnetic moments of the AMB-1 mutant deduced from magnetic  
612 measurements.

### 613 **3.6 FORC measurements**

614 The FORC diagrams of the wild-type and the mutant AMB-1 (Figure 7) share many  
615 similarities with the numerical simulations of single- and double-stranded chains of equi-  
616 dimensional crystals, but feature also important differences. The central ridge of wild-  
617 type cells extends to the origin and is accompanied by a vertical ridge along  $B_c = 0$ ,  
618 located mainly in the lower quadrant. These are the typical signatures of thermal  
619 relaxation in systems containing particles close to the lower SD stability limit (Pike et al.,  
620 2001; Lanci and Kent, 2018), and has been observed in the growing phase of MTB  
621 cultures (Carvallo et al., 2009). In case of single-stranded chains of equidimensional  
622 crystals, the lower SD stability limit is comprised between 12 and 17 nm (Newell, 2009)  
623 and is compatible with the smallest crystal sizes observed with TEM (Figure 3). The  
624 hysteresis squareness ( $M_{rs}/M_s = 0.475$ ) is slightly smaller than expected for single-  
625 stranded chains, probably because of a minor superparamagnetic contribution associated  
626 with immature chains, as confirmed by electron microscopy (Figure 3). The coercivity  
627 distributions obtained from FORC measurements of the wild-type cells (Figure 7c) are  
628 unimodal with a peak at 28–30 mT and the right tail extending to a maximum of 60–70  
629 mT. Contrary to the micromagnetic simulations of single-stranded chains of  
630 equidimensional magnetosomes (Figure 5a) and to some examples of cultured MTB  
631 producing single-stranded chains (e.g., Wang et al., 2015), the coercivity distributions are

632 left-skewed and include a small, non-zero contribution at  $B_c = 0$  caused by thermal  
633 relaxation.

634 The mutant AMB-1 strain shares the same FORC features (i.e., central ridge, viscous  
635 component and rotations of magnetic moments in the applied field), albeit over different  
636 field ranges, but also exhibits additional contributions (Figure 7b), consisting of a doublet  
637 of positive lobes at  $(B_c, B_u) \approx (12, \pm 8)$  mT, and a doublet of negative lobes at  $(B_c, B_u) \approx$   
638  $(25, \pm 3)$  mT, almost symmetrically arranged above and below the central ridge. These  
639 lobes are the typical hallmark of FC nucleation and annihilation (Egli, 2021), as seen with  
640 VO particles (Dumas et al., 2007; Roberts et al., 2017) and small magnetosome clusters  
641 produced by the  $\Delta mamJ$  mutant of MSR-1 (Katzmann et al., 2013). The hysteresis loop is  
642 constricted (Figure S8), and has a much smaller squareness (Table1, Figure 1) caused by  
643 the instability of high-moment magnetic states predicted by micromagnetic simulations of  
644 magnetosome rings (Section 3.1). This instability is associated with FORC contributions  
645 extending beyond the memory region of the FORC diagram (Figure 7b, left of the dashed  
646 lines). Constricted hysteresis loops are typically the result of bimodal coercivity distribu-  
647 tions, which, in this case, consist of a main peak at  $\sim 2$  mT, and a shoulder at  $\sim 25$  mT  
648 (Figure 7d). The main peak of the central ridge, close to the origin, is caused by thermal  
649 relaxation of high-moment states, which, as predicted by numerical simulations (Section  
650 3.1), are unstable at room temperature. FC nucleation from the negative high-moment  
651 state (feature 4 in Figure 7b) contributes additionally to the main peak of the other two  
652 coercivity distributions, explaining their larger amplitude with respect to the central  
653 ridge. A single mechanism, namely the annihilation of FC states around  $+25$  mT,

654 explains the existence of a shoulder with similar amplitude in all three coercivity  
655 distributions.

656 About 50% of the high-moment states in looped chains of the AMB-1 mutant possess  
657 a stable remanence, as indicated by the portion of the positive lobes above and below the  
658 central ridge located within the memory region (i.e., right of the dashed lines in Fig. 7b).  
659 This is explainable by the stability of smaller loops with  $N \leq 16$  magnetosomes predicted  
660 by numerical simulations (Table 2).

## 661 **4. Discussion**

### 662 **4.1 Distinctive characteristics of the magnetofossil signature**

663 Magnetic assemblages showing coexisting FORC signatures of UNISD particles  
664 (central ridge) and non-SD or interacting SD particles (positive contributions above and  
665 below the central ridge) were previously interpreted as mixings of several magnetite sour-  
666 ces including intact and collapsed magnetofossil assemblages, and non-SD particles of  
667 detrital origin (Heslop et al., 2014a; Lascu et al., 2015; Chang et al., 2019). However,  
668 mixings of the above-mentioned magnetic sources cannot provide a satisfactory explana-  
669 tion for the elevated hysteresis squareness typical of secondary magnetite in  
670 magnetofossil-rich sediments (Ludwig et al., 2013). Our work demonstrates that the  
671 magnetic signatures of these sediments can be explained by the sole presence of MTB  
672 producing single- and multi-stranded magnetosome chains, as well as specific alterations  
673 of these native configurations, such as fold-collapse, which maintain the original strong  
674 uniaxial anisotropy. Fold-collapsed chains form a uniform trend with the hysteresis  
675 properties of intact chains and UNISD particles (Figure 1), which is characterized by a  
676 very limited decrease of the hysteresis squareness ( $M_{rs}/M_s \geq 0.47$ ), and  $B_{cr}/B_c$  values

677 comprised between  $\sim 1.2$  and  $\sim 1.6$ , close to the limits for narrow and wide SD coercivity  
678 distributions, respectively (Dunlop, 2002).

679 Other putative chain collapse products, such as disordered magnetosome clusters and  
680 looped chains, might possess compatible FORC signatures, but lack the elevated  
681 hysteresis squareness of systems with stable SD-like remanent states. The hysteresis  
682 properties of large clusters of extracted magnetosomes (Kobayashi et al., 2006; Li et al.,  
683 2012) follow a trend characterized by a steep  $M_{rs}/M_s$  decrease (Figure 1) typical of  
684 densely packed synthetic SD magnetite particles (Muxworthy et al., 2003). This decrease  
685 is associated with a vertical widening of the FORC function beyond the limits of the  
686 memory region (Chen et al., 2007), due to large random internal fields associated with  
687 magnetostatic interactions (Muxworthy and Williams, 2005). FORC diagrams of SD  
688 particle clusters lack a central ridge (Carvallo et al., 2005); minor central ridge  
689 contributions in magnetosome extracts (e.g., Li et al., 2012) are therefore associated with  
690 incomplete chain collapse.

691 Micromagnetic simulations of magnetofossil collapse by chain axis randomization  
692 (Chang et al., 2019) produce a trend of hysteresis properties that is intermediate between  
693 the two cases described above (Figure 1). This trend, which includes the looped chains  
694 produced by our mutant AMB-1 as the endmember with lowest squareness, is associated  
695 with the intermediate dimensionality of chain loops ( $D \approx 2$ ) and of the partially collapsed  
696 chains generated by the random walk algorithm of Harrison and Lascu (2014) ( $1 < D <$   
697  $2$ ), compared to intact or fold-collapsed chains ( $D \approx 1$ ) and dense clusters ( $D \approx 3$ ),  
698 respectively. FORC diagrams with non-central ridge contributions and  $M_{rs}/M_s \approx 0.5$  are  
699 therefore important hallmarks of SD particle systems with a uniaxial anisotropy that is

700 sufficiently strong to stabilize SD-like remanent states. The only known natural way for  
701 secondary SD magnetite particles to develop such a strong uniaxiality is by inheritance of  
702 native magnetosome chain structures, which must therefore survive diagenesis without  
703 becoming fully randomized. Fold-collapse is one of the possible fates of single-stranded  
704 chains that are not immediately stabilized by electrostatic adhesion to other sediment  
705 particles. Multi-stranded chains, on the other hand, are expected to be more resistant to  
706 mechanical solicitations, due to the staggered magnetosome arrangement, and might  
707 survive diagenesis with little structural modifications.

708 The bell shape of the central ridge coercivity distribution is the second distinctive ele-  
709 ment of magnetofossil signatures. It is generated by the denucleation of magnetic states  
710 with largest switching field: specifically, the high-moment, SD-like state of single-  
711 stranded chains, and the low-moment, FC state of multi-stranded chains. Our simulations  
712 show that the switching fields of these states tend to form two relatively narrow  
713 distributions with medians of  $\sim 40\text{--}50$  mT in the case of equidimensional magnetosomes  
714 and  $\sim 70\text{--}80$  mT in the case of prismatic magnetosomes, prior to maghemitization. These  
715 distributions are similar to the biogenic components BS and BH discovered in AF  
716 demagnetization curves of ARM (Egli, 2004a) and later identified also in the central  
717 ridge of magnetofossil-rich sediments (Ludwig et al., 2013; Heslop et al., 2014a). The  
718 existence of a minimum uniaxial anisotropy provided by the chain structure ensures that  
719 the coercivity distributions of BS and BH are inferiorly limited by a non-zero switching  
720 field of  $\sim 10$  mT (BS) and  $\sim 25$  mT (BH). This limit is absent in isolated SD particles and  
721 in interacting clusters of such particles (Egli, 2021). An interesting counterexample is  
722 provided by a mutant MTB producing distant magnetosomes (Wang et al., 2019): in this

723 case, the combined action of magnetic viscosity and lack of strong in-chain magnetostatic  
724 interactions shifts the central ridge distribution peak to  $B_c = 0$ .

725 ARM and the central ridge are expected to have different sensitivities towards single-  
726 and double-stranded chains. In case of single-stranded chains, ARM represents the room-  
727 temperature thermodynamic equilibrium between two symmetric SD states in the  
728 decaying AF field, like in UNISD particles (Egli and Lowrie, 2002). The case of systems  
729 featuring two symmetric SD-like states with denucleation field  $B_{n1}$  and two symmetric  
730 FC states with higher denucleation field  $B_{n2}$ , as in double-stranded and fold-collapsed  
731 chains, is more complex: once the AF field has decayed below  $H_{n2}$  during ARM  
732 acquisition, the system becomes trapped into one of the two FC states. In this case, the  
733 acquired ARM is a room-temperature thermodynamic equilibrium between two  
734 symmetric FC states. This ARM is reset to zero only in AF fields with initial amplitude  
735  $\gtrsim B_{n2}$ . The similarity between  $B_{n2}$  and the switching field of single-stranded chains made  
736 of the same type of magnetosomes (Figure 5), yields comparable ARM and central ridge  
737 coercivity distributions. However, while the central ridge response is proportional to the  
738 mean amplitude of the magnetization jumps associated with FC denucleation, which  
739 amounts to  $\sim 40\%$  of the saturation moment ( $M_{cr}/M_s$  in Table 1), the ARM response is  
740 proportional to the remanent moment of FC states, which, in case of identical strands, is  
741 nearly zero. Therefore, the ARM of double stranded chains reflects the residual net  
742 magnetic moment of asymmetric strands, which is significantly smaller than the  
743 saturation moment. FC states are therefore expected to lower the ratio  $\chi_a/M_{rs}$  between  
744 the ARM susceptibility and the saturation remanence. A marked decrease of  $\chi_a/M_{rs}$  has  
745 been observed for the BS and BH components of lake sediments during a eutrophication

746 event and was tentatively attributed to the presence of greigite magnetofossils (Egli,  
747 2004a,b). However, greigite-producing MTB appear to have similar magnetic signatures  
748 as magnetite-producing MTB (Chen et al., 2014), so that multi-stranded chains are the  
749 most likely explanation for  $\chi_a/M_{rs}$  variations of magnetofossil components.

750 Coercivity distributions obtained from other types of magnetization curves, such as the  
751 commonly employed isothermal remanent magnetization (IRM) acquisition (Kruiver et  
752 al., 2001), contain contributions from all transitions between magnetic states, which, in  
753 the case of multi-stranded chains, include the denucleation of SD-like states in  $B_{n1}$ . This  
754 additional contribution is easily identifiable as a secondary low-coercivity peak in the  
755 case of fold-collapsed chains of equidimensional magnetosomes (Figure 5c), while it  
756 merges with the distribution of  $B_{n2}$  in the other case, lowering the median field. As a  
757 result, coercivity distributions obtained from IRM acquisition curves respond to a larger  
758 number of transitions between magnetic states with respect to the central ridge or ARM,  
759 yielding less constrained coercivity components that make the identification of BS and  
760 BH more difficult or even impossible. More importantly, these coercivity distributions  
761 respond also to unstable remanent magnetic states that are switched in arbitrarily small  
762 fields, yielding left-skewed curves with non-zero contributions at  $B_c = 0$ .

## 763 **4.2 Forward models of magnetofossil FORC signatures**

764 The FORC signature of single-stranded chains is identical to that of UNISD particles:  
765 both systems possess only a pair of antisymmetric SD-like states, and the in-field  
766 transition between these states produces the central ridge. The transition is preceded by a  
767 reversible rotation of magnetic moments, which generates additional FORC contributions  
768 in the lower quadrant. The coercivity distributions  $f_{hys}$  and  $f_{cr}$  associated with in-field

769 magnetization jumps produced by switching between SD-like states are identical and  
 770 proportional to the coercivity distribution derived from remanent magnetization curves  
 771 (e.g.,  $f_{\text{dcd}}$ ). The small differences between  $f_{\text{hys}}$  and  $f_{\text{cr}}$  in Figure 5a,d are due to the  
 772 numerical method used to isolate the central ridge from other FORC contributions. The  
 773 difference in amplitude between remanent and in-field coercivity distributions is  
 774 quantified by  $M_{\text{cr}}/M_{\text{rs}}$ , where  $M_{\text{cr}}$  is the magnetization associated with the central ridge  
 775 (Egli et al., 2010). Our micromagnetic simulations yield  $M_{\text{cr}}/M_{\text{rs}} \approx 0.704$  and  $0.711$  for  
 776 single-stranded chains of equidimensional and prismatic magnetosomes, respectively,  
 777 compared to  $0.544$  for the Stoner-Wohlfarth model (Egli et al., 2010), whereby all  
 778 estimates do not take thermal activations into account. The higher  $M_{\text{cr}}/M_{\text{rs}}$  values of  
 779 single-stranded chains are explainable by the fact that reversible magnetic moment  
 780 rotations is limited mostly to the end magnetosomes, while the magnetic moment of  
 781 central magnetosomes tend to maintain their remanent state. Non-central ridge  
 782 contributions in the lower quadrant of the FORC diagram are perfectly antisymmetric  
 783 with respect to  $B_{\text{u}} = -B_{\text{c}}$  and do not contribute to the total magnetization  $M_{\text{forc}}$  obtained by  
 784 integrating the FORC function, so that  $M_{\text{forc}} = M_{\text{cr}}$ .

785 The FORC diagrams of double-stranded and fold-collapsed chains contain additional  
 786 non-central ridge contributions originating from transitions between high- and low-  
 787 moment magnetic states. These contributions create nearly symmetric FORC amplitudes  
 788 around the central ridge, which contribute to  $M_{\text{rs}}$  and  $M_{\text{forc}}$ , but not to  $M_{\text{cr}}$ . The correspon-  
 789 ding ratios  $M_{\text{cr}}/M_{\text{forc}} \approx 0.47\text{--}0.57$  and  $M_{\text{cr}}/M_{\text{s}} \approx 0.38\text{--}0.42$  are therefore significantly  
 790 smaller than those of single-stranded chains (Table 3). For comparison, the FORC signa-  
 791 ture of secondary magnetite particles isolated from a magnetofossil-rich sediment

792 (Ludwig et al., 2013) is characterized by values of  $M_{cr}/M_{forc}$  and  $M_{cr}/M_s$  that are  
793 intermediate between those of simulated single-stranded and double-stranded or fold-  
794 collapsed chains. Mixtures of nearly equal parts of single- and double stranded chains  
795 (native and/or fold-collapsed) yield magnetization ratios that are compatible with those of  
796 magnetofossils (Table 3). Therefore, a composite FORC diagram has been generated  
797 using a mixture of equal amounts of all chain configurations simulated in this work,  
798 assuming a 2:1 proportion of equidimensional and prismatic magnetosomes (Figure 8b).  
799 This proportion has been chosen to reproduce at best the natural sediment example  
800 (Figure 8a). The corresponding FORC diagrams share striking similarities, but also some  
801 important differences. Both feature a central ridge, but the coercivity range of simulations  
802 is comprised between  $\sim 20$  and  $\sim 130$  mT, while the natural central ridge covers also the 0-  
803 20 mT range (see Section 4.4).

804 Other signatures of our composite FORC diagram are qualitatively similar to those of  
805 magnetofossil-bearing sediments, including the slight asymmetry between the upper and  
806 the lower quadrant, and the abrupt  $B_c$ -termination of FC contributions in the upper qua-  
807 drant. The contour lines of FORC simulation are clearly affected by localized  
808 contributions of FC nucleation and annihilation of individual chain endmembers, which  
809 are not completely merged into a smooth distribution as in the natural counterpart. Small  
810 negative amplitudes above the central ridge are also not completely cancelled. This is  
811 understandable considering that simulations were limited to few, well-defined  
812 geometries. For instance, single- and multi-stranded chains made of bullet- or tooth-  
813 shaped magnetosomes were not included. Multi-stranded chains of bullet-shaped  
814 magnetosomes are characterized by similarly elevated hysteresis squareness values as our

815 double-stranded simulations, with a central ridge peaking at ~60 mT (Li et al., 2010).  
816 This intermediate coercivity range fills the gaps between simulated chains of  
817 equidimensional and prismatic magnetosomes, making the resulting FORC diagram more  
818 similar to that of natural magnetofossils.

### 819 **4.3 Magnetofossil fingerprints and numerical unmixing**

820 Our numerical simulations show that magnetofossils possess a unique combination of  
821 magnetic properties related to the preservation of native or collapsed chain structures  
822 with a strong uniaxial anisotropy. This uniaxial anisotropy is at the basis of all magnetic  
823 criteria proposed so far for magnetofossil identification, which include (1) the central  
824 ridge (Egli et al., 2010; Heslop et al., 2014a), (2) relatively narrow coercivity components  
825 not extending to  $B_c = 0$  (Egli, 2004a), and (3) ferromagnetic resonance (FMR) spectra  
826 with positive anisotropy (Kopp et al., 2006; Charilaou et al., 2011; Kind et al., 2011). An  
827 additional criterion discussed in this work is the confinement of FORC contributions  
828 within the memory region, which ensures that  $M_{cr}/M_s \approx 0.5$  also in case of multi-stranded  
829 and fold-collapsed chains. Each of these criteria, if taken singularly, is fulfilled by an  
830 equivalent assemblage of isolated SD particles with appropriated equivalent anisotropy,  
831 but all known natural examples other than magnetofossils do not fulfill all of them. For  
832 instance, titanomagnetite needles in the Tiva Canyon Tuff do possess a central ridge  
833 (Berndt et al., 2018), but the associated coercivity distribution and vertical offset are  
834 different from those of magnetofossils. In another example (Till et al., 2017), magnetite  
835 derived from the inorganic breakdown of nanocrystalline goethite produces FORC  
836 diagrams similar to those of magnetofossil-rich sediments, but with a much lower  
837 hysteresis squareness. Finally, SD magnetite can form along dislocation lines of silicate

838 minerals, forming “strings of pearls” as documented in ancient zircons (Tang et al.,  
839 2018); however, the large irregular particle spacing resulting from this growth process is  
840 not expected to yield the narrow coercivity distribution of single-stranded chains.

841 Because natural sediments contain mixtures of magnetite particles with different pri-  
842 mary and secondary origins (e.g., Franke et al., 2007; Just et al., 2012; Li et al., 2020),  
843 magnetofossil signatures need to be isolated using numerical unmixing methods. Numeri-  
844 cal unmixing methods can be divided into parametric ones, which are based on model  
845 properties, such as coercivity distribution functions (Kruiver et al., 2001, Egli, 2003), and  
846 non-parametric ones, which are fundamentally linked to principal component analysis  
847 (PCA), such as non-negative unmixing of remanent magnetization curves (Heslop and  
848 Dillon, 2007) and FORC-PCA (Lascu et al., 2015; Harrison et al., 2018). Parametric  
849 coercivity analyses are very sensitive to noise and to subtle variations of the shape  
850 (skewness) of individual coercivity distributions (Egli, 2003; Zhao et al., 2018).  
851 Furthermore, individual coercivity components might be associated with the type of  
852 irreversible magnetization changes induced by a particular measurement protocol, rather  
853 than distinct types of magnetic particles. This is particularly evident in the case of fold-  
854 collapsed chains (Figure 5c), where  $f_{cr}$  is described by a single, unimodal distribution,  
855 while the other coercivity distributions are bimodal and require two coercivity  
856 components for a correct fit. In this case, the analysis of magnetization curves that are  
857 selective to specific magnetization processes, such as the central ridge and the AF  
858 demagnetization of ARM, helps with the identification of magnetofossil-specific  
859 coercivity components.

860 The correct individuation of endmembers in PCA-based unmixing methods is based  
861 on the assumption that individual magnetic components possess fixed magnetic  
862 properties within the set of analyzed samples. In this case, a single magnetofossil  
863 endmember is expected from PCA analyses. More than one endmember is needed to  
864 describe magnetofossil signatures that change in time, reflecting, for instance, variable  
865 proportions of equidimensional and elongated crystals (Hesse, 1994; Yamazaki and  
866 Kawahata, 1998; Wagner et al., 2021), or single- and multi-stranded chains.

867 Our micromagnetic simulations suggest that magnetosome elongation would control  
868 mainly the coercivity of magnetofossil endmembers (e.g., the proportion of BS and BH  
869 coercivity components), while higher proportions of multi-stranded chains would  
870 increase non-central ridge contributions to the FORC diagram. At least two magnetofossil  
871 endmembers are required to describe these variations. Splitting between these  
872 endmembers is controlled by the PCA covariance matrix, rather than by physical  
873 parameters. For instance, variable proportions of single- and multi-stranded chains could  
874 be described by the linear combination of a pure central ridge and a pure non-central  
875 ridge endmember, instead of the mixed FORC signatures of single- and multi-stranded  
876 chains. This might explain FORC-PCA results from the North Atlantic (Channell et al.,  
877 2016), where the three identified endmembers include one with the typical FORC  
878 signature of detrital magnetite (EM 3 in Fig. 11 of that study), one with a typical UNISD  
879 signature consisting of a central ridge, and almost no contributions in the upper quadrant  
880 (EM2, *ibid*), and one that is compatible with non-central ridge contributions from SV  
881 magnetite particles or multi-stranded magnetosome chains (EM3, *ibid*). In this example,  
882 the interpretation of the latter endmember is ambiguous; especially when considering that

883 PCA can group the signatures of magnetic components with completely different origins  
884 – such as multi-stranded magnetofossils and a fine detrital component SV signature – into  
885 a single endmember, if these components co-vary in time. Co-varying concentrations of  
886 primary and secondary magnetite particles can be expected if the abundance of  
887 magnetofossils is controlled by the flux of nutrients, which, in certain locations, is in turn  
888 controlled by primary mineral inputs (e.g., Roberts et al., 2011). Endmembers with  
889 characteristics similar to those of the above example are commonly found in marine  
890 sediments (Lascu et al., 2015; Yamazaki et al., 2020). FORC-PCA results are also  
891 sensitive to the number of principal components and the choice of the endmembers: for  
892 example, the FORC signature of a fourth endmember featuring two lobes around the  
893 central ridge similar to those of our micromagnetic simulations of double-stranded chains  
894 is distributed among the other three endmembers in the case of a three-endmember  
895 analysis of the same samples (Fig. 9-10 in Lascu et al., 2015).

896 The ambiguity of numerical unmixing results can be partially overcome by combining  
897 numerical methods with particle morphology statistics from TEM observations (Wagner  
898 et al., 2021) and with physical or chemical separation techniques, such as the selective  
899 dissolution of fine magnetite particles (Ludwig et al., 2013).

#### 900 **4.4 Authigenic magnetite in magnetofossil signatures?**

901 Fe(III)-reducing and Fe(II)-oxidizing bacteria are known to induce the precipitation of  
902 magnetite particles that are expected to provide an authigenic contribution to the  
903 magnetic signature of sediments affected by iron diagenesis. Ultrafine magnetite particles  
904 with broad volume distribution and irregular shapes have been often observed (e.g.,  
905 Gibbs-Eggar et al., 1999; Franke et al., 2007; Odlfield, 2007; Li et al., 2020), but their

906 magnetic signature is uncertain, owing to the uncontrolled grain size distribution and the  
907 unknown arrangement in the sediment matrix. Magnetite samples produced by these  
908 bacteria in the laboratory (Table 1) are characterized by a small squareness (Moskowitz  
909 et al., 1993; Carvallo et al., 2008) and the classical FORC signature of strong  
910 magnetostatic interactions (Miot et al., 2014). Because of size distribution overlapping  
911 with the stable SD range, authigenic magnetite is expected to have a similar preservation  
912 potential in geological materials (Roberts et al., 2012) and a magnetic signature that  
913 might be confused with that of magnetofossils. Irregularly shaped SD magnetite particles  
914 lacking a source of minimum uniaxial anisotropy, for instance by particle elongation or  
915 chain arrangement, are expected to produce a broad coercivity distribution with zero-  
916 coercivity contributions and median fields of 10-25 mT (Moskowitz et al., 1993).  
917 Coercivity components with similar characteristics have been found in freshwater and  
918 marine sediments, as well as in soils (EX and P in Egli, 2004a). These components are  
919 associated with moderately large  $\chi_a/M_{rs}$  values typical of non-interacting SD particles  
920 (Egli, 2004a), and, in the case of soils, with a central ridge (Geiss et al, 2008; Egli, 2021).  
921 Therefore, authigenic magnetite consists, at least in part, of isolated SD particles  
922 dispersed in the sediment matrix. The broad grain size distribution of biologically  
923 uncontrolled magnetite precipitation (e.g., Liu et al., 2005), which includes SV particles,  
924 is expected to yield also FORC signatures typical of non-SD particles, as indeed observed  
925 in FORC diagrams of well-developed soils (Egli, 2021). Isolated SD magnetite particles  
926 with random deviations from equidimensional shapes are also expected to produce low-  
927 coercivity FORC contributions above and below the central ridge (e.g., Fig 51 in Egli,  
928 2021), due to the competition between magnetocrystalline and shape anisotropy. Finally,

929 elevated local iron concentrations might lead to the formation of particle clusters with  
930 strong magnetostatic interactions that contribute to the vertical dispersion of the FORC  
931 function at low coercivities. Indeed, magnetite encrustation of Fe(III)-reducing or Fe(II)-  
932 oxidizing bacteria has been observed in culture (e.g., Miot et al., 2009). For instance,  
933 FORC signatures of non-interacting and interacting SD particles not produced by MTB  
934 have been identified in organic-rich methanogenic sediments (Ustra et al., 2021). Both  
935 non-SD and clustered SD magnetite contributions are expected to lower the hysteresis  
936 squareness, and might therefore be distinguishable from pure magnetofossil  
937 contributions.

938 Overall, the SD fraction of well-dispersed authigenic magnetite particles can produce  
939 magnetic signatures that might merge continuously with those of magnetofossils over the  
940 low-coercivity range. For instance, the low-coercivity FORC-PCA endmembers EM1 and  
941 EM2 in red clays from the Pacific Ocean (Yamazaki et al., 2020) provide altogether a  
942 signature that is similar to that of the pedogenic enhancement in soils. A low-coercivity  
943 component peaking at  $B_c = 0$  is also particularly evident in the central ridge of magneto-  
944 fossil-bearing ferromanganese crusts formed mainly through biomineralization (Jiang et  
945 al., 2020), while being absent in other crusts (Oda et al., 2018). The interpretation of the  
946 low-coercivity range (<20 mT) of the central ridge remains uncertain. Short chain frag-  
947 ments of 1-3 equant magnetosomes possess significantly lower coercivities than fully  
948 developed chains (Chang et al., 2019) and can therefore contribute to the central ridge  
949 over this range. It is not known whether such fragments are produced by MTB under  
950 natural, slow-growing conditions, or if longer chains are naturally fragmented through  
951 adhesion of segments of the same chain to different sediment particles. Overall, the

952 existence of low-coercivity contributions in the central ridge of most sediments means  
953 that a biogenic and an inorganic origin of SD magnetite particles, as postulated by  
954 different authors for the Paleocene-Eocene Thermal Maximum, are not mutually  
955 exclusive (Kent et al., 2003; Lippert and Zachos, 2007).

#### 956 **4.5 Paleontological and (paleo)environmental implications**

957 Discrimination of single- and multi-stranded chains based on the FORC signatures  
958 discussed above are of paleontological interest and could provide a temporal resolution  
959 on the evolution of magnetosome formation in MTB. Only bacteria belonging to the  
960 ancestral Delta-proteobacteria and Nitrospirae phyla were thought to produce multi-  
961 stranded chains of magnetosomes (Deng et al., 2016). However, they have been now  
962 identified in the more recent Alpha-proteobacteria and Gamma-proteobacteria phyla  
963 (Taoka et al., 2014; Zhang et al., 2017). Therefore, multi-stranded chain configuration  
964 has no specific phylogenetic distribution and might instead correspond to an adaptation to  
965 specific environments. For instance, single-stranded chain-producing cocci and the  
966 multistranded *M. bavaricum* display different responses to a sudden change of the oxygen  
967 gradient in sediment (Mao et al., 2014). In MTB, magnetosomes are aligned along  
968 cytoskeletal filaments made of actin-like proteins (Müller et al., 2020). Among them, the  
969 protein MamK is ubiquitously conserved in all known MTB. Bacteria forming multiple  
970 magnetosome chains contain several copies of genes encoding actin-like proteins in  
971 addition to MamK (Kolinko et al., 2016). We can thus hypothesize that genetic factors  
972 are responsible for multi-stranded chain configurations (Kolinko et al., 2016). They may  
973 include gene duplication events (Murat et al., 2010), or horizontal gene transfers (i.e., an  
974 exchange of genetic material through direct physical interactions between two organisms)

975 (Monteil et al., 2020). Once the genetic basis of chain configurations (Du et al., 2019) is  
976 fully understood, the methodology we describe in this work can be used to provide a  
977 temporal constrain on evolutionary events that occurred in one of the oldest and more  
978 diverse group of biomineralizing organisms.

#### 979 **4.6 Paleomagnetic implications**

980 Owing to the widespread occurrence of living MTB in the topmost ~10-20 cm of the  
981 sedimentary column (Petermann and Bleil, 1993; Flies et al., 2005; Mao et al., 2014) and  
982 cell dissolution in the same layer, magnetofossils are expected to contribute to  
983 sedimentary records of the Earth magnetic field like other magnetic particles. However,  
984 specific differences between the magnetic and mechanical properties of magnetosome  
985 chains and other carriers of a natural remanent magnetization (NRM) might affect  
986 relative paleointensity records (RPI) of magnetofossil-rich sediments (Larrasoña et al.,  
987 2014; Ouyang et al., 2014; Chen et al., 2017). Although the exact mechanism of NRM  
988 acquisition is unknown, it is possible to make some predictions on the influence of chain  
989 geometry on the RPI efficiency of magnetofossils on the basis of our findings.

990 Magnetofossils in non-varved sediments are expected to form close to the depth range  
991 inhabited by living MTB (Petermann and Bleil, 1993), inside the surface mixed layer  
992 (SML). In this case, magnetofossils would undergo the same continuous reorientation  
993 process of other remanence carriers, until they are definitively buried below the SML.  
994 The resulting NRM has been described as the result of a dynamic equilibrium between  
995 (1) the aligning effect of the Earth magnetic field on the net natural magnetic moment of  
996 isolated or grouped magnetic particles behaving as rigid mechanical units in the  
997 bioturbated sediment (e.g., clusters or inclusions in silicate minerals), and (2) the

998 rotational diffusion associated with sediment mixing (Egli and Zhao, 2015; Zhao et al.,  
999 2016). In this case, the resulting remanent magnetization  $M_{\text{nrm}} = M_0 S(m_0 B / \tau_s)$  is  
1000 proportional to the total magnetization  $M_0$  of the remanence carriers in the ideal case of  
1001 full alignment of their natural magnetic moments, and to a sigmoidal function  $S$ , with  
1002  $S(0) = 0$  and  $S(\infty) = 1$ , which describes the partial alignment of remanence carriers in  
1003 the Earth magnetic field  $B$  (Egli and Zhao, 2015). In small fields, this partial alignment is  
1004 proportional to the ratio between the magnetic torque  $m_0 B$  of individual remanence  
1005 carriers with net magnetic moment  $m_0$ , and the typical holding torque  $\tau_s$  that resists  
1006 particle reorientation. Writing  $M_0 = c m_0$ , where  $c$  is the concentration of remanence  
1007 carriers, gives  $M_{\text{nrm}} = c m_0^2 \kappa_{\text{nrm}}$  for the low-field limit of NRM acquisition, with  
1008  $\kappa_{\text{nrm}} \propto \tau_s^{-1}$  being a coefficient that describes the mechanical alignment efficiency of the  
1009 remanence carriers in sediments with specific mechanical properties.

1010 RPI records are obtained by normalizing  $M_{\text{nrm}}$  with a laboratory magnetization  $M_{\text{lab}}$   
1011 assumed to be proportional to  $M_0$ . In this case,  $M_{\text{lab}} = c m_{\text{lab}}$ , with  $m_0$  being the mean  
1012 magnetic moment component along the applied magnetic field, acquired by the  
1013 remanence carriers during the acquisition of a laboratory magnetization. The normalized  
1014 NRM is finally given by  $R = \kappa_{\text{nrm}} m_0^2 / m_{\text{lab}} B$ . As expected for valid RPI normalizations,  
1015  $R$  does not depend on the concentration of remanence carriers. Furthermore, a fixed  
1016 magnetic mineralogy yields a constant  $m_0^2 / m_{\text{lab}}$ , so that  $R$  is proportional to  $B$ .

1017 Each magnetic component contributing to the NRM is expected to possess a specific  
1018  $m_0^2 / m_{\text{lab}}$  value related to its magnetic properties, and a specific  $\kappa_{\text{nrm}}$  that reflects its  
1019 mechanical properties. Accordingly, sediments containing variable proportions of two or  
1020 more magnetic components (e.g., detrital and biogenic), yield RPI records that contain an

1021 unwanted environmental modulation caused by variations of  $\kappa_{\text{nrm}}m_0^2/m_{\text{lab}}$  within the  
1022 limit values of the individual components (Fabian and Leonhardt, 2009). The role of  
1023  $m_0^2/m_{\text{lab}}$  can be investigated by inspecting selected categories of remanence carriers. For  
1024 instance, the natural magnetic moment of silicate minerals containing  $n \lesssim 50$  SD  
1025 magnetic inclusions is proportional to the sum of  $n$  randomly oriented vectors, which  
1026 yields  $m_0 \approx m_{\text{SD}}\sqrt{8n/3\pi}$ , where  $m_{\text{SD}}$  is the mean magnetic moment of individual SD  
1027 particles (Heslop et al., 2014b). For comparison, intact chains of  $n$  magnetosomes are  
1028 characterized by  $m_0 = m_{\text{SD}}n$ , while fold-collapsed chains have a much smaller native  
1029 moment  $m_0 = m_{\text{SD}}\delta n$ , where  $\delta n$  is the mean absolute difference between the number of  
1030 magnetosomes in the two strands (e.g.,  $\delta n = 0$  for a chain that is folded exactly in the  
1031 middle). A similar reasoning can be applied to the estimation of magnetic moments  
1032 produced by the ARM and IRM magnetizations commonly used as RPI normalizers  
1033 (Table 4).

1034 Magnetofossil RPI values obtained with the above magnetic moment estimates display  
1035 different degrees of sensitivity to the chain structure. If IRM is used as normalizer,  
1036 similar RPI estimates are expected for intact single- and multistranded chains, since they  
1037 carry a saturated magnetic moment in their native state and after application of a  
1038 saturating IRM. Fold-collapsed chains, on the other hand, have a small net native  
1039 moment, making them inefficient NRM carriers. If ARM is used as a normalizer, intact  
1040 double stranded chains are expected to yield larger RPI values than intact single-stranded  
1041 chains, because the ARM sets multistranded chains in a FC state with low magnetic  
1042 moment (See Section 4.1). In case of comparable mechanical alignment efficiencies  
1043 ( $\kappa_{\text{nrm}}$ ), intact magnetofossils are expected to possess larger RPI efficiencies relative to

1044 silicate minerals containing SD magnetite inclusions with the same saturation moment, as  
1045 reported by Ouyang et al. (2014) and Chen et al. (2017), because the magnetic moments  
1046 of individual crystals add arithmetically to the native net moment, instead of randomly.

## 1047 **5. Conclusions**

1048 Rock and sediment magnetism methodologies have been extensively used for the  
1049 search and identification of magnetofossils. The central ridge observed during FORC  
1050 analyses was established as a distinctive feature of the strong uniaxial anisotropy of  
1051 isolated magnetosome chains. Our findings show that intact multi-stranded and fold-  
1052 collapsed chains can generate additional signatures in FORC diagrams through the  
1053 nucleation and annihilation of FC magnetic states while maintaining high hysteresis  
1054 squareness ( $M_{rs}/M_s$ ). FC magnetic states in multi-stranded chains, which can be described  
1055 by individual strands possessing opposed magnetic polarities, are similar to FC states  
1056 observed in small magnetosome clusters and looped magnetosome chains forming after  
1057 cell dissolution in aqueous solutions, which might serve as term of comparison for  
1058 diagenetic chain collapse in sediment. However, these artificial magnetosome structures  
1059 are characterized by a significantly lowered hysteresis squareness that is not observed in  
1060 magnetofossil-rich sediments. Micromagnetic calculations show that native multi-  
1061 stranded chains and fold-collapsed chains feature stable SD states with large magnetic  
1062 moments and the same hysteresis squareness of intact single-stranded chains. This  
1063 stability, which has been confirmed experimentally in the case of native chains (Hanzlik  
1064 et al. 2002; Thomas et al., 2008), originates from the strong uniaxial anisotropy of such  
1065 structures and explains the coexistence of (1) magnetic signatures typical for systems of  
1066 isolated SD particles and single-stranded magnetosome chains (central ridge and

1067  $M_{rs}/M_s \approx 0.5$  ), and (2) signatures typical of SD particle systems with random  
1068 magnetostatic interactions (non-central-ridge contributions in the FORC diagram).

1069 Full chain collapse leading to a complete loss of the original structure is likely  
1070 prevented by the electrostatic adhesion of magnetosomes to sediment particles.  
1071 Therefore, the strong uniaxial anisotropy of intact and fold-collapsed magnetosome  
1072 chains appears to be a key feature for the preservation of a unique magnetic signature of  
1073 magnetofossils, which, besides the elevated hysteresis squareness and a central ridge,  
1074 includes two coercivity components (BS and BH in Egli, 2004a) with inferiorly limited,  
1075 Gaussian-like switching field distributions distinct from those of isolated or clustered SD  
1076 magnetite particles. Our micromagnetic models suggest that the low-coercivity portion of  
1077 the central ridge of natural sediments (Figure 8) likely represents the contribution of  
1078 isolated SD particles of authigenic origin. ARM is another key parameter of  
1079 magnetofossil fingerprints: its coercivity distribution is similar to that of the central ridge,  
1080 but, unlike to the central ridge, it is more selective towards single-stranded chains.

1081 Preservation of a distinctive magnetofossil fingerprint, as demonstrated in our work,  
1082 is pivotal for the interpretation of the origin of secondary SD magnetite particles in sedi-  
1083 ments, since this fingerprint is the only practical mean for verifying, in a quantitative  
1084 manner, the existence of isolated chain-like structures of SD magnetite particle as the  
1085 most essential magnetofossil identification criterion. The detailed characteristics of  
1086 magnetofossil fingerprints depend on the relative abundances of equidimensional and  
1087 elongated magnetosomes, which affect the coercivity distribution, and on the relative  
1088 abundances single- and multi-stranded chains, which affect the fraction of magnetic  
1089 remanence carried by the central ridge. Magnetosome shape and chain structure reflect

1090 environmental conditions controlling the growth of different MTB strains. Therefore,  
1091 detailed magnetofossil records obtained with high-resolution FORC measurements,  
1092 combined with statistically significant TEM observations, will provide novel  
1093 methodologies to discriminate distinct populations of ancient MTB and improve our  
1094 understanding of paleomagnetic and environmental records of magnetofossil-rich  
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1106 [https://figshare.com/collections/Magnetic\\_Signatures\\_of\\_Magnetofossils/5579547](https://figshare.com/collections/Magnetic_Signatures_of_Magnetofossils/5579547).

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1634 **Tables**

1635 **Table 1.** Summary of measured and modelled magnetic properties of MTB, magneto-  
 1636 fossils, and other SD particle assemblages.  $M_{rs}/M_s$  is the ratio between the central ridge  
 1637 magnetization and the saturation remanent magnetization,  $\chi_a/M_{rs}$  is the so-called ARM  
 1638 ratio, and  $M_{cr}/M_s$  the ratio between the total magnetization of the central ridge and the  
 1639 saturation magnetization.

Structure	Reference	$M_{rs}/M_s$	$\chi_a/M_{rs}$ (mm/A)	$M_{cr}/M_{rs}$
<i>Natural sediment</i>				
Lake Baldeggersee	Egli (2004), Wagner et al., (2021)	0.41	2–4	0.37
Lake Ely	Egli et al. (2010)	0.47	—	0.48
Pelagic carbonate (CBD) <sup>1</sup>	Ludwig et al. (2013)	0.47	2–3	0.65
Paleosol S1 (CBD) <sup>1</sup>	Egli (2004, 2021)	0.20	1.7	0.32
<i>Single-stranded chains</i>				
Cultured MTB	Li et al. (2012), Moskowitz et al. (1993)	0.50	3.1–3.7	0.65
AMB-1	This study, Li et al. (2012)	0.48–0.50	1.38	0.79
Simulated	This study	0.49–0.50	—	0.71–0.72
Simulated	Chang et al. (2019)	0.32–0.50	—	—
<i>Multistranded chains</i>				
Wild-type MTB	Pan et al. (2005)	0.47–0.51	0.5–0.8	—
Simulated (2 strands)	This study	0.47–0.49	—	0.40–0.42
Simulated (fold-collapsed)	This study	0.47–0.50	—	0.37–0.38
<i>Clumps and loops</i>				
AMB-1 extract	Li et al. (2012)	0.22	0.23	—
MV-1 extract	Wang et al. (2013)	0.31	—	0.092
$\Delta mamJ$ mutant	Katzmann et al. (2013)	0.23	—	0.36
$\Delta mamJ \Delta limJ$ mutant	This study	0.31	—	0.53
<i>Extracellular magnetite</i>				
<i>Geobacter metallireducens</i>	Moskowitz et al. (1993)	0.03	0.25	—
<i>Shewanella putrefaciens</i>	Carvallo et al. (2008)	0.14	—	—
<i>Acidovorax</i> on green rust	Miot et al. (2014)	—	—	0

1640 <sup>1</sup> Citrate-Bicarbonate-Dithionite (CBD) extractable component calculated from the difference  
 1641 between pre- and post-CBD measurements.

1642 **Table 2.** Boltzmann factors  $\beta_0$  associated with the denucleation of high-moment states  
1643 (HMS) and low-moment states (LMS) for various chain geometries with of  $N$  equidimen-  
1644 sional magnetosomes of 50 nm diameter, separated by a diameter-normalized gap  $g$ .

Chain geometry	Gap $g$	$N$	$\beta_0$ (HMS)	$\beta_0$ (LMS)
Single-stranded	0.1	2	439.9	—
	0.1	7	763.9	—
	0.1	8	784.2	—
	0.1	9	795.0	—
	0.1	15	835.9	—
	0.1	16	839.7	—
	0.1	17	842.9	—
	0.05	17	969.2	—
Double-stranded (native)	0.1	10+9	667.8	800.4
	0.1	10+10	688.5	803.1
	0.1	11+10	705.2	801.6
	0.1	11+11	751.5	829.2
	0.05	11+11	864.0	953.4
Double-stranded (fold-collapsed)	0.1	10+9	235.0	1119
	0.1	10+10	268.4	1345
	0.1	11+10	277.7	1210
	0.1	11+11	242.2	1367
	0.05	11+11	278.5	1572
Ring	0.1	12	65.2	1518
	0.1	16	55.5	1606
	0.1	20	27.0	1633
	0.05	20	31.0	1877

1645 **Table 3.** Central ridge magnetization  $M_{cr}$  and total FORC magnetization  $M_{forc}$  from  
 1646 micromagnetic simulations of (1) single- and double-stranded chains, (2) a composite of  
 1647 intact chain configurations with a 2:1 proportion of equant vs. prismatic magnetosomes,  
 1648 (3) a composite of all chain configurations with 2:1 proportion of equant vs. prismatic  
 1649 magnetosomes (Figure 8b), and (4) the CBD-extractable fraction of a magnetofossil-rich  
 1650 pelagic carbonate from the Equatorial Pacific (Ludwig et al., 2013).

SD system	$M_{cr}/M_s$	$M_{forc}/M_s$	$M_{cr}/M_{rs}$	$M_{cr}/M_{forc}$
Stoner-Wohlfarth	0.272	0.272	0.544	1.0
Single-stranded equidimensional	0.347	0.379	0.704	0.914
Single-stranded prismatic	0.355	0.374	0.711	0.947
Double-stranded equidimensional	0.194	0.396	0.407	0.489
Double-stranded prismatic	0.209	0.367	0.424	0.570
Fold-collapsed equidimensional	0.171	0.397	0.366	0.431
Fold-collapsed prismatic	0.187	0.354	0.381	0.528
Composite chains (intact)	0.274	0.382	0.561	0.718
Composite chains (all)	0.242	0.382	0.500	0.632
Pelagic carbonate (CBD-extractable)	—	—	0.653	0.666

1651 **Table 4.** RPI parameters for different types of SD remanence carriers made of  $n$  SD  
 1652 crystals with mean magnetic moment  $m_{SD}$ . Other symbols:  $m_0$  — native magnetic  
 1653 moment,  $m_{IRM}$  — magnetic moment after IRM acquisition,  $m_{ARM}$  — magnetic moment  
 1654 after ARM acquisition,  $r_a$  — ARM/IRM of isolated SD crystals.

<b>SD configuration</b>	<b>NRM</b> $m_0/m_{SD}$	<b>IRM</b> $m_{IRM}/m_{SD}$	<b>ARM</b> $m_{ARM}/r_a m_{SD}$	<b><math>R</math> (IRM)</b> $m_0^2/m_{IRM}$	<b><math>R</math> (ARM)</b> $r_a m_0^2/m_{ARM}$
Silicate inclusions	$\sim 0.9\sqrt{n}$	$\sim 0.5n$	$\sim 0.9\sqrt{n}$	$\sim 1.7$	$\sim 0.9\sqrt{n}$
Single-stranded chains	$n$	$0.5n$	$n$	$2n$	$n$
Double-stranded chains	$n$	$0.5n$	$\delta n$	$2n$	$n^2/\delta n$
Fold-collapsed chains	$\delta n$	$0.5n$	$\delta n$	$2\delta n^2/n$	$\delta n$

1655 **Figure captions**

1656 **Fig. 1.** So-called Day diagram (Dunlop, 2002) showing the hysteresis properties  $M_{rs}/M_s$   
1657 and  $B_{cr}/B_c$  of intact cultured cells (Li et al., 2012; Moskowitz et al., 1993; Pan et al.,  
1658 2005), SD particles in a magnetofossil-rich sediment (Ludwig et al., 2013), the AMB-1  
1659 mutant producing looped magnetosome arrangements (this work), and a  $\Delta mamJ$  mutant  
1660 producing magnetosome clusters (Katzmann et al., 2013). The properties of extracted  
1661 magnetosomes (Li et al., 2012), micromagnetically simulated chains with increasing  
1662 degree of axis randomization (Chang et al., 2019), and our micromagnetic simulations of  
1663 intact and fold-collapsed chains are shown for comparison. Departures from  $M_{rs}/M_s =$   
1664 0.5 for ideal, non-interacting, uniaxial SD particles (cultured cells), follow trends with  
1665 increasing slopes, from intact and fold-collapsed configurations with strong uniaxial  
1666 anisotropy to complete randomization (extracted magnetosomes), through the  
1667 intermediate trend of looped and randomized chains.

1668 **Fig. 2.** Representative examples of native and collapsed double-stranded magnetosome  
1669 chains obtained from TEM micrographs. **(a)** Native, twisted double-stranded chain of  
1670 equant magnetosomes produced by *M. gryphiswaldense*. Notice the magnetosome size  
1671 tapering at both ends. **(b)** Native double-stranded chain of prismatic magnetosomes  
1672 (Lefèvre et al., 2011). Notice the staggered magnetosome arrangement. **(c)** Top: kinked  
1673 single-stranded chain of prismatic magnetosomes (Shcherbakov et al., 1997). Bottom:  
1674 complete folding of a single-stranded chain around a kink point. Notice the side-by-side  
1675 arrangement of magnetosomes, and one-sided tapering of magnetosome size. **(d)** Two  
1676 examples of rings obtained from magnetophoresis of magnetosome chains extracted from  
1677 cultures of *M. magnetotacticum* (Philipse and Maas, 2002).

1678 **Fig. 3.** Electron microscopy images of wild-type and mutant AMB-1 cells.

1679 **Fig. 4.** Numerically simulated zero-field magnetic states in idealized chains of identical  
1680 magnetosomes with no magnetic anisotropy and dipolar interactions. The magnetic mo-  
1681 ments of individual crystals are indicated by arrows with the color coding corresponding  
1682 to the axial component. **(a)** High-moment (SD-like) state of a single-stranded chain with  
1683 15 magnetosomes. **(b)** Two-domain state of the same chain as in (a), during a thermally  
1684 activated magnetization reversal. **(c)** High-moment state of a ring with 20 magnetosomes,  
1685 consisting of two symmetric domains with opposed vorticity. **(d)** Low-moment (FC) state  
1686 of the same ring as in (c). **(e)** High-moment (SD-like) state of a double-stranded chain  
1687 with 11+10 magnetosomes and staggered arrangement. **(f)** Low-moment (FC) state of the  
1688 same double-stranded chain as in (e). See Supporting Movies S1-S4 for the  
1689 corresponding transitions between states.

1690 **Fig. 5.** Simulated FORC diagrams of single-stranded (left), native double stranded  
1691 (middle) and fold-collapsed (right) chains of equidimensional (top) and prismatic  
1692 (bottom) magnetite magnetosomes. Each FORC diagram corresponds to  $\sim 10^5$  randomly  
1693 oriented chains with a realistic distribution of geometric parameters as explained in the  
1694 text. Coercivity distributions obtained from the simulated FORC data ( $f_{\text{ded}}$  — DC  
1695 demagnetization of saturation remanence,  $f_{\text{hys}}$  — irreversible component of the ascending  
1696 hysteresis branch,  $f_{\text{cr}}$  — central ridge) are shown below, together with coercivity  
1697 distributions of the biogenic component BS (gray lines in a-c) and BH (gray lines in d-f),  
1698 obtained from AF demagnetization curves of ARM (from Egli, 2004a). All FORC  
1699 diagrams share the same color scale (blue — negative values, green to violet — positive  
1700 values) with  $q = 5, 10, 20, 30, 40, 50, 60, 70, 80,$  and 90% quantile contours. The FORC  
1701 region enclosed by the  $q$ -quantile contour contributes to a fraction  $1 - q$  of the total  
1702 FORC integral (Egli, 2021). Dashed lines indicate the left boundary of the so-called  
1703 memory region.

1704 **Fig. 6.** Native magnetic states of wild-type AMB-1 and the AMB-1 mutant.  
1705 Magnetization of a suspension of (a) wild-type and (d) mutant AMB-1 cells in small  
1706 fields varying between  $\pm 2$  mT, before (black) and after (gray) saturation in a 200 mT  
1707 field. Electron microscopy and corresponding magnetic phase contours determined by  
1708 off-axis electron holography images of (b-c) wild-type and (e-f) mutant magnetite chains.

1709 **Fig. 7.** Magnetic properties of wild-type AMB-1 and the AMB-1 mutant. (a-b) FORC  
1710 diagrams with 2, 5, 10, 20, 30, 40, 50, 60, 70, 80, 90% quantile contours. Insets are  
1711 schematic representations of the magnetization of an individual cell as a function of the  
1712 applied field. Numbers highlight the following features: 1 – central ridge created by the  
1713 magnetization jump through which the lowest curve merges with curve I; 2 – positive and  
1714 negative contributions from reversible magnetic moment rotation (difference between the  
1715 slopes of consecutive curves); 3 — signatures of magnetically viscous particles (vertical  
1716 ridge and central ridge extending to the origin); 4 — nucleation of a FC state from a  
1717 negative SD state (contribution of the first magnetization jump in curve III to the  
1718 difference between curves II and III); 5 — annihilation of a FC state (contribution of the  
1719 magnetization jump in curve II to the difference between curves I and II); 6 — same as 5,  
1720 but for the difference between curve II and III; 7 — annihilation of a FC state  
1721 (contribution of the second magnetization jump in curve III to the difference between  
1722 curves II and III). (c-d) Coercivity distributions of wild-type AMB-1 and the AMB-1  
1723 mutant, obtained from subsets of FORC data:  $f_{\text{hys}}$  — irreversible component of the  
1724 ascending hysteresis branch,  $f_{\text{dcd}}$  — DC demagnetization of  $M_{\text{rs}}$ ,  $f_{\text{cr}}$  — central ridge. The  
1725 shaded area represents the  $f_{\text{hys}}$  contribution of SD magnetic states that cannot exist in a  
1726 null field.

1727 **Fig. 8.** Comparison between the FORC signature of SD particles in a magnetofossil-rich  
1728 sediment and a simulated magnetofossil composite. **(a)** FORC diagram of in-situ  $<1\mu\text{m}$   
1729 magnetite particles (mostly SD) in a pelagic sediment (data from Ludwig et al., 2013).  
1730 **(b)** FORC diagram of a simulated composite obtained from the six micromagnetically  
1731 model-led chain structures, with the following relative contributions to the saturation  
1732 magnetization, chosen for a visual match with the FORC diagram in (a): 1/3 single-  
1733 stranded chains of equant magnetosomes, 1/6 single-stranded chains of prismatic  
1734 magnetosomes, 1/3 native double-stranded chains of equant magnetosomes, 1/6 native  
1735 double-stranded chains of prismatic magnetosomes, 1/3 fold-collapsed chains of equant  
1736 magnetosomes, 1/6 fold-collapsed chains of prismatic magnetosomes. The same field  
1737 range and contour levels with respect to the maximum amplitude are used in both plots to  
1738 ease the comparison. Numbers highlight the following features: 1 —  
1739 nucleation/annihilation of FC states, 2 — high-field limit of FC state nuclea-  
1740 tion/annihilation (asymmetric about the central ridge), 3 — residual negative amplitude  
1741 from the annihilation of positive FC states, uncompensated by positive amplitudes from  
1742 intermediate coercivity contributions.  
1743

Figure 1.

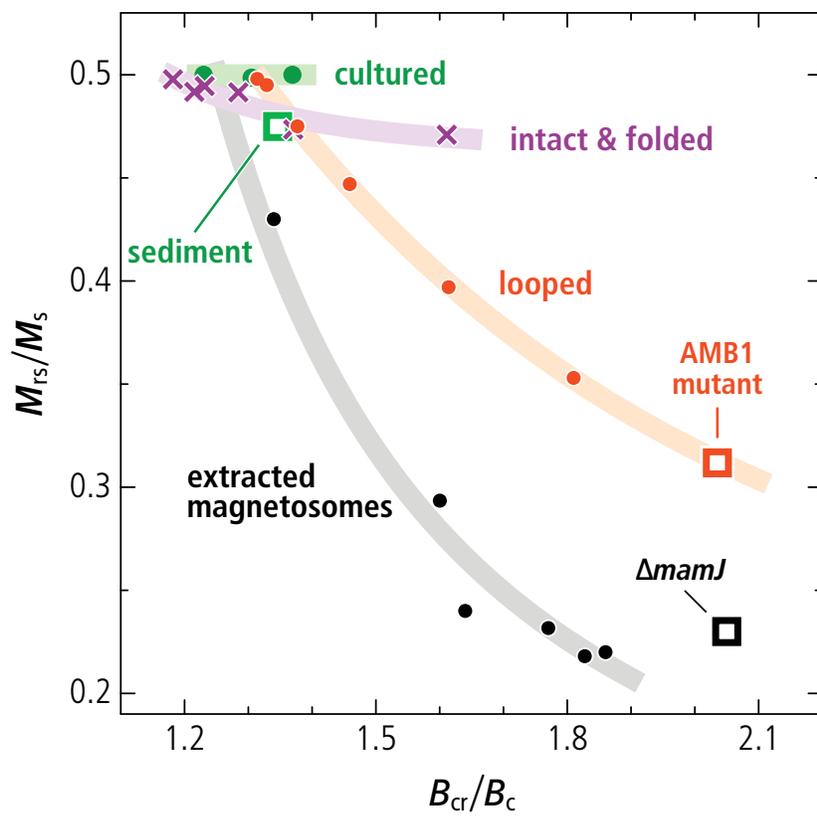
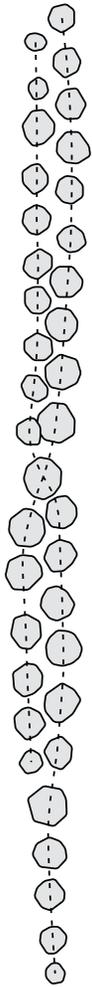
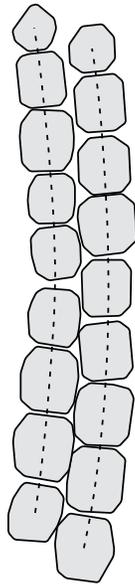


Figure 2.

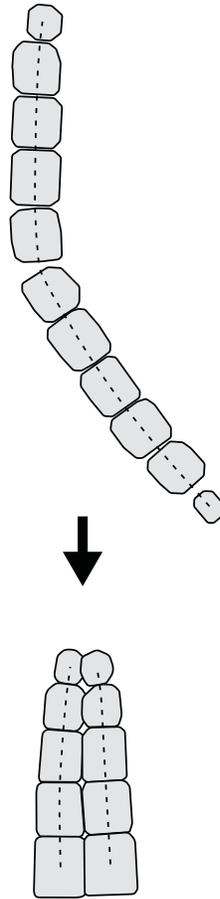
(a)



(b)



(c)



(d)

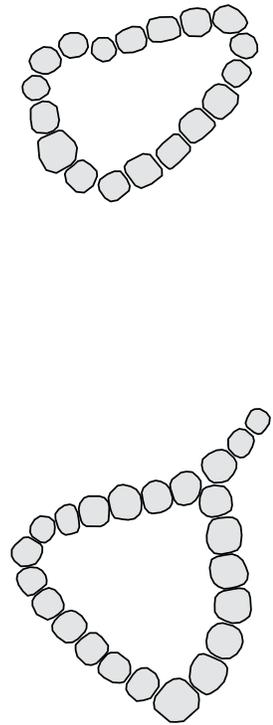
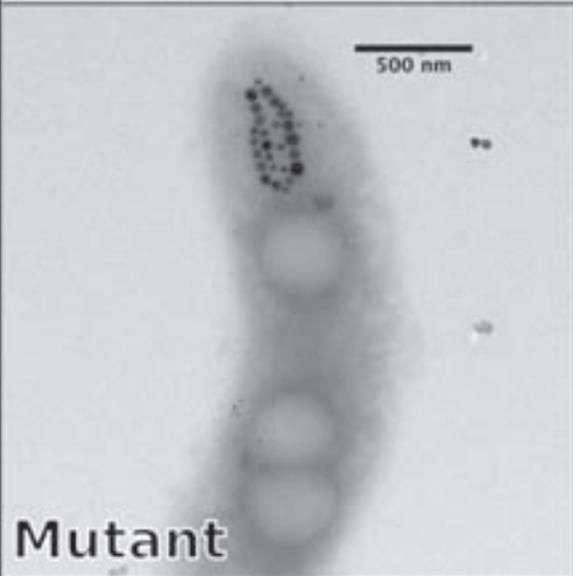
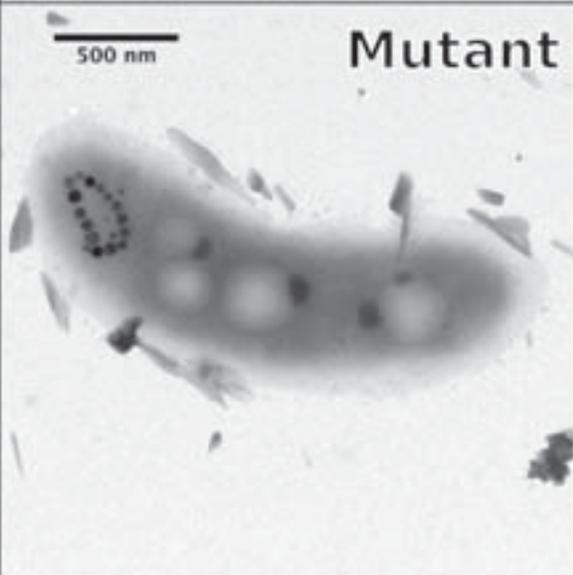
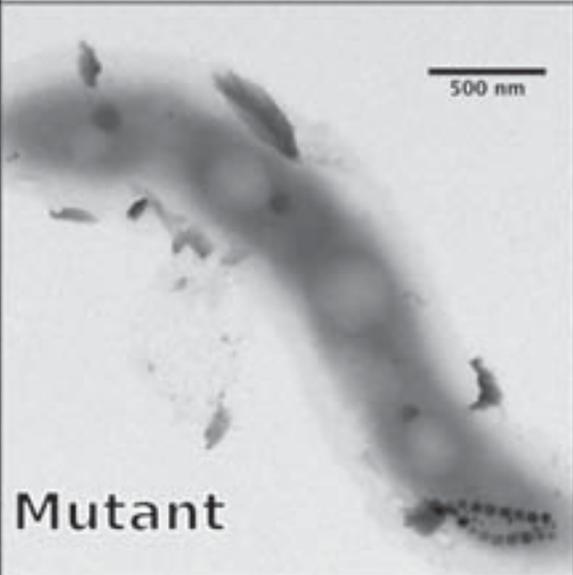
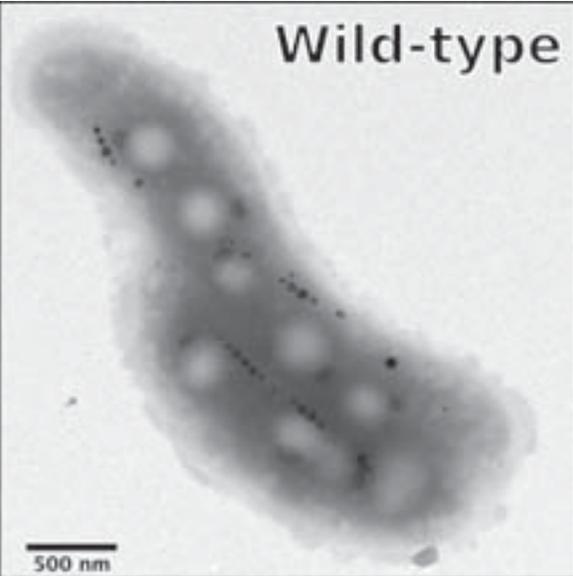
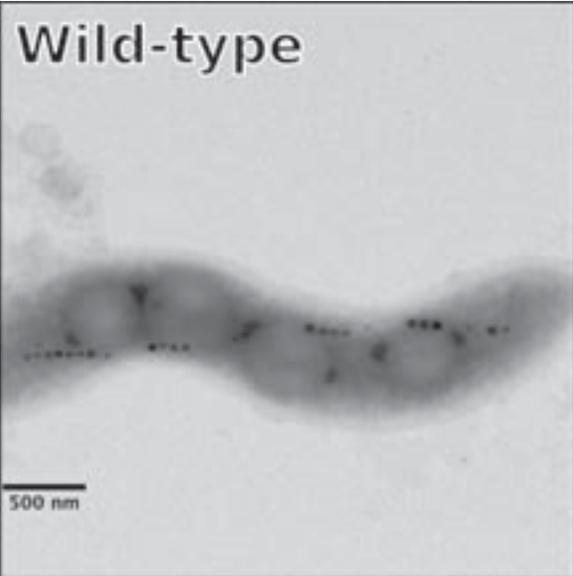


Figure 3.



**Figure 4.**

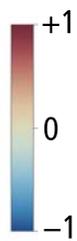
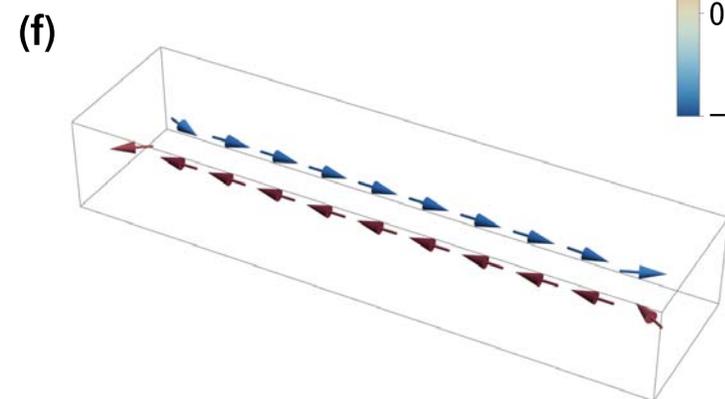
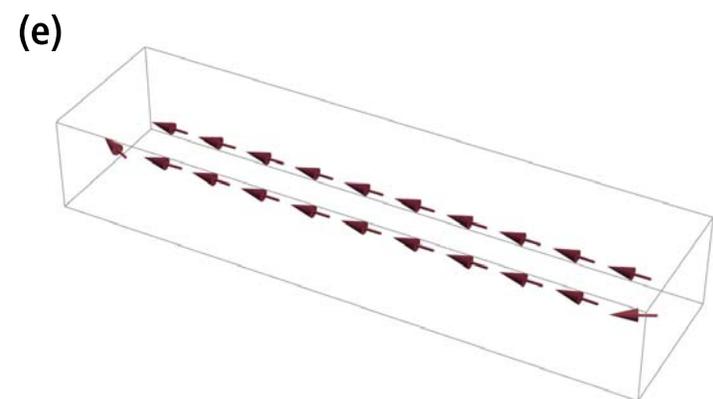
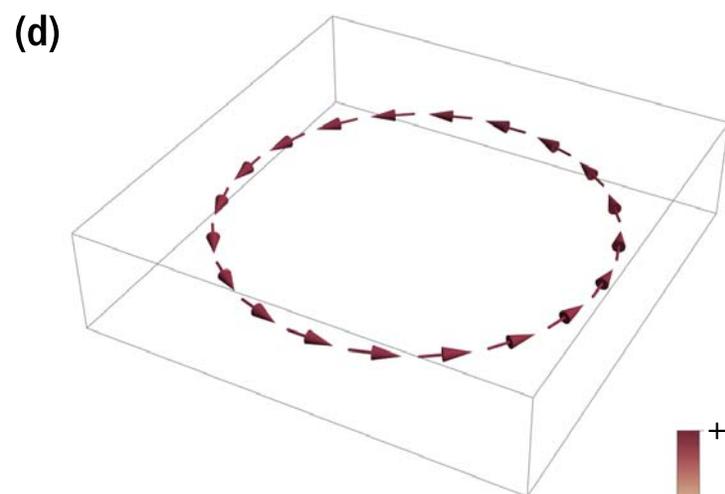
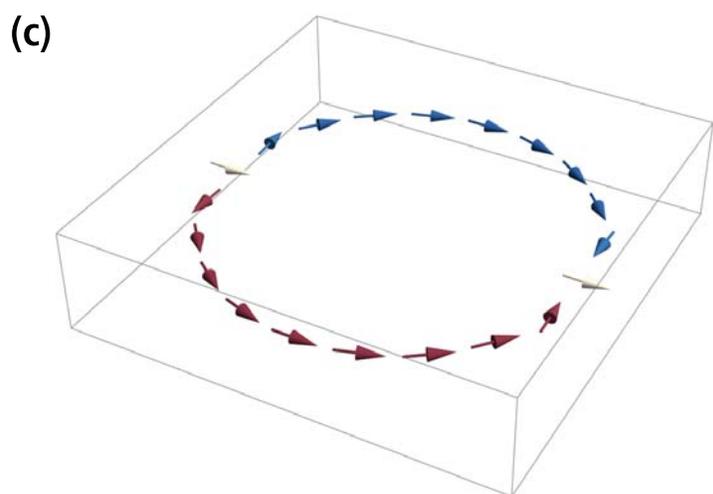
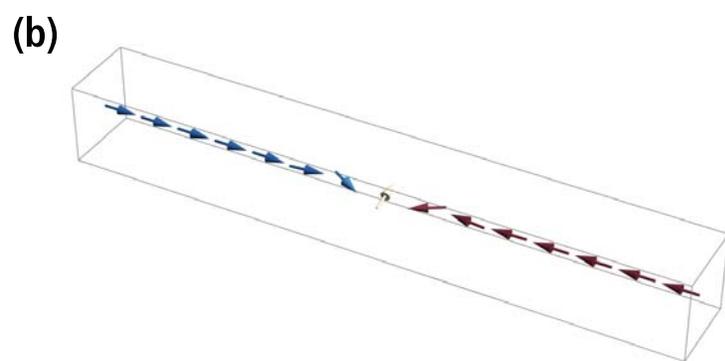
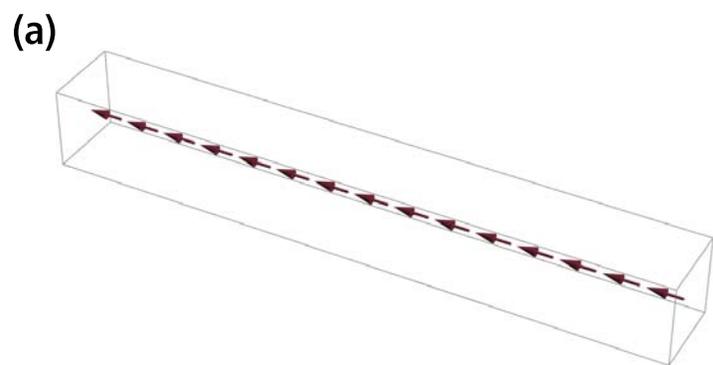


Figure 5.

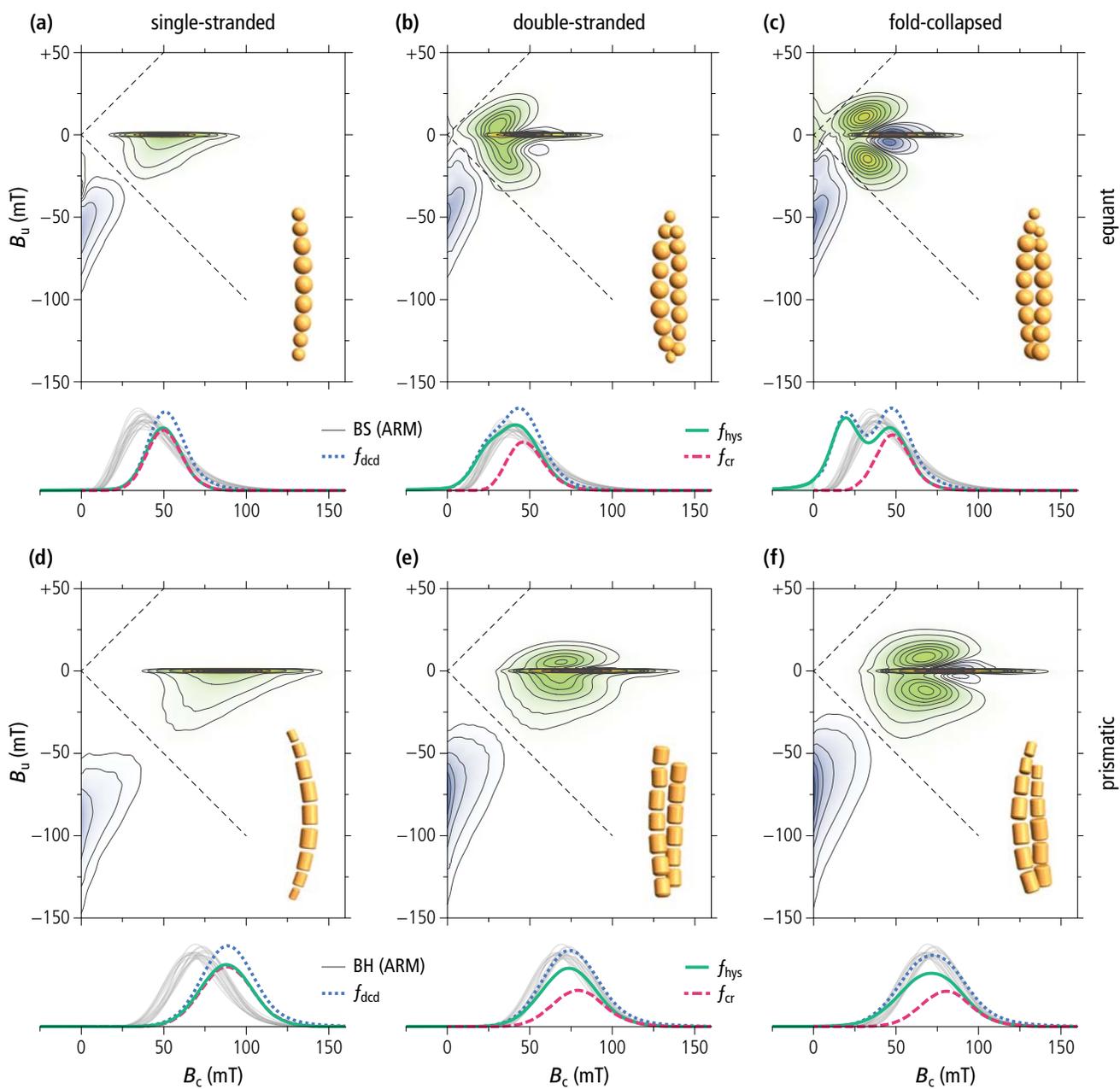
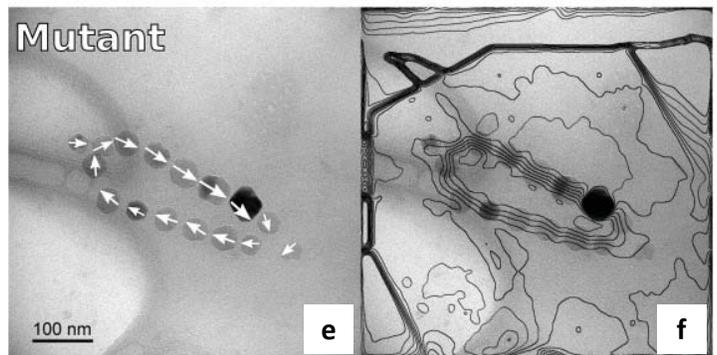
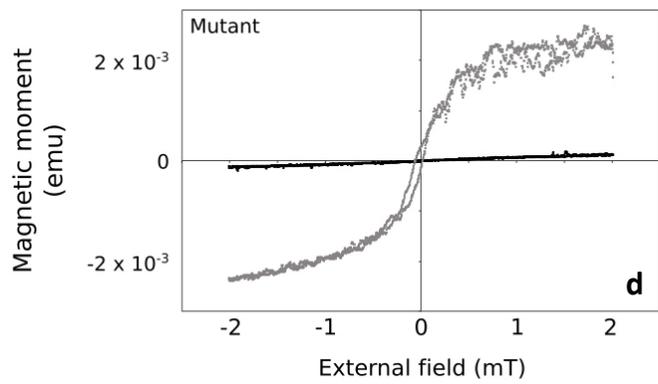
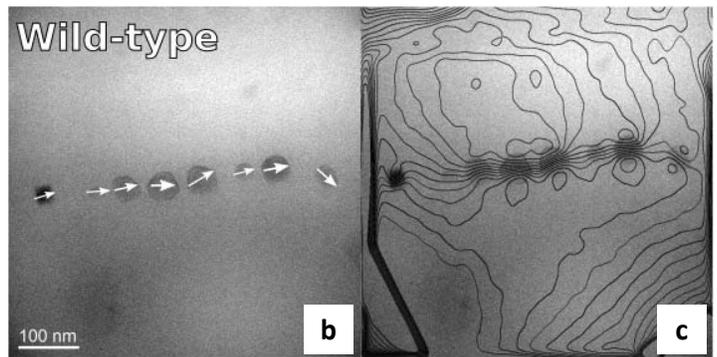
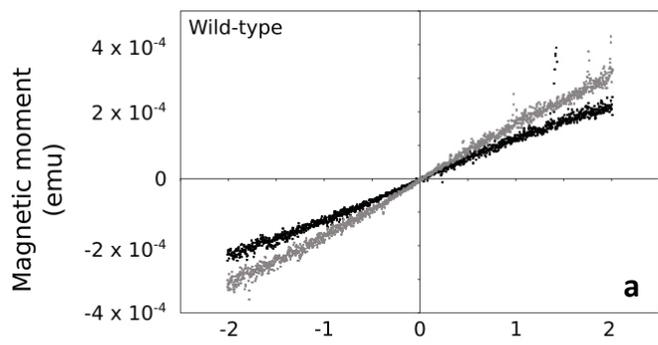


Figure 6.



**Figure 7.**

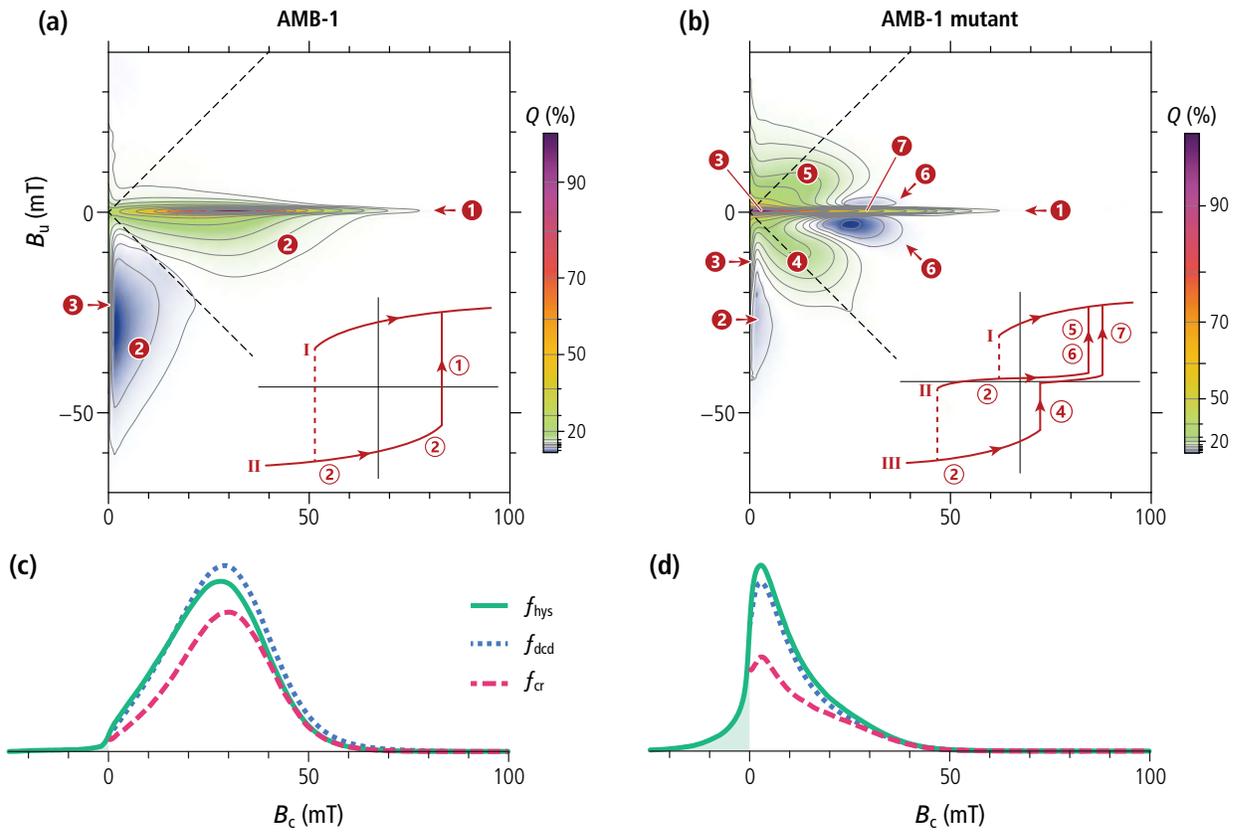


Figure 8.

