

Paleomagnetic evidence for fossil biogenic magnetite in western Crete

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Previous paleomagnetic research has shown that the concentration of fine-grained magnetite preserved in Miocene marine clays of western Crete drops during two successive geomagnetic transitions, although the mechanism responsible for this effect was not known. Magnetite precipitation by magnetotactic bacteria offers a straightforward explanation for this decrease. Reduced field strengths during a reversal will strain the competitive advantage of having intracellular magnetite and will force bacteria to precipitate correspondingly more magnetite if they are to maintain the same alignment in the geomagnetic field. Their ability to do this is limited by several magnetophysical constraints which should act to reduce the numbers of magnetite-precipitating cells, particularly in fields of less than about 12% of the present level. This would lead to a decrease in the supply of bacterial magnetite to the sediments. Recovery of intact magnetotactic bacterial fossils may lead to a new method for estimating paleointensities from sedimentary rocks.

1. Introduction

Valet and Laj [1] recently described paleomagnetic results from two successive geomagnetic polarity transitions recorded in a nearly uniform sequence of Miocene marine clays from the province of Potamida in western Crete. Using extensive thermal and AC demagnetization techniques along with saturation isothermal remanent magnetization (sIRM) and anhysteretic remanent magnetization (ARM) experiments, the authors concluded that the main carrier of the stable magnetic remanence was probably fine-grained magnetite. All remanence in their clay samples was lost by 600°C, the median destructive field of the stable NRM was found to be near 50 mT, and the saturation IRM was obtained rapidly between 200 and 250 mT.

As part of their investigation, Valet and Laj accurately measured the relative concentration of magnetic particles in each sample. In addition to the expected decrease in NRM intensity observed

during most transitions, they observed that the total influx of magnetic material producing the NRM dropped at the same time, as indicated by both the sIRM and ARM levels. Furthermore, during the two transitions the ratio of the ARM to the sIRM decreased, implying that it was a significant portion of the *fine-grained* magnetite fraction which disappeared. The authors noted that they were unable to provide an explanation as to how a geomagnetic reversal could produce this change in sedimentary conditions.

2. The biogenic magnetite hypothesis

Magnetite precipitation by magnetotactic bacteria [2,3] or its possible formation by magnetotactic algae [4] offers a straightforward explanation for this decrease in fine-grained magnetic material during geomagnetic transitions. Magnetotactic bacteria live at the mud/water interface and have been found in almost all freshwater and

marine environments examined to date [2,5–9]. Using the initial bacterial population densities and generation times measured by Moench and Konetzka [9] and a typical sedimentation rate of $1 \text{ cm}/10^3 \text{ years}$, Kirschvink and Lowenstam [10] calculated that magnetotactic bacteria could by themselves yield detrital remanent magnetizations (DRMs) on the order of 10^{-4} A/m . Towe and Moench [11] revised this estimate upwards to between 10^{-3} and 10^{-2} , based on more extensive measurements of natural population densities. Although the measured sedimentation rate for the sequence in Crete is higher than that used in these estimates ($5 \text{ cm}/10^3 \text{ years}$ [1]), their measured intensities are in the 10^{-3} to 10^{-2} range, consistent with the hypothesis that at least some fraction of the stable remanence is of biological origin. It is also interesting to note that the median destructive fields revealed by AC demagnetization of the samples from Crete ($\sim 50 \text{ mT}$) are very similar to the magnetic field pulse required to reverse the polarity of half of the magnetic bacteria naturally present in the marine pond near Woods Hole [12]. Although this similarity in coercivity does not by itself imply a biologic origin for the magnetite, it would be an expected consequence of bacterial activity.

As of this writing, very little is known about the magnetotactic algae, other than that their total moment per cell is about 10 times larger than that of the magnetotactic bacteria [4]. These algae do not appear to be as ubiquitous as the bacteria, and so would probably not contribute very much to the DRM. Photosynthetic organisms like these are probably non-existent to rare below the euphotic zone on the sea floor.

If a significant amount of the fine-grained magnetite in this marine clay is of bacterial or algal origin, the next problem is to understand how and why a geomagnetic reversal would lead to a drop in the population of magnetotactic micro-organisms and a corresponding decrease in the concentration of the fine-grained, single-domain magnetic material preserved in the sediment. Kirschvink [8] and Kirschvink and Lowenstam [10] predicted that this effect might be observed during a transition as a result either of the local magnetic inclination passing through horizontal or if the

field decayed to near zero levels; either condition was thought to reduce or remove the survival advantage which orientation in the geomagnetic field normally gives these organisms [13]. However, the recent report by Frankel et al. [7] that equal numbers of north- and south-seeking magnetotactic bacteria coexist in freshwater muds near the geomagnetic equator in Brazil makes this first possibility seem unlikely. Non-magnetic, flagellated bacteria are normally only able to move in a random walk; the comparative efficiency of powered swimming motion using ferromagnetic orientation alone is apparently high enough to permit survival even in the absence of a vertical geomagnetic component. In higher latitudes the presence of a vertical component to the local field merely biases the bulk of the population to be either north- or south-seeking [5,8], depending on the hemisphere in question.

In view of this, the decrease in geomagnetic intensity often associated with the reversal process remains as the most likely cause for the bacterial or algal populations to drop. Clearly, in a completely null magnetic field magnetite is of no use to either organism, and the metabolic energy required for its biochemical precipitation and for the formation of the internal magnetosome [14] would give them a severe competitive disadvantage in relation to non-magnetic strains. This is clearly a continuous process; in a strong magnetic field only a small volume of single-domain magnetite would be enough to align these organisms, whereas larger amounts are required for alignment in weaker fields. Individual magnetotactic bacteria living in natural environments today are found to precipitate just enough magnetite such that their magnetic energy product, μB , is about 16 times the one-dimensional thermal background energy, kT (where μ is the magnetic moment of the cell, B is the strength of the local geomagnetic field, k is the Boltzmann constant, and T the absolute temperature [13]). This relationship apparently holds for high-latitude bacteria, as well as in the low latitude of Rio de Janeiro, Brazil (H. Lins de Barros, personal communication, 1982), where the background geomagnetic field reaches the lowest global value of $29 \mu\text{T}$. From this it follows that if the background geomagnetic field were to drop to 10

or 20% of its present value during a transition, natural selection would tend to yield bacterial strains which make 5–10 times more single-domain magnetite than modern types.

There are some simple physical constraints on the amount of intra-cellular magnetite that a bacterium could precipitate. First, they cannot make more magnetite than the total volume of their cells. A typical bacterial cell has a volume of about $1 \mu\text{m}^3$, and a saturated magnetite crystal of this size would have a magnetic moment of $4.8 \times 10^{-13} \text{ J/T}$. At 300°K , $kT = 4.1 \times 10^{-21} \text{ J}$, so a magnetic field of only $0.14 \mu\text{T}$, or about 0.3% of

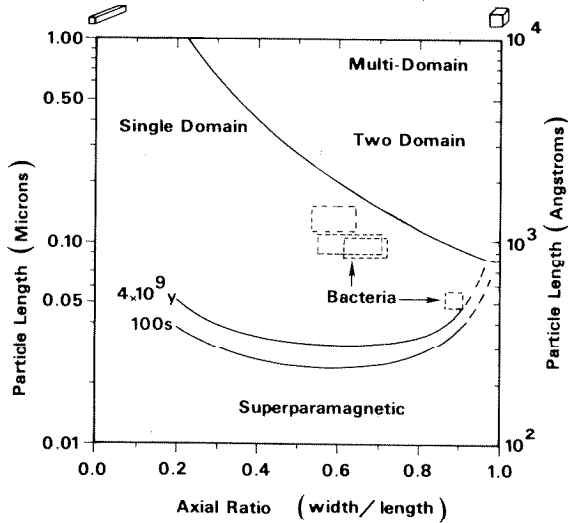


Fig. 1. Size-shape relationships and magnetic properties of magnetite crystals [15,17]. Each point on this diagram represents a rectangular magnetite crystal of specified size and shape. Points which plot in the upper right area labeled "multi-domain" or "two domain" represent crystals with two or more differently magnetized sub-regions within them; their net external magnetism is consequently reduced. Crystals which plot in the single-domain field (central part of the diagram) are those in which a single electron spin direction exists across their entire volume, they are magnetized fully to magnetite's saturation value of 48 mT. The particle shape constrains the magnetic remanence to lie permanently along its length unless forced to move by a strong magnetic pulse. Below the sharp transition zone bounded by the two lines labeled " $4 \times 10^9 \text{ y}$ " and " 100 s ", respectively, the remanence direction is no longer stable relative to the crystal and wanders freely in response to local fields and thermal agitation, giving rise to superparamagnetic behavior. Numerous bacterial magnetite crystals which have been measured by electron microscopy all plot in the single-domain field as shown.

the present level, would produce a 16 kT alignment energy. It is impossible that a bacterium could precipitate this much magnetite, however. A further problem is that a $1\text{-}\mu\text{m}$ cube of magnetite would normally not be single-domain as indicated by the calculations of Butler and Banerjee [15]. All bacterial magnetite crystals examined to date with high-resolution transmission electron microscopy fall in the single-domain stability field shown in Fig. 1 [3,6,10,11,13,14,16]. The reason for this is obvious—multi-domain and superparamagnetic crystals would be of no use to a bacterium. Natural selection would quickly weed out any new mutants which made particles in those size ranges. A $1\text{-}\mu\text{m}$ -long rectangular magnetite bar cannot be wider than about $0.2 \mu\text{m}$ before it would collapse into a pseudo-single-domain or multi-domain crystal which would be of little or no use to the organism. This largest possible single-domain crystal in this $1\text{-}\mu\text{m}$ -long bacterium would need a background field of only $3.4 \mu\text{T}$, or about 7% of the present level, to maintain a 16 kT alignment energy ratio. Again, this estimate is too high because these bacteria cannot reproduce properly with only one crystal per cell. Most magnetotactic bacteria which have been examined to date have many crystals aligned in their magnetosomes [2,5,6,9,14,16]. During cell division some of these crystals are passed on to each daughter, allowing them to inherit the north- or south-seeking swimming response of their parent [6]. Therefore, a minimum number of two, $0.5\text{-}\mu\text{m}$ -long crystals would be required per mature cell to allow this division process to continue. Once again using the diagram of Butler and Banerjee (Fig. 1 [15]), the maximum width for single-domain crystals of this length would be about $0.15 \mu\text{m}$, requiring a background field of $6.1 \mu\text{T}$ or about 12% of the present level to maintain a 16 kT orientation energy. These estimates therefore represent the smallest field in which $1\text{-}\mu\text{m}$ magnetotactic bacteria could probably maintain their presently observed alignment and still precipitate single-domain magnetite. Although these estimates have been made for a hypothetical, $1\text{-}\mu\text{m}$ -long bacterium, other sizes yield minimum field values in the same range.

Several other factors in addition to these magnetophysical limits probably reduce further the

ability of magnetotactic organisms to compete effectively in nature under low-field conditions. The precipitation of more magnetite implies the use of more iron, more metabolic energy to extract it from the medium, and more organic material with which to construct and organize the magnetosome. Another factor to consider is the internal strength of the magnetosome; it must be able to hold the crystals in a straight chain in order for it to function properly. Towe and Moench [11] report finding magnetococci with scrambled crystals, implying that this structure may on occasion collapse.

This observation might be explained by the following analysis. A straight chain is not a stable configuration for a string of single-domain magnetic particles because the total energy of the system can be reduced if the particles are allowed to clump. The energy of mutual attraction for two magnetite crystals, each with moment μ aligned lengthwise in a magnetosome, is given approximately by [17]:

$$E_{\text{chain}} = -2(\mu^2/L^3) \quad (1)$$

where the length of the particle, L , is also their center-to-center separation. Similarly, their energy after clumping is given by:

$$E_{\text{clump}} = -(\mu^2/W^3) \quad (2)$$

where the particle width, W , is now the center-to-center separation. Both (1) and (2) increase as the volume squared because $\mu = VJ_s$, where V is the volume and J_s is the saturation magnetization (48 mT for magnetite). Assuming a rectangular particle for simplicity, μ is given by $J_s L W^2$. The energy difference between the clumped and chain configurations for these two particles is then:

$$\Delta E = E_{\text{clump}} - E_{\text{chain}} = J_s^2 W L^2 [2(W^3/L^3) - 1] \quad (3)$$

The bacterial crystals of Towe and Moench [11] measured 99.3 by 62.3 nm, implying an energy difference of nearly $1.8 \times 10^3 kT$. Larger or more elongate particles increase this difference drastically; this value for the pair of $0.5 \times 0.15\text{-}\mu\text{m}$ crystals considered above is about $2 \times 10^5 kT$. Therefore when a bacterium builds a larger magnetosome, it must drastically increase the supporting strength of the adjacent organic material to

prevent the whole structure from collapsing. This in turn will place an increased metabolic burden on top of everything else associated with low-field conditions.

All of these factors taken together probably imply that either the $16 kT$ relationship observed in modern bacteria does not hold during transitions, or that a geomagnetic field intensity somewhat stronger than the 12% level estimated above would be enough to reduce the standing population of magnetotactic bacteria. In either case, one might expect to see a drop in the bacterial production of single-domain magnetite during the period of reduced magnetic intensity surrounding a geomagnetic reversal, as appears to be the case in Crete [1]. However, this analysis does not imply that bacterial strains genetically capable of magnetotaxis would go extinct during a reversal. Blake-more et al. [16] have found that the bacterium, *Aquaspirillum magnetotacticum*, is able to grow non-magnetically under certain conditions. If the geomagnetic environment temporarily shifts such that magnetotaxis no longer confers a competitive advantage, it seems likely that the small fraction of non-magnetic mutant forms will take over and dominate the population. Upon recovery of the field the reverse process should occur, and the magnetotactic varieties ought to re-establish themselves.

3. Discussion

This analysis suggests that the decrease in magnetic material during geomagnetic transitions found by Valet and Laj [1] is consistent with the hypothesis that magnetotactic bacteria were contributing to the DRM in the sediments under normal conditions. This reasoning predicts that samples away from the transition zones ought to have abundant fossil crystals of bacterial magnetite. Towe and Moench [11] note that these should be easy to recognize in the fossil record due their unique crystal morphology and grain size distribution. Crete is probably the best place to begin this search.

Perhaps this is an appropriate place to speculate on the importance of finding magnetotactic

bacteria in the fossil record. First, they are primitive organisms which may well have evolved during Precambrian time [18]. The presence of these crystals in rocks of Archean age would imply on paleontologic grounds the existence of the geomagnetic field and the prior formation of the core. Second, the constant $16 kT$ alignment energy ratio noted earlier for modern bacteria may provide a method for quantitatively making paleointensity estimates from sedimentary rocks, assuming that it also held true in the past. This method would require the complete recovery of *intact* magnetotactic bacterial fossils and the subsequent measurement of the total volume of magnetite within each cell. It remains to be seen whether these requirements can be met generally, or whether most sedimentary environments will destroy bacterial magnetite as appears to be the case near Woods Hole [19]. Numerous intact bacteria-like microfossils have been extracted and intensively studied from Precambrian rock [20,21], although magnetosomes have neither been searched for nor found in them. Finally, the selective pressures underlying the $16 kT$ orientation energy found in some modern bacteria need to be fully understood before one can confidently extrapolate this observation into the distant past.

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