Review

Magnetotactic Bacteria on Earth and on Mars

CHRISTOPHER P. MCKAY,[1] E. IMRE FRIEDMANN,[1] RICHARD B. FRANKEL,[2]
and DENNIS A. BAZYLINSKI[3]

ABSTRACT

Continued interest in the possibility of evidence for life in the ALH84001 Martian meteorite has focused on the magnetite crystals. This review is structured around three related questions: Is the magnetite in ALH84001 of biological or non-biological origin, or a mixture of both? Does magnetite on Earth provide insight to the plausibility of biogenic magnetite on Mars? Could magnetotaxis have developed on Mars? There are credible arguments for both the biological and non-biological origin of the magnetite in ALH84001, and we suggest that more studies of ALH84001, extensive laboratory simulations of non-biological magnetite formation, as well as further studies of magnetotactic bacteria on Earth will be required to further address this question. Magnetite grains produced by bacteria could provide one of the few inorganic traces of past bacterial life on Mars that could be recovered from surface soils and sediments. If there was biogenic magnetite on Mars in sufficient abundance to leave fossil remains in the volcanic rocks of ALH84001, then it is likely that better-preserved magnetite will be found in sedimentary deposits on Mars. Deposits in ancient lakebeds could contain well-preserved chains of magnetite clearly indicating a biogenic origin. Key Words: Mars— Magnetite—ALH84001—Life. Astrobiology 3, 263–270.

INTRODUCTION

THE SEMINAL PAPER by McKay *et al.* (1996) on the Martian meteorite ALH84001 cited four lines of evidence in support of the hypothesis that life existed on or in the ancient crust of Mars, ~4 billion years ago. Now more than 6 years later attention has focused on one of these lines of evidence, the nanodimensional magnetite (Fe_3O_4) grains found in fracture zones of the meteorite. The magnetite grains are similar in size and shape to those in the magnetosomes of terrestrial magnetotactic bacteria.

Since the original report of McKay *et al.* (1996), much research has been done on the physical and chemical structure of the magnetite grains in ALH84001 carbonate, some supporting their biogenic and others their non-biogenic origin. There has also been considerable progress in understanding the structure of magnetosomes, as well as the molecular biology, biophysics, and ecology of magnetotaxis and magnetite mineralization in magnetotactic bacteria. Against this backdrop, a NASA Astrobiology Institute-sponsored workshop was held at NASA Ames to consider three key questions:

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[1]Space Science Division, NASA Ames Research Center, Moffett Field, California.
[2]Department of Physics, California Polytechnic State University, San Luis Obispo, California.
[3]Department of Microbiology, Iowa State University, Ames, Iowa.

1. Is the magnetite in ALH84001 carbonate of biological or non-biological origin, or a mixture of both?
2. Does magnetite on Earth provide insight to the plausibility of biogenic magnetite on Mars?
3. Could magnetotaxis have developed on Mars?

In this report we summarize the main points raised at the meeting. Our goal was not to reach a definitive conclusion on the biological or non-biological nature of the magnetite but to provide a forum for the discussion of the current state of research and to point the direction toward promising and important areas for future research. In the following sections we consider each of the three questions addressed by the workshop.

IS THE MAGNETITE OF NON-BIOLOGICAL OR BIOLOGICAL ORIGIN, OR A MIXTURE OF BOTH?

At the workshop there was considerable debate on this question supported by detailed arguments related to the form, composition, and arrangement of the magnetite crystals. The biogenic hypothesis is based on two independent studies: Thomas-Keprta *et al*. (2000, 2001, 2002) suggested that there are six distinctive properties that, taken together, can be used to differentiate biogenic from abiogenic crystals of magnetite. Briefly these are: (i) narrow size range with a non-lognormal size distribution centered in the single-domain size range; (ii) restricted width-to-length ratios optimized for maximum overlap with the single-domain region of the Butler–Banerjee diagram of magnetite; (iii) chemical purity; (iv) very low density of crystal defects, with the exception of occasional twinning perpendicular to the [111] axis of elongation; (v) unusual truncated hexaoctahedral geometry described by the intersection of six {100} cubic faces, eight {111} octahedral faces, and only six of the possible 12 dodecahedral {110} faces (namely, those satisfying the relationship {110} · [111] = 0); and (vi) elongation along the [111] axis. Thomas-Keprta *et al*. (2000) suggested that these criteria comprise a restrictive and robust biosignature since even ~30% of magnetites produced by the magnetotactic bacterial strain, MV-1, would not display all these properties and therefore would not be confirmed as biogenic precipitates. To date no inorganic population,

whether produced by a natural or synthetic process, is known to simultaneously display all six properties. Up to ~25% of the magnetite crystals in the globular carbonate globules of ALH84001 display all six of the properties (Thomas-Keprta *et al*., 2000). The remaining ~75% of the magnetites lack sufficient characteristics to constrain their origin as either biogenic and/or inorganic.

The application of electron tomography to the magnetite crystals provides an important tool for determining their shape (Buseck *et al*., 2001). Following this suggestion, Clemett *et al*. (2002) have used electron tomography to show that the morphology of magnetite from magnetotactic bacterial strain MV-1 is truncated hexaoctahedral.

Friedmann *et al*. (2001) employed high-magnification three-dimensional backscattered scanning electron microscopy (SEM-BSE), a non-intrusive technique that permitted photographing through the intact surface the *in situ* arrangement of magnetite crystals embedded in the carbonate globules. With this method they were able to show magnetite crystal chains and chain fragments, among masses of single crystals, in the rim region of the globules. Chains of magnetite crystals, an energetically unstable configuration that does not occur in the mineral world, suggest biological origin, although such chains can be produced in the laboratory. However, the crystal chains in bacterial magnetosomes have additional unique morphological features. Six such features, observed in terrestrial magnetotactic bacteria, have been suggested as characteristic of magnetite crystal chains of biological origin, but absent in abiotically formed chains:

(i) Uniform crystal size. Despite the considerable variability in crystal size within the single domain size range (and within species or strain), crystals within a single chain are similar in size.
(ii) Uniform crystal shape within chains. Magnetite crystals in bacteria can be isodiametric, elongated, or teardrop-shaped, while within a chain they are of uniform shape. At the same time, crystals in chains produced in the laboratory randomly vary in both size and shape.
(iii) Gaps between crystals. Crystals in biogenic chains are separated by gaps, because of the organic substance (membrane material and others) between them. In abiotic chains held

together by magnetic forces there are no such gaps.

(iv) Orientation of elongated crystals. In biogenic chains of elongated crystals the crystals are oriented along their long axis, while in abiotic chains they would form a flat band.

(v) *Postmortem* bending of chains. Biogenic chains undergo such changes because they are flexible owing to the elasticity of the organic matter between crystals while abiotic chains are not.

(vi) Presence of a biological membrane around crystals.

The first five of these features are generally visible in the SEM-BSE images from ALH84001 (Friedmann *et al.*, 2001). Fossil traces of the biological membrane are visible around chains as a darker halo (indicating low atomic number substances) only in cases where the chains lie on top of a larger carbonate crystal, which provides a light background. These characteristics are absent in magnetite chains produced in the laboratory, such as the one created by Golden *et al.* (2001, Fig. e). However, the microanalytical methods used by Friedmann *et al.* (2001) to determine the chemical composition of the chain-forming particles had only resolution sufficient to verify that groups of crystals but not single crystals were indeed magnetite.

The use of chains of magnetite crystals as a biosignature is novel and presents new problems of interpretation related to resolution, comparison with fossil samples from Earth, and possible presence of artifacts in the sample (Buseck *et al.*, 2001). However, the chains presented by Friedmann *et al.* (2001) are below the intact surface and surrounded by a low atomic number substance. Clearly the application of this same method to terrestrial fossils is needed.

The abiotic hypothesis, which has been developed by several groups, is based on the thermal decomposition of Fe-bearing carbonate to produce magnetite (Golden *et al.*, 2000, 2001; Barber and Scott, 2002), with the implication that in ALH84001 such an event occurred through impact shock heating. Evidence for this process comes from the observation that in addition to magnetite, nanodimensional periclase (MgO) crystals are also associated with the carbonate globules in ALH84001, particularly the Mg-rich carbonate. Both magnetite and periclase crystals are frequently associated with voids in the carbonate, suggesting a mineralization process in which CO_2 is released. Some faceted magnetite and periclase crystals in carbonate are crystallographically oriented with respect to the carbonate crystal lattice (Bradley *et al.*, 1998; Barber and Scott, 2002). This is powerful evidence that these magnetites formed *in situ* abiogenically. Golden *et al.* (2001) demonstrated that thermal decomposition of pure siderite ($FeCO_3$) above 450°C results in magnetite crystals with size-range and shapes similar to those found in ALH84001 (Golden *et al.*, 2001). Some of these magnetite crystals are elongated along [111], as are the magnetite crystals in a number of magnetotactic bacteria, although there are differences in the relative sizes of facets of the low index forms {100}, {110}, and {111}.

Paleomagnetic measurements (Kirschvink *et al.*, 1997; Weiss *et al.*, 2002a) and inert gas measurements (Bogard and Garrison, 1998, 1999; Weiss *et al.*, 2002b) present evidence for little to no post-formation thermal processing of the carbonate globules necessary to produce magnetites. The paleomagnetic data show heterogeneous magnetization in the carbonates, suggesting that the carbonates were never heated above the superparamagnetic blocking temperature, experimentally measured to be above 80°C. $^{39}Ar/^{40}Ar$ radiogenic age dating of ALH84001 indicates that the rock did not approach the closure temperature for Ar, which is ~300°C, as does mass fractionation in the $^{36}Ar/^{132}Xe$ and $^{84}Kr/^{132}Xe$ ratios.

As to the question of whether the magnetite in carbonate globules is a mixture of crystals of biogenic and non-biogenic origin, the results of Thomas-Keprta *et al.* (2000, 2001, 2002) suggest that a population (~25%) of ALH84001 magnetite crystals are identical to biologically produced crystals. But this identity does not in itself prove biological origin. The remaining ~75% may have been formed by inorganic processes including, but not limited to, chemical precipitation from a hydrothermal fluid and/or allochtonous accumulation during carbonate formation.

In summary, there are credible arguments and supporters for both the biogenic and abiogenic hypothesis for the origin of the magnetite in the ALH84001 meteorite. Further examination of the meteorite might help resolve the matter. In addition, alternative sources of information about the problem obtained on Earth, on Mars, or from other ancient Martian meteorites may help address this issue.

DOES MAGNETITE ON EARTH PROVIDE INSIGHT TO THE PLAUSIBILITY OF BIOGENIC MAGNETITE ON MARS?

Magnetotactic bacteria were first recognized on Earth by Blakemore (1975), and magnetite in magnetotactic bacteria was first reported by Frankel *et al.* (1979). Most magnetotactic bacteria are microaerophiles, living in aquatic environments in the redox transition zone between oxygen-rich upper waters and oxygen-depleted, sulfide-rich, lower waters or sediments. Their metabolism is typically based on the oxidation of carbon compounds with oxygen, nitrate, or nitrous oxide as electron acceptors. Magnetotactic bacteria use their magnetic response in conjunction with aerotaxis to navigate to an optimal location in the oxygen gradient (Frankel *et al.*, 1997). As the bacteria swim through the water the torque exerted by the geomagnetic field on the magnetic dipole moment of their internal magnetite chain keeps them oriented along magnetic lines of force, and the bacteria thus swim in a one-dimensional path. Presumably this reduces the effort required to find the optimal oxygen concentration compared with a search in three dimensions. The magnetic grains contained within magnetotactic bacteria are termed magnetosomes. In some species the magnetite particles are enveloped in an organic membrane structure that secures them within the cell and provides an enclosed microenvironment for precise biological control of magnetosome size and morphology. The most common magnetosome arrangement is one or more linear chains traversing the long axis of the cell (see Fig. 1). To maximize the magnetic moment per unit mass of magnetite most, but not all, magnetotactic bacteria produce magnetite grains that are between ~30 and 100 nm. This is the optimal size range for stable, single magnetic domain magnetite. Smaller particles are unstable because of thermally induced orientation fluctuations of their magnetic moment, whereas larger particles are unstable with respect to magnetic domain formation. The magnetic moment per unit mass of magnetite is enhanced by the organization of the magnetite grains in chains. Some non-magnetotactic microorganisms perform dissimilatory iron reduction, which can result in magnetite formation under certain condtions of E_h and pH, but the crystal shapes and sizes are not genetically controlled as they are in magnetotactic bacteria. For this reason, such magnetite crystals are not distinct from those precipitated from inorganic solutions.

Biochemistry and gene expression

The study of magnetotactic bacteria on Earth is still developing. Further understanding of the biochemical and genetic controls on magnetite production, the ecology and morphology of magnetotactic bacteria, and their evolutionary history as part of the phylogenic and fossil record could provide essential background information for a biogenic interpretation of Martian magnetite. Little is known about how magnetotactic bacteria synthesize their magnetic minerals at the chemical/biochemical/gene levels.

Magnetotactic bacteria are microaerophiles, anaerobes, or both, and it seems clear that magnetite magnetosome synthesis occurs only under these conditions (Blakemore *et al.*, 1985; Bazylinski *et al.*, 1988; Sakaguchi *et al.*, 1993; Schüler and Baeuerlein, 1998). Much of the discussion at this meeting focused on the determination of the genes involved in magnetite synthesis by the magnetotactic bacteria and how to identify these genes. Most researchers use two different approaches to find these genes: (1) by examining the proteins present in the magnetosome membrane (e.g., Arakaki *et al.*, 2003) and then using "reverse genetics" to obtain the gene sequences for these proteins; and (2) biochemical comparison of mutants that do not produce magnetosomes with wild-type strains and then again using "reverse genetics" to determine gene sequences.

The mam (magnetosome membrane) genes appear to be conserved within several magnetotactic bacteria (*Magnetospirillum* species and strain

FIG. 1. Electron micrograph of the bacterium *M. magnetotacticum* showing the chain of magnetite-containing magnetosomes that result in the alignment of the cell along magnetic-field lines as it swims. The magnetite grains have an average length of 45 nm.

MC-1) and may be involved in magnetite biomineralization in magnetotactic bacteria (Grünberg *et al.*, 2001). These researchers cloned and sequenced some of the mam genes in *Magnetospirillum gryphiswaldense* that were assigned to two different genomic regions. These proteins exhibited the following homologies: mamA to tetratricopeptide repeat proteins; mamB to cation diffusion facilitators; mamE to HtrA-like serine proteases. The sequences of mamC and mamD showed no homology to existing proteins. A gene cluster containing homologues to mamA and mamB was found in *Magnetospirillum magnetotacticum* and strain MC-1 that also contained genes that showed no homology with known genes or proteins in established genomic databases. Definitive functions have not yet been ascribed to these proteins.

The magA gene found in *M. magneticum* strain AMB-1 encodes for a protein that is homologous to the cation efflux proteins, the *Escherichia coli* potassium ion-translocating protein, KefC, and the putative sodium ion/proton antiporter, napA, from *Enterococcus hirae*. MagA has been expressed in *E. coli*, and membrane vesicles prepared from these cells that contained the magA gene product took up Fe but only when ATP was supplied, indicating that Fe uptake was energy-dependent. It was also shown, using a magA-luc fusion protein, that magA is a membrane protein localized in the cell membrane and possibly the magnetosome membrane as well (Nakamura *et al.*, 1995). Interestingly, the magA gene was expressed to a much greater degree when wild-type *M. magneticum* cells were grown under Fe-limited conditions rather than Fe-sufficient conditions under which they produce more magnetosomes. Moreover, a non-magnetotactic Tn5 mutant (that does not produce magnetosomes) overexpressed the magA gene under Fe-limited conditions, although it did not make Fe_3O_4. This suggests that the magA protein is involved in Fe transport.

Three other genes that encode the magnetosome-membrane-specific proteins mms6, mms16, and mpsA have been obtained from *Magnetospirillum* strain AMB-1 (Matsunaga *et al.*, 2000; Okamura *et al.*, 2001). These genes were also found in the genome of *M. magnetotacticum*. MpsA exhibits homology to an acyl-CoA transferase. Mms16 shows GTPase activity and is possibly involved in magnetosome membrane vesicle formation by invagination and budding from the cytoplasmic membrane. Mms6, the most abundant of the

three, is apparently bound to magnetite and may function in regulation of crystal growth (Arakaki *et al.*, 2003).

Lastly, another major point brought up at the meeting is the need for a genetic system in the magnetotactic bacteria (Schultheiss and Schüler, 2003). It is necessary to have this in order to determine the functions of the above and other proteins in magnetite synthesis in magnetotactic bacteria.

DOES MAGNETITE ON EARTH PROVIDE INSIGHT TO THE PLAUSIBILITY OF BIOGENIC MAGNETITE ON MARS?

The carbonates in the ALH84001 meteorites were shown to be 3.9 ± 0.04 Gyr old (Borg *et al.*, 1999). If the magnetite is of biological origin then this implies that there were magnetotactic bacteria on Mars long before they are found in the geological record on Earth. But this is based on our current understanding of the evolution of magnetotaxis on Earth. Observations from ancient rocks suggest that biogenic magnetite from magnetotactic bacteria is present in some terrestrial rocks as old as ~2 billion years (Chang *et al.*, 1989). We presently do not know how long magnetotactic bacteria have been on the Earth or even how widely this phenotype is distributed among contemporary prokaryotes. Phylogenetic analyses, based on 16s rRNA gene sequences of many cultured and uncultured magnetotactic bacteria, show that most of the magnetite-producing strains are members of the alpha-subgroup of the Proteobacteria in the Domain Bacteria (Bazylinski and Frankel, 2000; Spring and Bazylinski, 2000). There are several exceptions, including *Desulfovibrio magneticus*, a member of the delta-subgroup of the Proteobacteria (Kawaguchi *et al.*, 1995), and the uncultured species *Magnetobacterium bavaricum*, which is phylogenetically associated with the newly designated Nitrospira group in the Domain Bacteria (Spring and Bazylinski, 2000). Neither the Proteobacteria nor the Nitrospira group is a deeply branching evolutionary line in the Domain Bacteria, and therefore these groups are not generally considered to be ancient groups of bacteria (Woese, 1987). However, dating the evolutionary origins of most bacterial groups is currently impossible or extremely difficult at best. Moreover, phylogenetic analyses suggest that magnetotaxis and perhaps magnetite

synthesis may have evolved several times in the past (DeLong *et al.*, 1993; Spring and Bazylinski, 2000). Clearly more studies are necessary on the distribution of magnetotaxis in the Archaea and in the deeply rooted branches of the tree of life, as well as more complete searches for magnetofossils in the sedimentary record on Earth.

A biological explanation for magnetosomes on Mars requires not only that there was life on Mars but also that magnetotaxis developed—presumably independently from Earth. The logical possibility exists that magnetotactic bacteria that originated on Mars were transported to Earth via meteorites, since it has been shown that sterilizing temperatures are not reached during meteorite transfer from Mars to Earth (Weiss *et al.*, 2001).

If the biochemistry and ecology of magnetactic bacteria on Earth are a guide, then the development of magnetotaxis on Mars implies the presence of liquid water habitats, magnetic fields, and oxygen in the atmosphere at low levels. The presence of liquid water early in Martian history is well established. The recent detection of strong crustal magnetism in linear features in the cratered southern highlands on Mars (Acuña *et al.*, 1999; Connerney *et al.*, 1999) suggests that there was a strong dipole field on Mars early in its history. High levels of oxygen on early Mars are more problematic, but there have been suggestions that, given a similar biological source of oxygen as on the Earth, Mars would have experienced high oxygen levels much more rapidly than the Earth (Hartman and McKay, 1995; McKay, 1996). Thus if the magnetite in ALH84001 is of biological origin it has implications for understanding the geochemical history of Mars. Certainly, the geological history of Mars is consistent with the possibility of the presence of magnetotactic bacteria on Mars 3.9 Gyr ago.

It is interesting to note that prokaryotic microorganisms (bacteria) rarely produce morphologically distinct inorganic intracellular components other than magnetite. The organic remains of any Martian bacterial biota would have been destroyed by the oxidant that is presumed to be responsible for the Martian surface oxidation and lack of organics detected by the Viking Landers. But even under these conditions, magnetite would be preserved as a signature of life. In the oxidizing Martian surface soil and sediments, biogenic magnetite may be the only remaining signature of microorganisms once present.

RECOMMENDATIONS

The question of the biogenic origin of the magnetite in the ALH84001 meteorite remains disputed. The potential importance of a biogenic origin for understanding the biological and geochemical history of Mars makes the question compelling for Astrobiology. Recommendations for future research centered on four areas:

1. More studies of ALH84001 and laboratory simulations. The way forward will certainly involve more studies on the ALH84001 meteorite as well as laboratory simulations to reproduce the structures of the carbonate and magnetite inclusions.
2. Studies of magnetotactic bacteria on Earth. It is also clear that a much better understanding of the biochemistry, genetics, ecology, morphological diversity, and paleontology of magnetotactic bacteria, and other prokaryotes that produce magnetite, as found on Earth is needed to guide investigations of Martian magnetite.
3. Martian magnetic soils. Magnetite grains produced by bacteria provide one of the few inorganic traces of past bacterial life on Mars that could be recovered from surface soils and sediments. Better understanding of the magnetic phase on Mars would help determine the mineralogical stability and weathering history of magnetic phases on Mars and the possible contribution of biogenic magnetite to the soil magnetic fraction.
4. Sample return from Mars from paleolake sediments. If there was biogenic magnetite on Mars 3.9 Gyr ago in sufficient abundance, then it is likely that better-preserved magnetite will be found in sedimentary deposits on Mars. Lake deposits such as those identified in Gusev and Gale Craters (e.g., Cabrol *et al.*, 1999) could contain well-preserved chains of magnetite clearly indicating a biogenic origin.

ACKNOWLEDGMENTS

ABBREVIATION

SEM-BSE, backscattered scanning electron microscopy.

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Address reprint requests to:
Dr. Christopher P. McKay
Space Science Division
NASA Ames Research Center, Code 245-3
Moffett Field, CA 94035

E-mail: cmckay@mail.arc.nasa.gov