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Biogenic Magnetite in Stromatolites. II. Occurrence in Ancient Sedimentary Environments

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Abstract

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In this paper we report the discovery of fossil bacterial, single-domain magnetite particles in ancient stromatolites. The biogenicity of the crystals was determined by the following criteria: (1) distinctive morphology and habit, (2) composition and (3) environment of deposition. Stromatolites ranging in age from the Middle Archean to Pleistocene, composed of both carbonate and chert, were analyzed for the presence of single-domain magnetite using rock magnetic methods. The granulometry and composition of the ultra-fine-grained magnetite crystals extracted were determined by transmission electron microscopy and electron diffraction. The oldest magnetofossils were extracted from stromatolitic chert of the Gunflint Iron Formation which is approximately 2000 Ma old. The implications of these findings and the potential uses of fossil bacterial magnetite in studies of the evolution of biomineralization and prokaryotic metabolic processes, paleomagnetism, and as an indicator of ancient oxygen levels are discussed. Bacterial magnetite represents the oldest evidence of biomineralization yet discovered in the fossil record.

Introduction

Biomineralization producing hard parts was a major innovation in the history of life (Lowenstam and Margulis, 1980). The most profound biomineralization event took place at the base of the Cambrian System, some 570–540 Ma ago, when cyanobacteria, algae and numerous phylogenetically distant invertebrates developed the ability to secrete hard parts. Although the cause(s) of this event is unknown, studies on extant organisms indicate that the mineral-forming mechanisms range from matrix-mediated to biologically induced (Lowenstam, 1981; Lowenstam and Weiner, 1983). Biologically induced minerals have crystal habits and chemical signatures that are governed by the same equilibrium principles that control the crystallization of their inorganic counterparts. In contrast to this, matrix-mediated minerals are usually grown in a pre-formed organic framework (the matrix). A high level of biochemical control makes their size, shape and

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chemical signature distinguishable from possible inorganic counterparts.

Biogenic magnetite may be produced by either biologically induced or matrix-mediated biomineralization (Stolz et al., 1989b). Dissimilatory iron reducing bacteria convert amorphous ferric oxide to magnetite by coupling iron reduction to the oxidation of organic compounds (Lovley et al., 1987). The biologically induced precipitate is deposited extracellularly and the crystals have the typical octahedral shape for magnetite. Magnetotactic bacteria on the other hand, produce magnetite by a matrix-mediated process. The magnetite is formed intracellularly in a membrane-bounded structure, the magnetosome, and has morphologies which can be easily distinguished from biologically induced or abiotically produced magnetite (Stolz et al., 1989b). Although the biologically induced magnetite produced by dissimilatory iron reducing bacteria has been implicated for the occurrence of magnetite in some rock formations (Lovley et al., 1987), we restrict our discussion in this paper to the magnetite formed by magnetotactic bacteria and the criteria to distinguish it in the fossil record.

When Blakemore (1975), discovered magnetotactic bacteria, he recognized that these bacteria not only have the ability to biomineralize magnetite within their cells, but that it is a clear example of a matrix-mediated mineral (Lowenstam and Kirschvink, 1985; Lowenstam, 1986). The morphology, structure and composition of these bacterial magnetites have been well studied (Frankel et al., 1979; Towe and Moench, 1981; Blakemore, 1982; Matsuda et al., 1983; Mann et al., 1984a,b). The crystal morphologies generally fall into one of three categories: (1) hexagonal prisms (Towe and Moench, 1981; Matsuda et al., 1983; Mann et al., 1984a), (2) cuboid (Frankel et al., 1979; Mann et al., 1984b) and (3) tear drop (Blakemore et al., 1980; Blakemore, 1982). These shapes are all quite different from the typical octahedral morphology of inorganically formed magnetite. In addition, biogenic magnetites are chemically pure (Towe and Moench, 1981; Mann, 1985), in contrast to igneous and metamorphic magnetites which often have higher levels of some other transition metals such as titanium (Haggerty, 1976).

Besides their distinctive shape and composition, bacterial magnetites have a unique size distribution. All of the bacterial magnetite crystals studied by high resolution transmission electron microscopy (TEM) to date have sizes ranging from 0.05 to 0.3 μm and are within the size range of the stability field for single-domain magnetite (Towe and Moench, 1981; Chang et al., 1987) (Fig. 1). The restricted size range for these biogenic magnetites has been interpreted to be the result of natural selection operating on organisms that use their internally formed magnetite for directional sensitivity (Blakemore et al., 1985; Kirschvink, 1983). These characteristic properties, combined with the widespread distribution and abundance of magnetotactic bacteria (Moench and Konetzka, 1978; Chang et al., 1987), suggest that biogenic magnetite should be present and recognizable in the rock record.

The formation of magnetite in *Aquaspirillum magnetotacticum* is known to require some amount of free oxygen (Blakemore et al., 1985); the maximum yield of magnetite is obtained with an initial oxygen concentration of 1 kPa and virtually no magnetite is formed with <0.5 kPa. The study of bacterial magnetite crystals in the fossil record could, therefore, provide constraints on the chemistry of bottom waters through the Phanerozoic and may ultimately shed light on the evolution of free oxygen during the Precambrian. Furthermore, because magnetotactic bacteria use the magnetite they produce as a compass orientation (Frankel, 1984), the presence of fossil bacterial magnetites in the Precambrian would imply the existence of a geomagnetic field.

The purpose of this study was to establish whether magnetotactic bacteria occur in stromatolitic environments and if their magnetofossils can be found in fossil stromatolites and

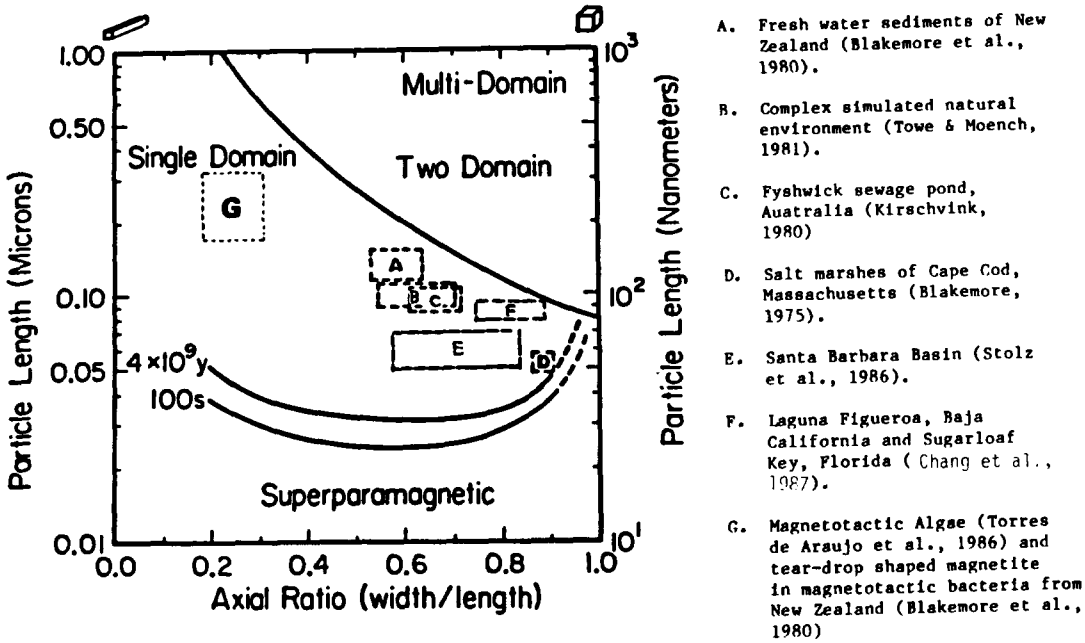

Fig. 1. Size and shape distribution of magnetite particles found in magnetotactic bacteria and magnetotactic algae from previously reported occurrences as plotted in the theoretically derived stability field diagram of magnetite (Butler and Banerjee, 1975).

microfossiliferous cherts. The previous paper (Stolz et al., 1989a) reported on modern stromatolitic environments while this paper presents the results of our study on fossil bacterial magnetites.

Materials and methods

Samples from 16 localities spanning almost 3500 Ma of geological time, from the middle Archean to the late Cenozoic, were examined for biogenic magnetite (Table 1). Obsidian samples that were known to contain single-domain magnetite as their major remanence carrier were studied as a reference for examining the morphology of typically inorganically formed ultrafine-grained magnetite particles.

The rock magnetic techniques used in this study have been described elsewhere (Stolz et al., 1989a). Saturated isothermal remanent magnetization (SIRM) acquisition analysis and alternating field (AF) demagnetization (coercivity spectra) analysis were employed to determine the major magnetic phase in each sample. If magnetite was found as the main magnetic carrier, the revised Lowie–Fuller test (Johnson et al., 1975) was then performed to determine the size distribution of these particles. Only those samples that were shown by these methods to contain single-domain magnetite particles of the characteristic size underwent magnetic extraction.

The magnetic extraction procedure is basically the same as that used by Chang and Kirschvink (1985) for marine sediment. Two minor differences are that the chert samples were pulverized to a submicron-sized powder to separate the magnetic particles from the chert matrix and the limestone samples were treated with 5 N acetic acid (Chang et al., 1987) to dissolve carbonate phases before the general extraction procedure. For testing the effects of grinding on the geometry of ultra-fine-grained magnetite particles, magnetite particles (around 0.2 μm in size) were also ground and

TABLE 1

Occurrence of fossil bacterial magnetites

Locality	Age	Description	Extract	SQUID
Furnace Creek, CA (1)	Pliocene	Stromatolite	ND	H
Ocean sediment, Bahamas (2)	Pliocene	Carbonate sediments	Prismatic, euhedral, teardrop	SD
Potomida Clay, Crete (3)	Miocene	Marine sediments	Prismatic, hexagonal	SD
Deep-sea core, DSDP 522 (4)	Oligocene	Deep ocean sediments	Prismatic, euhedral	SD, MD
Deep-sea core, DSDP 523 (5)	Eocene	Deep ocean sediments	Prismatic, euhedral	SD, MD
Green River, WY (1)	Eocene	Limestone stromatolite	ND	SD, MD
Sinskian, Siberia, U.S.S.R. (6)	Cambrian	Black marine limestone	Cuboidal	SD
Beck Spring, CA (1)	>800 Ma	Stromatolic chert	Octahedral	SD, MD
Bittersprings, Australia (1)	850 Ma	Stromatolitic chert	Cuboidal, octahedral	SD, MD
Bittersprings, Australia (1)	850 Ma	Intercolumnar chert	ND	H
Skillogalee, Australia (7)	1000 Ma	Black chert	Octahedral	SD, MD
Dismal Lake, Canada (7)	1200 Ma	Black chert	Octahedral	SD, MD
Vempalle, India (7)	1400 Ma	Stromatolitic chert	Prismatic	SD
Gunflint, Canada (1)	2000 Ma	Stromatolitic chert	Cuboidal	SD, MD
Fortescue, Australia (7)	2800 Ma	Stromatolitic chert	ND	MD
Warrawoona, Australia (7)	3400 Ma	Stromatolitic chert	ND	MD

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ND = not determined; SD = single-domain magnetite; MD = multi-domain magnetite; H = hematite.

examined by TEM.

The final magnetite extracts were placed on carbon-coated grids and observed with a Phillips 201 transmission electron microscope at 80 kV. Several magnetite extracts were also examined on a JEOL JSM-840 high resolution scanning electron microscope. Electron diffraction on the transmission electron microscope (Towe, 1985) and energy dispersive X-ray analysis on the scanning electron micro-

scope were used to determine the phase and composition of the extracts.

Results and discussion

Cenozoic stromatolites

Two Cenozoic stromatolite samples were studied: one from the Pliocene Furnace Creek Formation, Death Valley, CA (Pitts, 1983) and the other from the Eocene Green River Formation, CO (Surdam and Wray, 1976). Both stromatolites are columnar, well laminated, composed of limestone and formed in lacustrine environments. No organic-walled microbial fossils have been observed in this material. Although single-domain biogenic magnetite has been detected in extant lacustrine stromatolites from several localities (Stolz, et al., 1989a), the rock magnetic studies of these samples did not reveal the presence of any single-domain magnetite.

The Furnace Creek sample is heavily leached and superficially stained by reddish iron oxides, probably hematite. Coercivity spectral analysis (Fig. 2a) suggest its remanence resides in some high coercivity phases, like hematite or goethite. In contrast, both the coercivity spectral analysis and the Lowrie–Fuller test (Fig. 2b) for the Green River sample show some very low coercivity phases (e.g., multi-domain magnetite or maghemite) as their major remanence carriers.

The mesoscopic and microscopic nature of the lamination of the Green River stromatolite is superficially similar to the microstructure found in many extant laminated stromatolites and microbial mats, such as those forming in the hypersaline marine environment of Hamelin Pool, Shark Bay, Western Australia (Surdam and Wray, 1976) and in Laguna Figueroa, Baja California, Mexico (Magulis et al., 1980). We have detected both magnetotactic bacteria and bacterial magnetite in microbial mat samples from the surface of these two extant stromatolite localities (Chang et al., 1987; Stolz et al., 1989a). Our study of the magnetic grain-size variations in laminated microbial sediments from Laguna Figueroa revealed the disappearance of single-domain magnetite crystals with depth, which we interpret as the result of iron reduction coupled with decay of organic matter (Stolz et al., 1989a). The same type of biologically induced chemical dissolution processes could have occurred in the Eocene Green River environment and account for the absence of single-domain magnetite from the sample. Early cementation/lithification of degrading microbial mat material, which may have not occurred with the Green River samples and does not occur at Laguna Figueroa, may be conducive for the preservation of biogenic magnetite.

Cenozoic marine sediments

In contrast to the Cenozoic lacustrine stromatolites, previous studies on Cenozoic and other ancient marine sediments have demonstrated a widespread distribution of fossil bacterial magnetite (Kirschvink and Chang, 1984; Chang and Kirschvink, 1985; Patterson et al., 1986). No Cenozoic marine stromatolites were available for comparison in this study. The discrepancy concerning the preservation of bacterial magnetite in different depositional environments led us to reassess our selection of material for analysis.

If the proposed mechanism for the disappearance of single-domain magnetite (iron reduction coupled with decay of organic matter) (Karlin and Levi, 1983, 1985; Stolz et al., 1986, 1989a) is correct, we should be able to see an inverse correlation between the abundance of bacterial magnetite preserved and the total organic carbon (TOC) content of the sediment. Johnson-Ibach (1982) has compiled analyses of TOC in numerous DSDP core samples and obtained a relationship between the TOC and sedimentation rate. Generally speaking, TOC decreases with increasing sedimentation rate because of the clastic dilution of the organic input. In the same study he also found that, at a

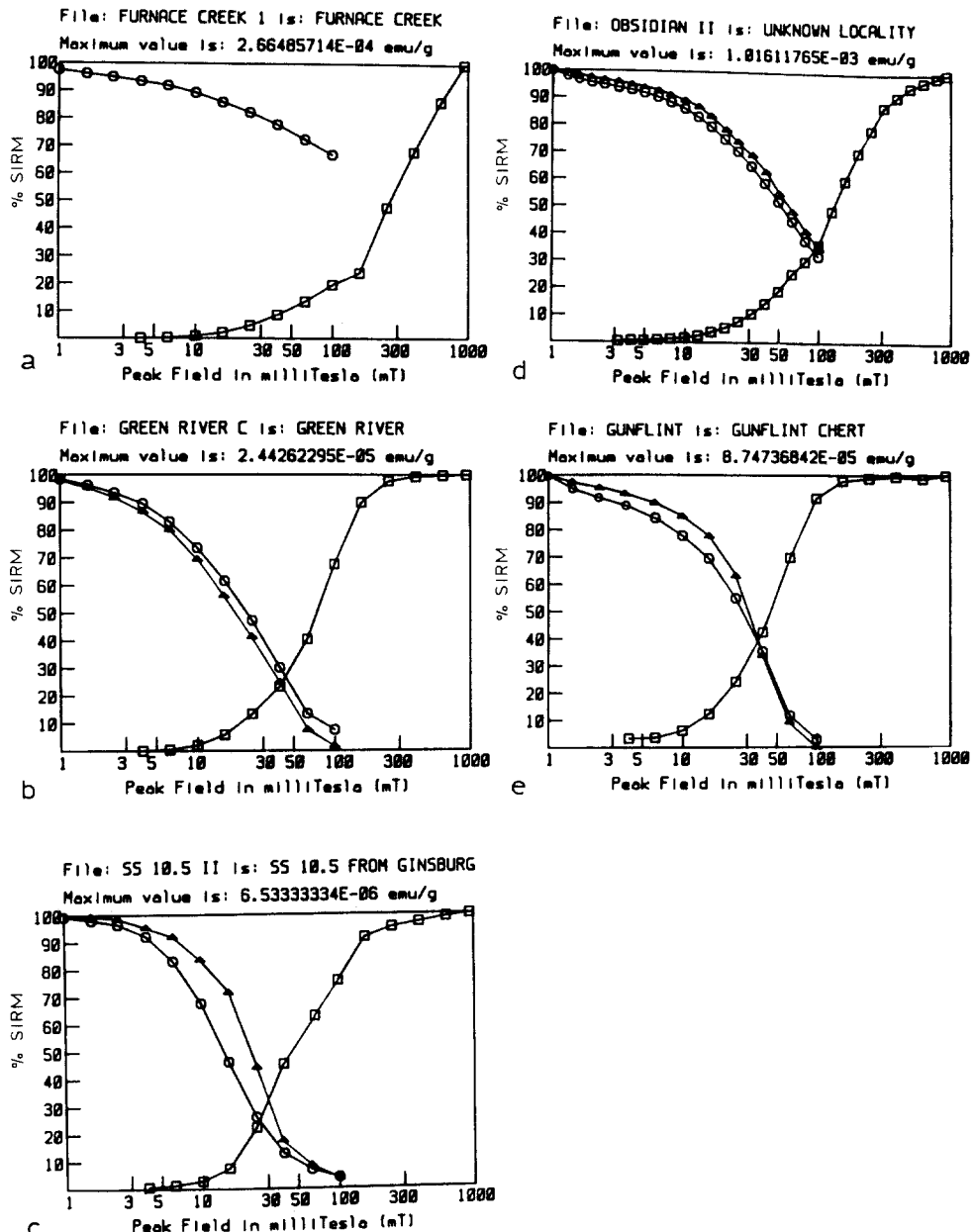

Fig. 2. Spectra with IRM (□), AF demagnetization of SIRM or IRM gained at 1000 G (○), and AF demagnetization of ARM (△). The intersection point of the IRM acquisition and the AF demagnetization of IRM curves generally represents the coercivity of a sample. Comparing the median destructive field (MDF) of the SIRM and the ARM (Lowrie-Fuller test) determines whether single-domain ($MDF_{ARM} > MDF_{IRM}$) or multi-domain ($MDF_{ARM} < MDF_{IRM}$) magnetite is the major remanence carrier (Johnson et al., 1975). (a) Limestone stromatolite from Pliocene Furnace Creek Formation, Death Valley, CA, (b) limestone stromatolite from Eocene Green River Formation, WY, (c) carbonate core from San Salvador Island, Bahama Islands, (d) obsidian sample from unknown locality, (e) stromatolitic chert from 2000 Ma Gunflint Formation which is representative for all six Proterozoic samples examined. 1 mT = 10 G.

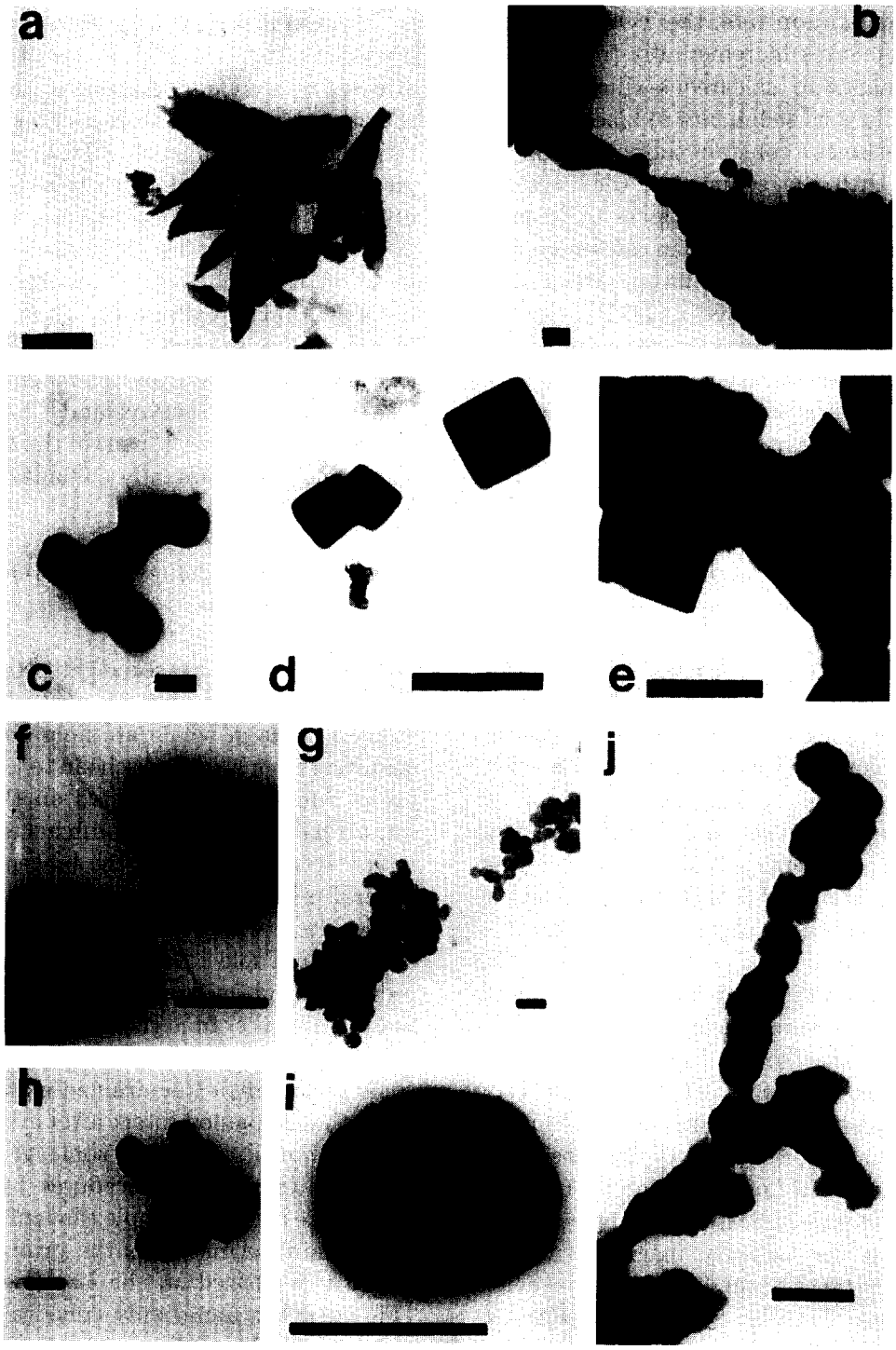

Fig. 3. Ultra-fine-grained magnetite from (a-c) ancient stromatolites and (f-g) cherts, (e) obsidian, and (d) after grinding. (a-b) Carbonate core from San Salvador Island, (c) Cambrian Sinskian Formation, Labaia Lena River, Siberia, (f) 1000 Ma Skillogalle Formation showing octahedral crystals that could be identified in all the Proterozoic samples, (g) 850 Ma Bitter Springs Formation chert, (h) 1400 Ma Vampelle stromatolitic chert, (i-j) Gunflint stromatolitic chert. Scale bars 100 nm, except (d-f) 500 nm.

given sedimentation rate, the TOC by weight per cent increases incrementally from calcareous sediments to calcareous–siliceous sediments to siliceous sediments to black shale. If one then assumes a constant supply of bacterial magnetite into the sediments, the bacterial magnetite particles should appear to be most abundant and best preserved in calcareous sediments with a high sedimentation rate. This is exactly what was observed in DSDP site 522 and other deep-sea core samples (Kirschvink and Chang, 1984). Similarly, bacterial magnetites are well preserved in the flood-derived sediments at Laguna Figueroa, an observation that can also be explained by the clastic dilution of organic material during the flood period (Stolz et al., 1989a).

Another potential complication in our study of Proterozoic stromatolites is the effect of the long term geological processes on the bacterial magnetite. Until now, reports of bacterial magnetite crystals have been restricted to clays and deep-sea soft sediments, with no definitive reports from consolidated sedimentary deposits. To test for possible effects of lithification on biogenic magnetite, we studied a set of marine carbonate core samples of Pliocene to Recent age from the island of San Salvador in the Bahamas that had been subjected to minimal diagenetic alteration (McNeill et al., 1987). We have previously detected both magnetotactic bacteria and bacterial magnetite in the surface sediments of the Florida Keys (Chang et al., 1987; Stolz et al., 1989a, 1989b), which has a similar depositional setting as the Bahama Banks (Ginsburg, 1964). A typical coercivity spectrum and ARM Lowrie–Fuller test (Fig. 2c) for these samples indicate that single-domain magnetite is the primary magnetic mineral present. Two types of single-domain magnetite particles were identified from the magnetic extracts; one that has a teardrop shape (Fig. 3a) and another that is cuboidal (Fig. 3b). Both of these types are commonly observed in magnetotactic organisms (e.g., Blakemore, 1982; Torres de Araujo et al., 1986), strongly suggesting a biogenic origin. The edges of the crystals are well defined and do not seem to have been affected by secondary diagenetic processes. On the other hand, single-domain magnetite crystals recovered from much older limestone samples of the Early Cambrian Sinskian Formation of the Siberian Platform (Chang et al., 1987) (Fig. 3c) show less distinct outlines. This degradation of morphology is probably due to partial oxidation and alteration of the crystal surface to maghemite and other iron oxides, which are then removed during the magnetic extraction process (Kirschvink and Chang, 1984). Nevertheless, the alignment of the crystals in a chain and their generally cuboidal shape still imply a bacterial origin.

Proterozoic stromatolites and microfossiliferous cherts

Table 1 lists data for eight representative stromatolitic chert samples which we have studied, some of which are microfossiliferous, spanning from Middle Archean to Late Proterozoic. Samples were selected on the basis of known paleontological significance and availability to us. Details on the biogeology and a general overview on the geology of each formation from which the samples were collected are also in Table 1. Each of the samples were reduced to sub-micrometer sized powders in a motor-driven ceramic grinder before subjecting them to magnetic extraction. Figure 3d shows some of the ultra-fine-grained magnetite particles that remained intact after grinding. As a control, we also applied some grinding and magnetic extraction procedures to a cryptocrystalline obsidian sample that contained single-domain magnetite as the primary remanence carrier based on the Lowrie–Fuller test (Fig. 2d). We found only euhedral single-domain magnetite with no evidence of abrasion due to the grinding. The shape of these inorganically formed magnetite particles is mostly octahedral (Fig. 3e), which is easily distinguished from that of bacterial magnetite.

Rock magnetic analyses of Archean Warrawoona Group and Fortescue Group samples show their remanence to reside mainly in a high coercivity phase (the former) or multi-domain magnetite particles (the latter). In contrast, rock magnetic analyses of Proterozoic samples have a mixture of multi-domain and single-domain magnetite as their major remanence carrier. In three of them (Skillogalee, Dismal Lake and Beck Spring) multi-domain and single-domain octahedral crystals are the dominant type observed in the magnetic extracts (Fig. 3f). Magnetic extracts of the Bitter Springs (Fig. 3g), Vampalle (Fig. 3h) and Gunflint (Fig. 3i,j) samples contain, in addition to octahedral crystals, prismatic and cuboidal single-domain magnetite crystals that resemble bacterial magnetite particles. Some multi-domain magnetite spheres, with a presumably diagenetic or authigenic origin, were found associated with the ultra-fine portion of magnetite extract. The paragenetic relationship between these spheres and the bacterial magnetite-like particles is difficult to determine.

Although we can not definitively prove a biogenic origin for these teardrop-shaped, prismatic and cuboidal single-domain magnetite crystals, the evidence for this is compelling. Modern analogs to the paleoenvironments we have studied in this paper indicate that magnetotactic bacteria commonly occur in these environments. Their magnetite is deposited and may be preserved in the sediments (Stolz et al., 1989a). The morphologies of the fossil magnetites (magnetofossils) extracted strongly resemble those seen in extant magnetotactic bacteria and are certainly distinguishable from single-domain magnetite particles isolated from abiogenic source rocks (e.g., obsidian). The identification of the crystals as magnetite was done using rock magnetic studies, followed by an extraction procedure that removed other iron oxides (e.g., maghemite), and by examination of the electron diffraction patterns from aggregates of crystals in the TEM preparations. The absence of titanium was also determined by energy dispersive X-ray analysis of the magnetite extract from the Gunflint (data not shown).

Implications

The ultra-fine-grained, single-domain magnetite identified in the Gunflint stromatolites is of biogenic origin based on the criteria of size, composition and environment of deposition. It represents the oldest evidence for matrix-mediated biomineralization. As for other implications, only certain speculations can be made from these results. These findings agree with a previously published report stating that the present level of the Earth's magnetic field strength appeared by 2000 Ma ago (Merill and McElhinny, 1983). The fossil bacterial magnetite in the Gunflint provides independent evidence that agrees with other evidence and conclusions that free oxygen had begun to accumulate in the environment before 2000 Ma ago (Walker et al., 1983). However, using bacterial magnetite as an indicator of paleooxygen level is somewhat tenuous because of the problems of localized oxygen production by cyanobacterial blooms and microbial mats. Whether the Gunflint bacterial magnetite reflects global atmospheric oxygen content that had reached 1 kPa is doubtful. In the future, sediments from well-mixed environments in which the magnetotactic bacteria are not associated with an oxygenic microbiota should be examined.

Conclusions

Fossil bacterial magnetite particles were identified from ancient carbonates and chert. Well-preserved magnetofossils were observed in consolidated carbonates from the Bahamas (Pleiocene) and the Sinskian Formation (Cambrian). Single-domain magnetite particles strongly resembling bacterial magnetite, but partially degraded, were seen in Proterozoic material from Gunflint, Vampelle and Bittersprings Formations. The occurrence of bac-

terial magnetite in the Gunflint implies that matrix-mediated biomineralization appeared at least as early as 2000 Ma ago, and supports the currently accepted hypotheses about the evolution of the Earth's magnetic field and Precambrian atmospheric oxygen concentration.

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