

polytypic, strictly monophyletic families are analysed, they find no evidence of a 26 Myr periodicity in extinction. They conclude that any periodicity evident in echinoderm and vertebrate families is an artefact of taxonomy and not a biological phenomenon.

At the core of Patterson and Smith's argument seems to be an assumption that taxonomic families are being treated as real evolutionary entities in the analyses of extinction patterns and that families can be subject to biological processes of extinction. This notion is mistaken. Extinction, as a dynamical process, operates at the population and (bio)species level. The higher taxa recognized by taxonomists become extinct only when all of their constituent species happen to be extinguished.

Throughout my analyses of taxonomic data, I have treated families as convenient proxies for species, either implicitly^{3,4} or explicitly⁵⁻¹¹. Each familial extinction, if properly dated, represents the extinction of one or more species; a collection of families therefore provides a sample of species extinctions, as Patterson and Smith note. The evidence that families provide a good sample of species extinctions is admittedly indirect but includes the observations that (1) empirical studies show that familial diversity correlates well with estimated species diversity over the Phanerozoic¹¹, indicating that the traditionally recognized families are capable of reflecting species-level evolutionary patterns; and (2) Monte Carlo simulations of phylogenies indicate that noncladistic taxa, with paraphyletic groups of highly variable size (including frequent monotypy), track patterns of diversity and extinction at the lineage level⁵⁻¹¹.

Families, however, are not the only sources of information on Phanerozoic extinction patterns. Although it is true that the initial evidence for periodicity rested upon stratigraphic ranges of marine families, subsequent analyses of other kinds of data have corroborated the preliminary results. Much larger data sets for marine genera^{4,9}, even after partial correction for Lagerstätten and monographic effects^{10,11}, exhibit patterns of extinction similar to the families over the Mesozoic and Cenozoic. The patterns include peaks of extinction in the upper Pliensbachian (and not in the Toarcian, containing the Posidonienschiefer), upper Tithonian (and not lower Tithonian, containing the Solnhofen), and Upper Eocene (and not Middle Eocene, containing the Monte Bolca fish beds); this indicates the data are reflecting more than mere variation in fossiliferousness of localities.

Even more importantly, most of the peaks in extinction in the familial (and the generic) data correspond to events initially recognized in detailed biostratigraphic studies, as I have repeatedly emphasized^{8,9,11,13}. Biostratigraphers are no fools, deluded by paraphyletic taxa and shifting facies. Their painstaking studies have revealed faunal discontinuities of varying magnitude in the Upper Permian, uppermost Triassic, Pliensbachian (actually lowermost Toarcian), Tithonian, Cenomanian, Maastrichtian, and Upper Eocene. These times form a periodic array with a 26 Myr spacing.

Why, then, do cladistically culled data for echinoderms and vertebrates fail to exhibit periodicity? A variety of explanations can be offered, ranging from taxonomic artefact as argued by Patterson and Smith, to an unrepresentative nature of echinoderms and vertebrates, to bias in cladistic classification. I believe the hypothesis of taxonomic artefact can be rejected quickly. Patterson and Smith's 'clade extinctions' at the top of their Fig. 1 (ref. 1) fail to show several well-documented species-level events, including the Cretaceous/Tertiary mass extinction, known since the mid-nineteenth century. This indicates something is awry with their data. It could very well be that echinoderms and vertebrates are not representative of the marine fossil record. Vertebrates have a notoriously incomplete and spotty fossil record, and the echinoderm record is hardly ideal, especially compared to the frequently fossilized molluscs. Thus, the familial record of the two groups may indeed primarily reflect fossilization noise.

But the Cretaceous/Tertiary event does seem to appear among paraphyletic taxa. (Remember that the dinosaurs, the symbol of the Cretaceous/Tertiary extinctions, constitute a paraphyletic group.) Thus, there may be a problem with cladistic classification in this context: cladistic culling may be biasing the data away from the underlying species patterns. Cladistic classification is based upon phylogenetic geometry. Thus, anything that alters the geometry may alter the classification as well. Extinction events, and especially mass extinctions, can alter phylogenetic geometries radically, and therefore cladistic classifications may become altered around these events. Polytypic, monophyletic clades thus may not approach unbiased samples of species and may no longer be useful for studying extinction time series, such as used to argue for periodicity. This suggestion should not be construed as a general criticism of cladistic taxonomy or phylogenetic systematics; cladistics is immensely valuable in many situations. It is simply an exposition of a possible limitation of the technique and a testable explanation for why Patterson and Smith failed to find periodicity, or even the well-known extinction events, in the culled sample of echinoderm and vertebrate families.

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Anaerobic production of magnetite by a dissimilatory iron-reducing microorganism

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The potential contribution of microbial metabolism to the magnetization of sediments has only recently been recognized. In the presence of oxygen, magnetotactic bacteria can form intracellular chains of magnetite while using oxygen or nitrate as the terminal electron acceptor for metabolism¹. The production of ultrafine-grained magnetite by magnetotactic bacteria in surficial aerobic sediments may contribute significantly to the natural remanent magnetism of sediments²⁻⁴. However, recent studies on iron reduction in anaerobic sediments suggested that bacteria can also generate magnetite in the absence of oxygen⁵. We report here on a sediment organism, designated GS-15, which produces copious quantities of ultrafine-grained magnetite under anaerobic conditions. GS-15 is not magnetotactic, but reduces amorphous ferric oxide to extracellular magnetite during the reduction of ferric iron as the terminal electron acceptor for organic matter oxidation. This novel metabolism may be the mechanism for the formation of ultrafine-grained magnetite in anaerobic sediments, and could

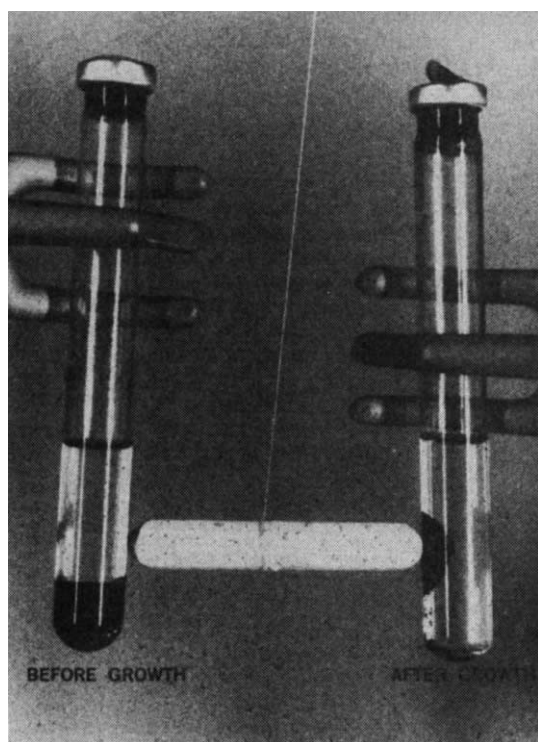


Fig. 1 Appearance of anaerobic culture medium prior to and after growth of GS-15. The brown amorphous ferric oxide at the bottom of the tube prior to growth was not attracted to the magnet. The metabolism of GS-15 resulted in the production of a large quantity of black magnetic precipitate.

account for the accumulation of magnetite in ancient iron formations and hydrocarbon deposits.

Although microbial reduction of ferric iron plays an important role in the iron geochemistry and organic matter mineralization of aquatic sediments, the pathways for organic matter metabolism and the organisms which carry out these reactions are only beginning to be identified⁵⁻⁷. Previously described bacteria which reduced ferric iron during anaerobic growth reduced iron as a minor reaction, with fermentation being the major mode of organic matter metabolism⁷. GS-15, which was isolated from sediments of the Potomac River, is the first organism known to effectively couple organic matter oxidation to ferric iron reduction during growth under anaerobic conditions. For each mole of acetate GS-15 oxidizes, two moles of carbon dioxide are produced and eight moles of ferric iron are reduced to ferrous iron. As iron serves as the terminal electron acceptor for metabolism, this reduction is termed dissimilatory iron reduction to distinguish it from the reduction of iron during microbial assimilation of intracellular iron. It was observed that dissimilatory iron reduction by GS-15 resulted in the formation of a highly magnetic black precipitate. A detailed characterization of this organism will be published separately. Here we present the analysis of the black precipitate and its implications.

The medium in which GS-15 is grown contains acetate as the sole electron donor, various major and minor minerals, and approximately 0.2 moles of ferric iron per litre in the form of amorphous ferric oxide. The amorphous ferric oxide is synthesized by neutralizing a ferric chloride solution, and has no distinct diffraction maxima detectable by powder X-ray diffraction analysis⁵. The medium contains less than 200 μ M sulphate and no reducing agents (for example, sulphide, thioglycolate, titanium). Oxygen is removed from the medium by degassing with nitrogen. Typically, the ferrous iron that is transferred with the inoculum provides an initial ferrous iron concentration in

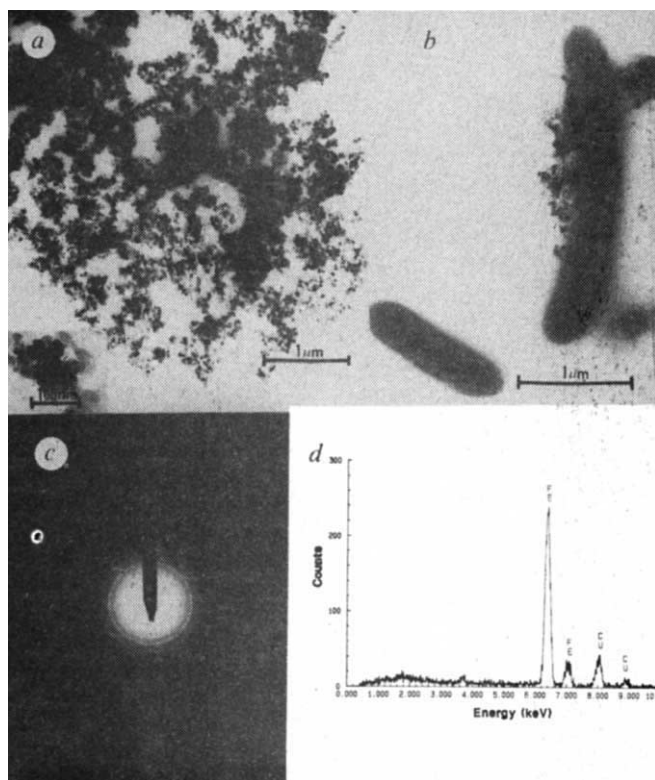


Fig. 2 Transmission electron micrographs of black precipitate and GS-15. An aggregate of the particles (*a*, bar 1 μ m) and cells of GS-15 with extracellular particles (*b*, bar 1 μ m) were observed with a JEOL 100CX operating at 80 kV. Micrographs of particles at higher magnification (inset of *a*, bar 100 nm), electron diffraction pattern (*c*) and X-ray energy dispersive analysis of the crystals (*d*) were obtained in a JEOL 200B operating at 200 kV. Copper peaks in (*d*) are from the grid.

the newly inoculated medium of 10 mM, which is more than enough to scavenge any residual oxygen.

During its growth GS-15 converted the non-magnetic brown amorphous ferric oxide to a black solid material which was strongly attracted to a magnet (Fig. 1). The black precipitate was not formed if the culture medium was not inoculated with GS-15, if the culture was incubated at temperatures too high for growth (for instance, 50 °C), or if the inoculated medium was sterilized prior to incubation. Furthermore, no black material was produced if ferrous iron (as ferrous chloride or ferrous ammonium sulphate) was added to uninoculated medium. These results indicated that the metabolism of GS-15 was necessary for formation of the black precipitate.

Examination of the black precipitate with transmission electron microscopy (TEM) revealed aggregates of small crystals ranging in size from 10 to 50 nm (Fig. 2*a*). The crystals were clearly external to the cells and were not aligned in chains (Fig. 2*b*). Further evidence for the lack of intracellular magnetite was the observation that, unlike magnetotactic bacteria, in wet mounts, GS-15 did not orient in response to an applied magnetic field. A selected area electron diffraction pattern taken from an aggregate of the crystals gave a diffuse ring pattern and a few single crystal diffraction spots (Fig. 2*c*). The lines 220, 311, 400, 422, 440, and 551 were identified by spacing and relative intensity. This diffraction pattern is characteristic of magnetite⁸. The black precipitate was not dissolved by a sodium dithionite-citrate solution which dissolves hematite, maghemite, goethite, and pyrrhotite, but not magnetite⁹. X-ray energy dispersive analysis of the crystals in the TEM detected only iron in the crystal aggregates (Fig. 2*d*).

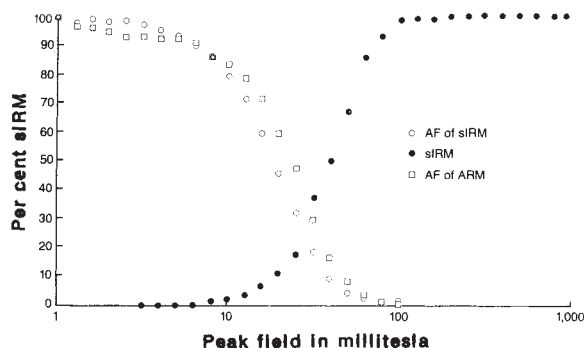


Fig. 3 Coercivity spectrum (sIRM, closed circles; AF of sIRM, open circles) and AF of ARM (squares) data for the black precipitate.

The magnetic properties of the black precipitate were determined using a SQUID magnetometer¹⁰. Anhysteretic remanent magnetization (ARM) in a biasing field of 2.5 G with subsequent alternating field demagnetization (AF) was followed by saturation isothermal remanent magnetization (sIRM) and AF demagnetization. The coercivity spectrum generated (Fig. 3) is indicative of a ferromagnetic mineral like magnetite and is similar to the coercivity spectra observed in marine sediments that contain ultrafine-grained magnetite^{2,3}. A Lowrie-Fuller test was performed by comparing the values for the median destructive field (MDF, peak field at 50% sIRM) of the AF of sIRM and AF of ARM. The MDF_{ARM} was greater than MDF_{sIRM} which suggests that the particles are magnetically single domain^{11,12}.

These results demonstrate that nonmagnetotactic bacteria can produce large quantities of ultrafine-grained magnetite under anaerobic conditions by coupling the oxidation of organic matter to the reduction of ferric iron. This has several important implications to iron geochemistry and interpretation of the sedimentary magnetic record.

Ultrafine-grained magnetite is an important carrier of remanent magnetism in sediments¹³. The recovery of magnetite crystals with morphologies characteristic of the magnetite of magnetotactic bacteria has demonstrated that magnetite production by magnetotactic bacteria contributes to the magnetization of sediments^{2-4,9,14}. However, there is substantial evidence that not all of the ultrafine-grained magnetite that is produced in sediments originates from magnetotactic bacteria. In a detailed study of the morphology of sedimentary magnetite, Chang and Kirschvink found that much of the ultrafine-grained magnetite could not be unequivocally attributed to magnetotactic bacteria and suggested that the magnetite was authigenic⁹. Karlin and co-workers have recently reported data which suggests the authigenic formation of ultrafine-grained magnetite in anaerobic sediments within the zone of iron reduction¹⁵. Although magnetotactic bacteria were considered to be the probable source, this is unlikely because they require oxygen for growth and magnetite synthesis¹. However, the data is consistent with the formation of magnetite by dissimilatory iron-reducing bacteria, such as GS-15. Further studies to ascertain the relative contributions of magnetotactic bacteria and dissimilatory iron-reducing bacteria to the magnetization of sediments are warranted.

Carbon isotope data suggests that the formation of magnetite in ancient iron formations resulted from the oxidation of organic matter coupled to the reduction of ferric oxide to magnetite^{16,17}. We propose that dissimilatory iron-reducing bacteria, similar to GS-15, were the catalysts for this reaction. Once formed, the magnetite could have persisted in the absence of significant subsequent sulphide production, because it is resistant to further microbial reduction⁵. Magnetotactic bacteria have also been proposed as a source of magnetite in these iron formations¹⁸. However, ferric iron was probably precipitated first and then

reduced under anaerobic conditions^{17,19}. This view is in accordance with metabolism of dissimilatory iron-reducing organisms but not magnetotactic bacteria. It has also been suggested that the magnetite associated with hydrocarbon deposits results from the microbial degradation of hydrocarbons²⁰. Although no bacteria have been identified yet, the finding that dissimilatory iron-reducing bacteria can produce magnetite during organic matter metabolism makes this proposed mechanism more plausible. From these considerations, it is apparent that magnetite formation by dissimilatory iron-reducing bacteria is likely to have an important influence on the geochemistry of sedimentary environments.

We thank E. Landa, D. Webster, C. Lawson, S.-R. Chang, J. Kirschvink, S. Goodwin, P. Toth, and S. Haggarty for their assistance and helpful discussions.

Received 10 July; accepted 1 October 1987.

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Experimentally induced alteration in the polarity of developing neurons

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Despite the great diversity of shapes exhibited by different classes of nerve cells, nearly all neurons share one feature in that they have a single axon and several dendrites. The two types of processes differ in their morphology, in their rate of growth, in the macromolecular composition of their cytoskeletons and surface membranes, and in their synaptic polarity^{1,2}. When hippocampal neurons are dissociated from the embryonic brain and cultured, they reproducibly establish this basic form with a single axon and several dendrites, despite the absence of any spatially organized environmental cues, and without the need for cell to cell contact³⁻⁷. We have cut the axons of young hippocampal neurons within a day of their development: in some cases the initial axon regenerated, but more frequently one of the other processes, which if undisturbed would have become a dendrite, instead became the axon. Frequently the stump of the original axon persisted following the transection and subsequently became a dendrite. Evidently the neuronal processes that first develop in culture have the capacity to form either axons or dendrites. The acquisition of axonal characteristics by one neuronal process apparently inhibits the others from becoming axons, so they subsequently become dendrites.

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