Big discovery for biogenic magnetite

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One of the most significant characteristics of the Anthropocene (the present age of geologic time) is the rate at which humans are perturbing the global carbon cycle. The potency of carbon dioxide and methane as greenhouse gases and their effects on Earth's temperature balance is well established (1), and the myriad of climate and ecological changes and feedbacks in response to this abrupt warming is the focus of much ongoing research (1, 2). The geologic record is one of our greatest assets in understanding the short- and long-term environmental responses to extreme fluctuations in the carbon cycle, and the Paleocene–Eocene Thermal Maximum (PETM), which occurred ≈55 million years ago, is an ideal analogue for the Anthropocene. The PETM is marked by an abrupt negative carbon isotope excursion that indicates a massive injection of light carbon into the oceans and atmosphere over a period of a few thousand years. This perturbation to the carbon cycle resulted in super-greenhouse conditions that persisted for as long as 180,000 years. Mean annual temperatures and deep and surface ocean temperatures at all latitudes rose by 5–8°C (3). Terrestrial plants and mammals diversified and radiated, and new marine microorganisms evolved and flourished while others disappeared forever. In this issue of PNAS, Schumann *et al.* (4) report evidence for new microorganisms that appeared and disappeared with the PETM, signaling another specific ecological response to the biogeochemical changes associated with this extreme warming event.

Using high-resolution transmission electron microscopy and nanometer-scale chemical analyses, Schumann *et al.* (4) found exceptionally well-preserved, uniquely-shaped stoichiometric magnetite (Fe_3O_4) particles in PETM-age marine sediments from a drill core from New Jersey. The elongate prism and spearhead morphologies are unlike any magnetite crystals previously reported and are inconsistent with a hydrothermal, volcanogenic, or diagenetic origin. Instead, the crystal morphologies are most consistent with a biogenic origin.

In addition to the discovery of large and unique forms of biogenic magnetite, Schumann *et al.* (4) present the first application of fossilized biogenic magnetite (magnetofossils) as a paleothermometer. Previous studies demonstrated the temperature-dependent fractionation of oxygen isotopes between cultured biogenic magnetite crystals and the water from which those crystals precipitated (5). Using nanometer-scale secondary ion mass spectroscopy (NanoSIMS), Schumann *et al.* (4) measured oxygen isotope compositions in magnetofossils that are consistent with independent paleotemperature estimates of marine waters during the PETM (6). Although the utility of the NanoSIMS results presented here is compromised by their low precision, they lead the way in the development and application of this underutilized marine paleothermometer and bolster the evidence for abundant and unique biogenic magnetite in PETM-age sediments.

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The discovery of magnetofossils in PETM-age marine sediments is not new, however. Two independent studies (7, 8) recently demonstrated that the unusual abundance of ≈30- to 120-nm-sized magnetite (Fe_3O_4) particles in PETM-age sediments from several drill cores from New Jersey (9) was produced by magnetotactic bacteria. Rock magnetic data from similar studies on marine sediments from New Zealand (10) and Egypt* are consistent with the occurrence of magnetofossils at these locales as well. What is remarkable about the findings of Schumann *et al.* (4) is the size and morphology of the magnetofossils, which are unlike any previously reported.

Most magnetofossils are produced by various species of magnetotactic bacteria that biomineralize cubic, cubo-octahedral, or bullet-shaped magnetite or greigite (Fe_2S_4) crystals called magnetosomes (11, 12). Magnetosomes are typically arranged in elongate chains within the cell to orient the organism along magnetic field lines to aid the organism's search for nutrients and might even be used as an intracellular energy or iron supply (12). Although these chains can reach several hundred nanometers in length, individual particles rarely exceed a few hundred nanometers and most are less than 120 nm. In contrast, individual magnetite particles discovered by Schumann *et al.* (4) range from 1 to 4 micrometers in length. These dimensions are similar to or exceed the cellular size of most common aquatic bacteria, leading the authors to suggest these large crystals were produced by eukaryotes. Exceptionally large prokaryotes (cellular diameters up to 750 μm) replete with sulfur or calcite inclusions are common in some high-productivity shelf sediments (13, 14), however, suggesting that these new forms of magnetofossils may be unique environmental adaptations of prokaryotes and not necessarily eukaryotes. Thus, a key question is what function did these magnetofossils serve? Are they skeletal elements or part of a defensive carapace (4), or are they analogous to sulfur inclusions in giant sulfur-reducing bacteria (13) and function as batteries for the organism's iron-based metabolism? Although their function remains enigmatic, the environmental implications of these abundant and unique magnetofossils are nonetheless significant.

Magnetotactic bacteria commonly live in the oxic–anoxic transition zone of fresh, brackish, and marine aquatic environments where dissolved oxygen and sulfide are low and bioavailable iron is high [see review by Kopp and Kirschvink (12)]. These environments include suboxic sediments and seasonally-stratified euxinic estuaries and freshwater lakes. The co-occurrence of these newly discovered magnetofossils with abundant conventional magnetofossils suggests the organisms that synthesized them share a similar ecological niche. Most magnetofossils are removed from the geologic record by reductive dissolution with burial under steady-state redox conditions. Increased sedimentation rates or nutrient supply and productivity, however, lead to nonsteady redox conditions and suboxic sediments at a depth that fosters magnetite preservation. Thus, the restrictive ecological niche

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occupied by magnetotactic bacteria as well as their preservation as magnetofossils makes them useful biomarkers for environmental change.

But what does this mean for the PETM specifically, and for rapid global warming events in general? The PETM-age sediments from the New Jersey cores were deposited in subtropical near-shore waters on the shallow continental shelf (15). Moreover, a proximal deltaic system could deliver nutrient-rich sediment from the North American continent onto the shelf (15). The rapid warming associated with the onset of the PETM caused significant changes in the hydrologic cycle, with a shift toward stronger seasonality during the PETM. These changes would have been pronounced in the subtropical evaporative belts (e.g., see refs. 6, 16, and 17) where the New Jersey sediments were deposited (7) and are consistent with records of enhanced continental weathering and episodic sediment flux to the coastal oceans (e.g., refs. 17 and 18). Thus, strong seasonality would have established highly-stressed environments on the continental shelves in which short episodes of high nutrient availability punctuated longer, nutrient-lean periods. These variable environmental conditions would favor the diversification and proliferation of robust organisms adapted to exploit and tolerate periods of high and low nutrient availability, such as the dinoflagellate *Apectodinium* (e.g., ref. 19) or even an iron-metabolizing equivalent to the giant sulfur bacterium *Thiomargarita* (13).

The New Jersey magnetofossil record (4, 7, 8) clearly indicates high bioavailability of iron on the Atlantic coastal plain during the PETM. High magnetofossil abundance and diversity are coincident with increased kaolinite deposition (20), abundant high-productivity nannoplankton (21) and dinoflagellate (19) assemblages, and increased accumulation rates of organic and inorganic carbon (18) on the New Jersey shelf. These observations indicate significant changes in biogeochemical cycling, and by extension productivity, on the continental shelf.

What remains unresolved at this point is the extent to which biologic productivity increased and possibly functioned to sequester carbon on the continental shelves. Did shallow continental marine waters and sediments remain suboxic or did they episodically become euxinic? Schumann *et al.* (4) provide a compelling argument in favor of suboxic conditions, but additional geochemical studies that establish the organic carbon content, sedimentary redox conditions, and paleoproductivity of the magnetofossil-bearing sediments may be necessary to fully evaluate the environmental conditions on the North American continental shelf during the PETM.

Furthermore, are the environmental conditions that spurred the magnetotactic bacteria bloom and the diversification of iron biomineralizing organisms specific to the New Jersey continental margin or the subtropics in general, or are they globally extensive? Rock magnetic and microscopy results from the few PETM sections that have been investigated for the occurrence of biogenic magnetite (7, 8, 10, *, †) suggest the magnetofossil spike may be global, although limited to the shallow continental shelves and most pronounced along the eastern North American continental margin. With the discovery of anomalously large and unique magnetofossils, Schumann *et al.* (4) emphasize not only the sensitivity of continental shelf ecological communities to abrupt warming, but also that the evidence for such drastic changes is considerably larger than we expected.

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