## Anaerobes pumping iron

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SEVERAL microorganisms, including the bacteria Leptethrix, Sidorocapca and T. ferroxidans1, use ferrous iron as an electron (energy) source, oxidizing it to ferric iron while respiring O<sub>2</sub>. Some bacteria can use ferric iron at the other end of the electron-transport chain as the terminal electron acceptor. But there have been no indications that the latter is an important process in vivo. Now, Lovley and coworkers, on page 252 of this issue<sup>2</sup>, report the isolation and growth of a bacterium from anaerobic mud in the Potomac River basin that oxidizes organic acids to CO, while reducing hydrous ferric oxide to magnetite, Fe<sub>3</sub>O<sub>4</sub>. This finding has geochemical, evolutionary and palaeomagnetic implications.

The organism described by Lovley et al., cryptically designated GS-15, reduces 8 moles of ferric iron per mole of acetate consumed. The ferric iron in the culture medium is present as an amorphous hydrous iron-oxide precipitate resulting from the hydrolysis of ferric chloride. The production of Fe<sub>3</sub>O<sub>4</sub> presumably occurs extracellularly after the export of ferrous ions into the medium, where they subsequently interact with unreduced hydrous ferric oxide. Fe<sub>3</sub>O<sub>4</sub> is composed of two ferric and one ferrous iron per formula unit, and apparently cannot be further

reduced by the organism. Hence, only one-third of the ferric iron in the medium is available for respiration. Fe<sub>3</sub>O<sub>4</sub> production is nevertheless copious, potentially reaching 1 kilogram per 10 grams of biomass! By comparison, magnetotactic bacteria that use nitrate or oxygen as electron acceptors produce about 0.2 grams Fe<sub>3</sub>O<sub>4</sub> per 10 grams of biomass<sup>3</sup>. Of course, actual Fe<sub>3</sub>O<sub>4</sub> production by GS-15 in vivo could vary depending on the concentrations of anions such as carbonate, phosphate or sulphide that compete for ferrous ions. Whether the exported ferrous ions are incorporated into Fe<sub>2</sub>O<sub>4</sub> or into other iron minerals, it is clear that GS-15 and its relations can have a significant impact on the chemistry of iron in anaerobic sediments. Moreover, because the Fe<sub>2</sub>O<sub>4</sub> particles are in the singlemagnetic-domain size range, they can have a large effect on the palaeomagnetic intensity of those sediments. Karlin et al. recently reported4 magnetic evidence for Fe<sub>3</sub>O<sub>4</sub> production in suboxic marine sediments, and attributed it to iron reduction by microorganisms. Lovley et al. now point out2 that ancestors of GS-15 could have played a major role in the formation of Fe<sub>3</sub>O<sub>4</sub> in the banded-iron deposits during the Precambrian.

To investigate the chemistry of this

process, Tamaura et al.5 and Mann<sup>6</sup> have produced Fe<sub>3</sub>O<sub>4</sub> in vitro by adding ferrous ions to hydrous ferric-oxide precipitates. The process is thought to involve a solution reprecipitation sequence that begins with the binding of the ferrous ions on the surface of the iron-oxide particles. On the other hand, Lovley et al. did not obtain Fe<sub>3</sub>O<sub>4</sub> when they added ferrous ions to their uninoculated medium. This may result from inhibition by acetate or something else, either by chelating the ferrous ions or preventing binding to the surface of the oxide. In viable cultures, acetate would be consumed; that and other changes, such as in pH, could allow the process to proceed. Amorphous hydrous ferric oxide and ferrous ions are known to be precursors to intracellular Fe<sub>3</sub>O<sub>4</sub> formation in the bacterium A. magnetotacticum<sup>7</sup>.

Lowenstam has distinguished8 between biologically induced mineralization (BIM) and matrix-mediated, or boundaryorganized, biomineralization (BOB)6. In BIM, cellular export of metabolic products leads to extracellular mineral formation with materials in the environment. In BOB, the mineral phases are deposited in preformed organic matrices produced by the organism. Thus, Fe<sub>3</sub>O<sub>4</sub> production by GS-15 and A. magnetotacticum is biologically induced and matrix-mediated, respectively. In the former, Fe<sub>3</sub>O<sub>4</sub> particles have a broad size distribution and do not seem to be associated with an organic matrix, whereas in the latter the particles have a narrow size distribution, definite morphologies and are enveloped by a membrane9. Even in the BIM process the dimension of the particles is less than 50 nanometres.

In magnetotactic bacteria, Fe<sub>3</sub>O<sub>4</sub> serves as an aid to magnetic orientation and navigation, helping the motile cells to find and remain in the preferred microaerophilic zone<sup>10</sup>. For GS-15, Fe<sub>3</sub>O<sub>4</sub> could just be a metabolic by-product and have no other biological significance. But these non-motile cells seem to grow in intimate contact with the precipitates in the culture vessel and not in the water column above, which is sensible considering the very low solubility of hydrous ferric oxides and the very high iron requirement of the organism. Fe<sub>3</sub>O<sub>4</sub> has a density of 5 and in vivo could serve as an anchor for the cells in the habitat where their physiology gives them an advantage over other bacteria.

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