the authors assembled two nearly complete genomes and two partial genomes of the predominant symbionts. Gene function in the symbionts was inferred by identifying closely related genes in other well-characterized bacteria. With this information in hand, Dubilier and colleagues began to unravel the metabolic interactions that form this multispecies symbiosis.

The four characterized bacterial species seem to form a versatile system for supplying the host with organic carbon, amino acids and vitamins, and for eliminating nitrogenous waste. The authors identified bacterial genes that encode proteins that take up the nitrogen-containing compounds urea and ammonia, thus allowing the worm to conserve nitrogen rather than excreting these toxic waste products, and so possibly explaining the lack of excretory organs in the host.

Co-dependent interactions between the sulphide-oxidizing symbionts seem to be complex. All four symbionts can convert CO_2 into organic carbon, a process for which three distinct pathways exist, and the sulphate-reducing bacteria can also feed the host by taking up dissolved organic compounds from the environment. Together, the symbionts provide the worm with the enzymatic machinery to exploit various organic and inorganic energy sources, and to respire using molecules other than oxygen, such as sulphates, nitrates and fumarate.

The authors propose[3] that sulphide produced by the sulphate-reducing bacteria acts as an energy source for the sulphide-oxidizing bacteria, so creating an internal sulphur cycle that sustains both symbionts and also nourishes the worm. However, the compounds needed to drive this cycle may not all coexist in the same environment, as the preferred oxidants (oxygen or nitrate) for sulphide are found in surface sediments, whereas sulphate respiration is an anaerobic process that is only possible in deeper sediments that lack oxygen. It seems that the worm assists the bacteria by supplying another oxidant: the genomes show that the sulphide-oxidizing symbionts can respire using trimethylamine *N*-oxide (TMAO), a compound produced by the worm. This allows the bacteria to grow in the absence of oxygen or nitrate.

Furthermore, the host can move between the surface sediments and the deeper regions, so that an understanding of how the bacteria generate energy must also consider the worm's behaviour. One of the sulphide-oxidizing bacteria might partially oxidize sulphide using TMAO and store the resulting sulphur in globules for later use. When the worm migrates to the surface, this stored sulphur could then be fully oxidized to sulphate, and so the cycle continues. The sulphate-reducing bacteria, in turn, possess genes that enable them to grow in deep, oxygen-starved sediments by using molecular hydrogen to reduce sulphate and provide the host with carbon.

But the story remains incomplete. It is unclear why several species of sulphur-cycling bacteria are required, or what features of their co-dependent interactions sustain them. It also remains to be seen how the host fits into this web of interactions — for example, can the symbionts modify the worm's behaviour to direct it to different depths of the sediments? And what is the role of the fifth microbial partner in this complex symbiosis, the spirochaete bacterium? Studies of these 'lowly' worms should improve our understanding of many complex symbioses, including those found in the human body. ■

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GEOPHYSICS

Protons lead the charge

Greg Hirth

Is the anomalously high electrical conductivity seen in part of Earth's mantle caused by protons derived from hydrous defects in the mineral olivine? Two groups investigate this possibility — and draw different conclusions.

Many lines of evidence indicate that Earth's dynamic processes are controlled by water — more specifically, by the hydrogen ions (protons) present in minerals in its interior. What has been lacking is a reliable way to determine the concentration and distribution of this hydrogen. Theoretical considerations indicate that the magnitude of a mineral's electrical conductivity puts a constraint on its hydrogen content. In this issue, studies by Yoshino *et al.* (page 973)[1] and Wang *et al.* (page 977)[2] demonstrate that small amounts of hydrogen increase the electrical conductivity of olivine — a silicate that is the most abundant mineral in Earth's upper mantle — by between 100 and 1,000 times. These experimental results provide an initial verification of a process that has been proposed to explain high electrical conductivity in the upper mantle — but also supply several caveats.

Geoscientists have speculated that the apparently unique features of plate tectonics on Earth — the phenomenon does not seem to occur on any other Solar System body — are controlled by the presence of water. This hypothesis stems from the existence of oceans, the identification of tectonic processes that cycle volatile substances into and out of the mantle, and an appreciation of the influence of water on diffusion within the mantle, and on mantle viscosity and melting. For example, the melting temperature of mantle rocks decreases by some 700 °C in the presence of water[3]. Furthermore, although the interior of the convecting Earth is too hot for hydrous mineral phases, such as micas, to be stable, small concentrations (around 50 parts per million by weight) of hydrogen in olivine result in as much as a 30–100-fold reduction in viscosity[4]. At least another ocean's worth of water resides in Earth's interior[5], and such observations have stimulated studies on exactly how much water there is, and its role in the formation of tectonic plates and in the thermal evolution of Earth 4.5 billion years ago[6].

A technique known as magnetotellurics is used to study Earth's electrical conductivity by measuring its response to interactions between the solar wind and the ionosphere, the layer of Earth's atmosphere that is ionized by solar radiation. Specifically, electrical conductivity is determined as a function of depth by measuring variations in the magnetic and electric fields at Earth's surface over periods of months to years.

The electrical conductivity measured for some parts of the upper mantle using magnetotellurics is significantly greater than that of the minerals actually present in the mantle. In 1990, Shun-ichiro Karato proposed an explanation[7] for this apparent discrepancy based on experiments by Mackwell and Kohlstedt on the diffusion of hydrogen ions in olivine[8]. These experiments demonstrated two remarkable features. First, protons are extremely mobile in olivine — almost as mobile as electron holes (a hole is the absence of an electron, and changes ferrous iron to ferric iron, for example). Second, the diffusion rate of protons is exceptionally anisotropic, with the rate parallel to the shortest crystallographic axis (known as the *a* axis) being 50 to 100 times greater than that in other directions.

Karato's insight came from application of the

DEVELOPMENTAL BIOLOGY

Red-eye redirected

In most mammals, the cornea — the transparent part of the eye over the lens — has no blood vessels. This trait is obviously essential for optimal vision, but it also means the cornea is a useful experimental system for studying the factors that promote or inhibit the formation of blood vessels (angiogenesis). But why the cornea remains avascular despite the presence of the potent angiogenic factor VEGF-A and the proximity of other highly vascular tissues has remained unclear.

In this issue, B. K. Ambati *et al.* (*Nature* **443,** 993–997; 2006) show that in the cornea a soluble receptor, called sflt-1, traps VEGF-A, stopping it from directing the formation of blood vessels. When the authors blocked expression of sflt-1 using a variety of approaches, they saw an increase in free VEGF-A and in corneal vascularization, demonstrating that sflt-1 maintains corneal avascularity.

Blood vessels form spontaneously in the corneas of certain mutant mouse strains, as well as in those of people who suffer from a condition known as aniridia as a result of a similar mutation. Ambati and colleagues show that in all these cases, corneal vascularization is accompanied by a deficiency in the expression of sflt-1. In the mice, injections of sflt-1 reduced the corneal vascularization.

The authors surveyed different mammalian species to see whether the close relationship between the presence of sflt-1 and an avascular cornea is evolutionarily conserved. Manatees (pictured) are the only known organism with uniformly vascularized corneas. They compensate for their impaired vision with highly developed sensory bristles that enable them to navigate and locate food. Manatees live primarily in turbid freshwater areas, and corneal vascularization may result from or protect against this environment. Interestingly, no sflt-1 expression was detected in manatee corneas, whereas those of dugongs (which belong to the order Sirenia, like manatees) and of elephants — the manatee's closest terrestrial relatives — all produced sflt-1.

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Barbara Marte

Nernst–Einstein relation, which shows how electrical conductivity changes with the diffusion rate and concentration of charged species. Intriguingly, the *a* axis of olivine (the direction of potentially high conductivity) aligns parallel to the flow during viscous creep in the mantle. Because olivine deforms more easily along some crystallographic axes than along others, the alignment of olivine crystals can be observed using various seismic techniques. In regions of the oceanic mantle for which seismic and geochemical measurements have provided independent constraints on the alignment of olivine and on the water content, the Nernst–Einstein relation provides a good fit to both the magnitude and anisotropy of electrical conductivity. It also explains rapid changes in conductivity that occur in regions where water content is predicted to decrease[9]. Yet despite the apparent success of this approach, the idea that water affects conductivity met with scepticism owing to the lack of experimental verification.

Yoshino *et al.*[1] and Wang *et al.*[2] both report a huge increase in the conductivity of olivine with increased hydrogen content. But important differences in the results lead the authors to varying conclusions. Yoshino and colleagues' measurements[1], which were conducted on olivine single crystals, show an anisotropy of conductivity similar to that predicted by the hydrogen diffusion measurements. But the measured temperature dependence of conductivity for crystals oriented parallel to the *a* axis is significantly smaller than that of other directions. Thus, at face value the extrapolation of these data to conditions inside Earth (from the maximum experimental temperature of 723 °C to around 1,400 °C) indicates that the hydrogen effect is too small to explain the high conductivity of the mantle. The experiments were conducted at low temperatures to inhibit hydrogen loss from the sample by diffusion.

Wang and colleagues' experiments[2] were conducted on aggregates of fine-grained olivine at higher temperatures, and show a somewhat greater effect of hydrogen on conductivity, as well as a slightly greater temperature dependence. Extrapolating their data to mantle conditions provides excellent agreement with the observed conductivity. Based on these initial experiments, the influence of hydrogen concentration on conductivity is lower than that predicted by Karato's original hypothesis[7], although Wang *et al.* note[2] that the limited range of hydrogen content in their samples prevents a determination of the precise extent of this difference. Thus, these authors argue that only a fraction of dissolved hydrogen contributes to the conductivity during experiments — a conclusion drawn from similar measurements on wadsleyite, which is a form of olivine found at high pressures[10].

More work is required to resolve the differences between these studies. Variables such as grain size, other mantle mineral phases, aggregate anisotropy and the presence of small amounts of hydrous melt all need to be explored. But it is promising to note how well Karato's application of the Nernst–Einstein relation agrees with Wang and colleagues' data over the temperature range of the hydrogen diffusion experiments (800–1,000 °C; Fig. 2a on page 978). This agreement is even stronger if new constraints on the solubility of hydrogen in olivine are taken into account[11]: the technique that both Yoshino *et al.* and Wang *et al.* used to measure hydrogen content may underestimate the hydrogen concentration by a factor of three (meaning that the dashed lines in Wang and colleagues' Figure 2a are plotted a factor of three too low).

The discrepancy between the Nernst–Einstein relation and the data at lower temperature might then be explained by a fundamental difference between the conductivity and diffusion studies, as Wang and colleagues note in the supplementary information to their paper. During diffusion experiments, which measure the rate of hydration of olivine, hydrogen defects must first be created and then migrate. Activation energy must be supplied for both these processes. In the conductivity experiments, by contrast, the samples are 'doped' with hydrogen before the experiment, and activation energy is required only to get the hydrogen moving. As a result, the temperature dependence of the conductivity experiments is lower than that of the diffusion experiments. ■

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Correction

In the News & Views article "Greenland's ice on the scales" by Tavi Murray (*Nature* **443,** 277–278; 2006), the figures given in mass units for Greenland's ice loss are 1,000 times too small. The correct statement is that the Greenland ice sheet lost between 192 billion and 258 billion — not million — tonnes each year between April 2002 and April 2006. The equivalent volume figures given in the article — 212–284 km^3 — are correct. Our thanks to Mary Whitfield and her students at the Edmonds Community College, Lynnwood, Washington state, for pointing this error out.