altered to some degree. A first reading of the genome reveals, not unexpectedly, that some of the genes have been modified from ancient precursors. For example, a cluster descended from a single progenitor gene that encoded a member of the yellow protein family here prescribes the royal jelly used in caste determination and queen production. Others, including those that programme chemoreception and food management, seem to include innovations that have evolved since the bee lineage split from that of other insects.

This DNA sequence is a major step towards answering a basic question of social evolution: at the genomic level, what does it take to engineer an advanced colonial insect? As this work is extended, it will soon come to address a second, equally important question: what does it take to make a eusocial insect species in the first place? (In eusocial colonies, members comprise overlapping generations that are divided into reproductive and worker castes to care for the young.) Fortunately, a large fund of information can be gathered to settle this issue, because among the 16,000 or so living bee species known, some are solitary but close to the threshold of eusociality, others have barely made it across the threshold, a few have reverted back to the solitary state, and still others have settled at various degrees of social organization intermediate to the honeybee grade. The evolutionary histories of most of these lines have been worked out on the basis of anatomy[10], and in a few cases with the aid of partial molecular evidence. Among those closest to the honeybees are the solitary euglossines, the bumblebees and the meliponine stingless bees, the last of which seem comparable in complexity of social organization to the honeybees.

Box 1 | The honeybee genome and social lifestyle

The honeybee is the third insect to have its genome sequenced, following the fruitfly (*Drosophila*) and mosquito (*Anopheles*). We can therefore compare the honeybee gene number and content with those of the other two insects, which don't form colonies, to make some guesses at how its social lifestyle has evolved from and in turn shaped its genome.

Honeybees have more genes involved in producing royal jelly, which makes sense as they make it to feed their young, whereas the other two insects don't. They also have far more genes encoding odorant receptors — mirroring the importance of pheromones in sensory communication during the various bee dances, as well as in distinguishing different castes and bees alien to the colony.

A communal lifestyle lessens some of the hazards faced by a solitary insect. For instance, a hive environment means the honeybee can get away with a simpler outer cuticle than the other insects, and so it has fewer genes encoding cuticle proteins. It also has fewer taste receptors, possibly because most bees feed where another bee has already eaten, reducing the likelihood of ingesting poisonous food.

But not all the differences between the genomes are so easily explained. It seems odd that honeybees have fewer genes involved in immunity than the other insects. These bees live in crowded quarters, and diseases are easily transmitted in a small space. Perhaps novel pathways help them resist disease, or maybe they are protected sufficiently by social behaviours such as grooming.

The genome paper also reports initial studies of changes in gene expression during the honeybee lifespan. Significantly, developmental transitions, such as that at 2–3 weeks when bees begin to work outside the hive, are accompanied by altered activity of genes expressed in the brain. Moreover, there are prominent differences between the castes in terms of which metabolic genes are expressed. **Chris Gunter**

As pieces of this great mosaic are put in place with the aid of comparative genomics, a remarkable history will emerge, yielding many perspectives in developmental evolution and sociobiology.

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PALAEOCEANOGRAPHY

In hot water

Christina L. De La Rocha

There has long been scepticism about the geochemical evidence that the ancient ocean was markedly warm. A fresh approach bolsters the case for an ocean that, in the distant past, was indeed quite hot.

Reconstructing past ocean temperatures is an obsession for many Earth scientists. That's understandable — such data provide insights into climate and its links to biogeochemical cycling, ocean circulation and tectonics, not to mention mass extinctions, evolutionary radiations, and other ups and downs of the biosphere. It is the isotopic and trace-element compositions of sedimentary materials that provide the necessary information to quantitatively infer past temperatures. But that task is not straightforward, even for the past few hundred million years for which we have relatively pristine sediments to analyse. Go back to the Precambrian — roughly 4.5 billion to 0.5 billion years ago — and the job is even more daunting. Not only are there few sedimentary materials of that age left to work with, but all of those that do remain have been altered since they were laid down.

Thus, for decades we have not known what to make of geochemical estimates[1–3] indicating that, between 3.5 billion and 1.2 billion years ago, the ocean was as hot as 55–85 °C. Those estimates have been especially difficult to believe given the geological evidence for glaciations during this time[4]. Robert and Chaussidon[5] (page 969 of this issue), however, have now used the silicon-isotopic composition of ancient rock samples to support the earlier, intriguing results[1–3].

Deducing the environmental conditions of the Precambrian ocean would be a stunning achievement. This is, after all, the setting for the origin of life and the evolution of the great microbial diversity that led to and still supports plant and animal life today. The previous estimates of Precambrian ocean temperatures[1–3] are based on the oxygen-isotopic composition of chert, a siliceous rock that is formed when silica precipitates from sea water. Precipitated silica will have an ^{18}O to ^{16}O ratio that is higher than the fluid from which it formed, and the extent to which the ^{18}O to ^{16}O ratio is higher is inversely related to temperature. For a given fluid composition, then, the higher the temperature, the lower the resulting ^{18}O to ^{16}O ratio of the silica (reported as $\delta^{18}O$ when normalized to a standard). Thus, the remarkably low $\delta^{18}O$ values of Precambrian chert, and their

increase towards the Precambrian–Cambrian boundary, could indicate an ancient ocean that was scores of degrees warmer than the modern one and that cooled gradually. But caution dictates ascribing the strikingly low $\delta^{18}O$ values of ancient chert to other factors, such as the hydrothermal, metamorphic or other alteration of those rocks over billions of years, and not to superwarm Precambrian sea water.

But the low $\delta^{18}O$ values may indicate high temperatures after all. Robert and Chaussidon[5] point out that the Precambrian chert samples with the highest $\delta^{18}O$ values (that is, those least likely to have been altered) have $\delta^{18}O$ values that correlate strongly with their silicon-isotopic composition ($^{30}Si/^{28}Si$, reported as $\delta^{30}Si$). It is unlikely that such a relationship would have been maintained during alteration, suggesting that the isotopic signal of these particular chert samples (Fig. 1) is primary and robust. This evidence alone supports the contention that the Precambrian ocean was quite warm. But Robert and Chaussidon[5] have taken things a step further by using the silicon isotopes on their own to make an alternative temperature estimate.

The $\delta^{30}Si$ values of chert older than 1 billion years can be high[5,6] relative to the siliceous sediments and ocean waters of the modern day[7,8]. Precambrian concentrations of dissolved silicon were extreme, not far from the point of saturation, and were controlled largely by abiotic reactions[9]. Robert and Chaussidon assume that seawater $\delta^{30}Si$ was steady over time, and argue that the $\delta^{30}Si$ of chert and that of the silica precipitated during the circulation of hydrothermal fluids through ocean crust must have together equalled the $\delta^{30}Si$ of the mantle, the ultimate source of silicon to the system. Because precipitates have a lower $\delta^{30}Si$ than the dissolved silicon from which they formed, an increase in the proportion of hydrothermal silicon precipitated should be reflected in an increase in the $\delta^{30}Si$ of chert. And if the temperature of sea water controlled the extent of the hydrothermal silicification, the $\delta^{30}Si$ of Precambrian chert should reveal the temperature of the ocean at that time.

As with any model built to interpret isotopic results in the context of (bio)geochemical cycling, there are numerous assumptions at work here. One is that dissolved silicon input to the ocean has the same $\delta^{30}Si$ signal as that of Earth's mantle. This is not true in modern times, where the $\delta^{30}Si$ of the silicon input reflects the sequestration of silicon into clay minerals during weathering on the continents[8,10]. Ignoring clay formation might be fine for the part of the Precambrian lacking sufficient continental mass for the large-scale formation of clays. But this is not true for the entire Precambrian. Continental weathering and clay formation undoubtedly influenced the $\delta^{30}Si$ values of the younger Precambrian chert, throwing the modelled temperature estimates out of kilter.

Nonetheless, Robert and Chaussidon's
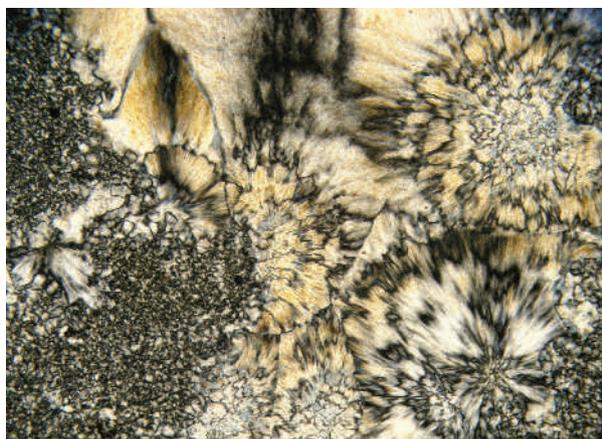
Figure 1 | Memory store. This example of a chert analysed by Robert and Chaussidon[5] comes from the Jinxian group, China, and is some 1.4 billion years old. Microcrystalline quartz within a sample such as this may have retained an isotopic memory of the conditions under which the chert initially formed — evidence that can be unlocked using the fine sampling beam of the ion microprobe.

M. CHAUSSIDON

temperature estimates[5] using silicon isotopes are in remarkable agreement with the earlier estimates based on oxygen isotopes[1–3]. Both records suggest that average ocean temperatures were between 60 °C and 80 °C for much of the time between 3.5 billion and 2.0 billion years ago. And both records imply cooling over the Precambrian, with more conventionally hospitable ocean temperatures of 20–30 °C reached by 1.5 billion years ago.

A Precambrian ocean that was at times warmer than 70 °C certainly gives pause for thought. No photosynthetic organism that can grow above 73 °C has ever been found[11]. Moreover, the declining solubility of oxygen gas with temperature would have exacerbated ocean hypoxia under the low oxygen levels of the Precambrian atmosphere, potentially impeding the development of multicellular animal life[3]. The silicon-isotope data from the Precambrian are striking. But given these points, and the existence of glacial deposits within the Precambrian, it will probably take

more than $\delta^{18}O$ and $\delta^{30}Si$ together to convince sceptics of a hot-tub Precambrian sea. ■

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PALAEONTOLOGY

Modern look for ancient lamprey

Philippe Janvier

It was once thought that lampreys evolved from armoured jawless vertebrates. But a recently discovered lamprey fossil dates from the twilight age of their supposed ancestors, and looks surprisingly modern.

Most living vertebrates have jaws. Such creatures comprise about 51,000 species ranging from sharks to four-legged land vertebrates. In contrast, living jawless vertebrates — known as cyclostomes — consist of only 60 species. These fall into two groups: hagfishes and lampreys (Fig. 1, overleaf). Both jawless groups lack paired fins, and many of their anatomical and physiological features are regarded as primitive relative to those of their jawed counterparts. As cyclostomes also lack scales and bone, their history is mostly undocumented by fossils, but a number of recent findings

have started to fill in the gaps. On page 981 of this issue, Gess et al.[1] report the oldest fossil lamprey to date, a discovery that calls for a reassessment of cyclostome evolution.

Until the late twentieth century, cyclostomes were assumed to be 'degenerate' descendants of armoured jawless vertebrates — known informally as ostracoderms — that lived from the Ordovician period to the Devonian period, 490 million to 358 million years (Myr) ago (Fig. 1). Hagfishes and lampreys were thought to share a common ancestor that derived from certain ostracoderms — either osteostracans