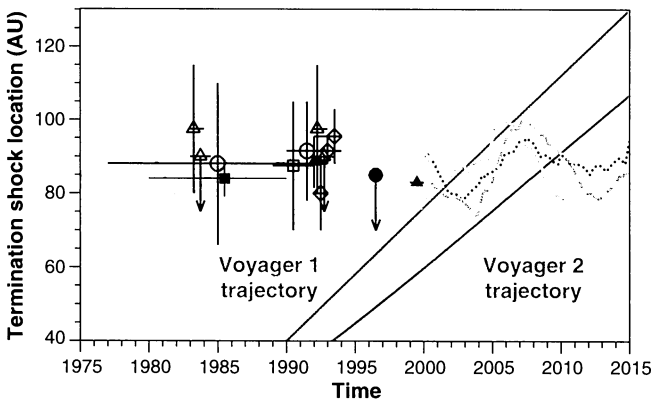

Where is the termination shock? Five methods have been used to estimate the distance to the termination shock. Each uses a different type of data: the solar wind dynamic pressure (open and filled circles, open diamonds), the timing of heliospheric radio emissions (open triangles), anomalous cosmic ray intensity gradients (filled squares), the duration of cosmic ray intensity decreases (filled triangles), and the intensity of solar ultraviolet backscattered from interstellar neutral H (open squares). Solid blue line, predicted variation in the shock location arising from observed changes in the solar wind pressure over the last three solar cycles (*1*). To illustrate the possible range of shock distances in the years ahead, the predicted location from the prior cycles (solid blue line) has been shifted 10 (blue dashes), 20 (black dots), and 30 (purple dashes) years.

rays diffuse and drift inward from the shock, establishing an intensity gradient that provides a fourth method for estimating the shock distance. Extrapolating the gradients observed inside 49 AU outward to the shock source gave a best fit shock location of 84 ± 5 AU for the 1980s (*13*).

The final approach is based on the observation that outward propagating shock complexes cause transient decreases in the intensities of anomalous and galactic cosmic rays. Model calculations indicate that the duration of such a decrease reflects the transit time of the interplanetary shock complex to the termination shock (*14*). Local temporal variations often perturb the observed recovery, but analysis of one such transient decrease in 1999 indicated that the termination shock was only 10 AU beyond Voyager 1 at 83 ± 1 AU (*15*). A related study used the duration of a transient inward flow of anomalous cosmic rays, leading to a shock distance of 88.5 ± 7 AU (*16*).

The assumptions and simplifications in each of the five methods introduce further uncertainties that are more difficult to quantify. Nevertheless, the models and observations are sufficiently different that the systematic uncertainties are unlikely to be correlated among the methods. The clustering of the estimates between 80 and 100 AU thus lends additional weight to the individual estimates.

The location of the termination shock is not fixed in time. Whang and Burlaga have incorporated the temporal variations observed by Voyager 2 into a two-dimensional magnetohydrodynamic model (*1*). They find that the location of the termination shock varies by about 20 AU over the solar cycle. The distance is smallest following times of maximum solar activity.

The shock is presently moving inward (see the second figure). Within the next few years, wind speed and pressure will increase, and with the arrival of the increased pressure, the termination shock will begin moving outward. This will affect when the Voyager spacecraft encounters the termination shock.

Voyager 1 is currently at ~82 AU and moves outward at 3.6 AU per year, followed by Voyager 2, now at ~66 AU and moving outward at 3.3 AU per year. Comparison with the Voyager 1 trajectory suggests the possibility of one or more encounters with the termination shock by 2005. If there has been no encounter by then, the shock will likely be moving outward again. It may then be 2 to 5 more years before it moves back into range for Voyager 1 to take a direct measure of the size of the heliosphere (*17*).

References and Notes

1. Y. C. Whang, L. F. Burlaga, *Geophys. Res. Lett.* **27**, 1607 (2000).
2. J. W. Belcher *et al.*, *J. Geophys. Res.* **98**, 15177 (1993).
3. R. von Steiger *et al.*, *Space Sci. Rev.* **78**, 1 (1996).
4. A. C. Cummings *et al.*, personal communcation.
5. G. Gloeckler *et al.*, *Nature* **386**, 374 (1997).
6. H. L. Pauls, G. P. Zank, *J. Geophys. Res.* **101**, 17081 (1996).
7. ____, *J. Geophys. Res.* **102**, 19779 (1997).
8. T. J. Linde *et al.*, *J. Geophys. Res.* **103**,1889 (1998).
9. G. Exarhos, X. Moussas, *Astrophys J.* **542**, 1075 (2000).
10. D. A Gurnett, W. S. Kurth, *Space Sci. Rev.* **78**, 53 (1996).
11. G. Zank *et al.*, in preparation.
12. D. Hall *et al.*, *J. Geophys. Res.* **98**, 15185 (1993).
13. E. C. Stone, A. C. Cummings, *Proc. 26th Int. Cosmic Ray Conf.* **7**, 500 (1999).
14. J. A. le Roux, H. Fichtner, *J. Geophys. Res.* **104**, 4709 (1999).
15. W. R. Webber *et al.*, *J. Geophys. Res.* **106**, 253 (2001).
16. F. B. McDonald *et al.*, *J. Geophys. Res.* **105**, 1 (2000).
17. E. C. Stone and A. C. Cummings [*Proc. 27th Int. Cosmic Ray Conf.* (2001)] give further details on estimates of the termination shock location.
18. G. P. Zank, *Space Sci. Rev.* **89**, 413 (1999).

PERSPECTIVES: MARINE BIOLOGY

Expansion of the Marine Archaea

David C. Smith

A remarkable consequence of the recent upheaval in the way we classify organisms has been the elevation of the Archaea (non-bacterial prokaryotes) to the rank of domain, making them equivalent to the Eukarya (eukaryotes) and Bacteria (*1*). The domain Archaea is subdivided into two kingdoms—Euryarchaeota and Crenarchaeota—and possibly a third, Korarchaeota. Karner *et al.* (*2*) calculate that the Archaea constitute about 20% of the total marine picoplankton biomass worldwide. Whereas Euryarchaeota thrive in a diverse array of environments, most Crenarchaeota seem to prefer hyperthermal habitats (>80°C). Indeed, the current record holder for growth at high temperatures (113°C) is a member of the Crenarchaeota isolated from a hydrothermal vent (*3*). However, molecular analyses of environmental samples indicate that some Crenarchaeota inhabit more mundane environments, such as terrestrial soils, lakes, and marine and freshwater sediments.

Although the Crenarchaeota have their roots in a hyperthermal environment, they have obviously expanded their range to occupy a variety of nonthermophilic habitats. But what prompted this expansion and when exactly did it take place? Possible answers are provided by Kuypers *et al.* (*4*) on page 92 of this issue. These investigators analyzed sediment samples "cored" from the ocean floor of the North Atlantic by the Ocean Drilling Program. They conclude that the Crenarchaeota expanded their habitat range dramatically by exploiting changing conditions during the mid-Cretaceous (124 to 83 million years ago). They pinpoint the precise time of the expansion by identifying unique membrane lipids characteristic of the Crenarchaeota in a ~45-cm-thick band of dark sediment deposited ~112 million years ago (see the figure). Their estimate of the archaeal expansion extends previous estimates (*5*) by about 60 million years.

What happened during the mid-Cretaceous that enabled the Crenarchaeota to branch out from the confines of their high-

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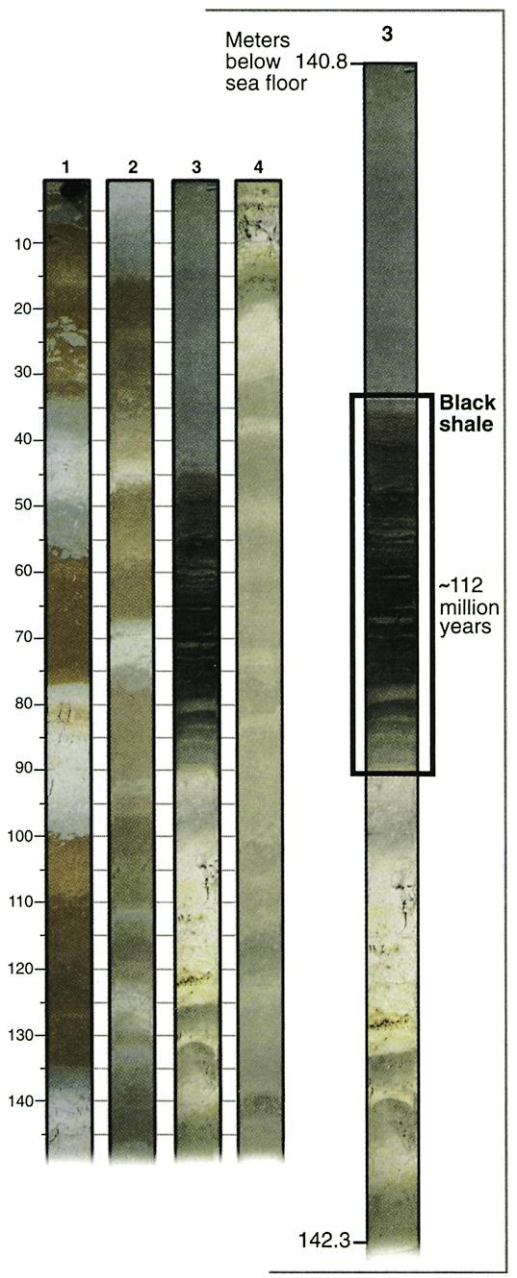
temperature habitats into cooler nonthermophilic regions of the oceans? Kuypers *et al.* propose that severe depletion of oxygen in the oceans at certain intervals during the mid-Cretaceous—called ocean anoxic events (OAEs)—resulted in the demise of many aerobic organisms, thereby allowing the predominantly anaerobic Crenarchaeota to flourish. Evidence for OAEs comes from layers of marine sediment called "black shales," which have a characteristic black color because the dead organic matter of which they are composed did not become oxidized. During an OAE called the Albian 1b—which occurred within the time frame that Kuypers *et al.* calculate for the archaeal expansion—there was greater stratification (that is, decreased mixing) of the Atlantic ocean due to excessive heat released during volcanic activity. The increased stratification of the Atlantic resulted in reduced ventilation of deeper waters, thereby decreasing the oxidation of organic matter as it rained down from above. An increase in global temperature at this time boosted freshwater runoff into the Atlantic, further fueling the stratification of the narrow Atlantic ocean basin (much narrower than it is today) resulting in stagnation of its lower depths.

How are Kuypers *et al.* able to determine the time of the archaeal expansion from a few hundred cubic centimeters of sediment, which they analyzed more than 100 million years after it was deposited? The answer lies in the lipids that make up the membranes of archaea, bacteria, and eukaryotes. These membrane lipids have unique structures that serve as molecular fingerprints for specific groups of organisms. Because membrane lipids cannot be readily degraded, they also serve as molecular fossils (biomarkers) for these groups. The ether linkage between the glycerol and isoprenoid side chains of archaeal membrane lipids is very different from the ester bonds of fatty acids favored by the Bacteria and Eukarya. Kuypers *et al.* discovered that the Albian 1b sediment is dominated by chemical structures characteristic of membrane lipids from nonthermophilic Crenarchaeota.

With compound-specific isotopic analysis, the authors squeezed even more information out of these molecular fossils (*6*). Just as archaeologists determine the eating habits of ancient civilizations by examining material preserved in middens (refuse heaps), these investigators infer the nutritional mode of the Crenarchaeota by analyzing the stable isotopes of carbon (^{13}C and ^{12}C) in lipid biomarkers of the Albian 1b sediment. The heavy isotope of carbon (^{13}C) is excluded during most enzymatic reactions in favor of its lighter isotope (^{12}C), resulting in organic carbon products that are depleted in ^{13}C. There is comparatively little ^{13}C in carbon compounds produced by light-driven reactions such as the "fixing" of CO_2 during photosynthesis (photoautotrophy). In contrast, organisms relying on chemical energy rather than light to "fix" CO_2 (chemoautotrophs) use enzymes that are far less discriminating so that the carbon compounds they produce (including lipids) are heavier. The ^{13}C isotopic composition of the archaeal lipid biomarkers in the Albian 1b sediment reveal a clear chemoautotrophic signature indicating that the Crenarchaeota preserved in this sediment were predominantly chemoautotrophs. The fact that the bulk of the lipid biomarkers in the Albian 1b black shale were produced chemoautotrophically suggests that this process was a far more important contributor of organic carbon to the world's oceans during the mid-Cretaceous than it is today.

Some scientists are busy developing new culture techniques to directly study the physiology of the Archaea, whereas others are circumventing the culture barrier and mining information directly from archaeal genome fragments extracted from the environment to figure out the metabolic capabilities of these organisms (*7*). Both strategies should yield additional information about the degree of specificity of archaeal lipid biomarkers, which is currently rather sparse. Molecular evidence suggests that the nonthermophilic representatives of the Crenarchaeota evolved on three separate occasions (*8*). We will have to await the discovery of other biomarkers or examination of additional sediment samples to see whether the first big expansion of the Archaea truly happened in the mid-Cretaceous or whether it was an even earlier event.



Drilling for molecular fossils. Sediment core samples recovered from the Atlantic ocean floor during the Ocean Drilling Program (Leg 171B). The dark layer of sediment in the middle of the core clearly records the ocean anoxic event (OAE) called the Albian 1b. The thickness of this "black shale" layer (about 45 cm, see scale to left) suggests that low oxygen conditions persisted for at least 30,000 years. During the Albian 1b OAE, decaying organic matter did not become oxidized, thus imparting a black color to the sediment. Under normal conditions when the oceans were well oxygenated, most of the organic matter in the sediments became oxidized, hence the light brown color of these sediments (above and below the black shale). A diverse array of lipid biomarkers associated with nonthermophilic Crenarchaeota preserved in the Albian 1b OAE indicate that these organisms branched out from their hyperthermal habitats about 60 million years earlier than previously estimated.

References

1. C. R. Woese, O. Kandler, M. L. Wheelis, *Proc. Natl. Acad. Sci. U.S.A.* **87**, 4576 (1990).
2. M. B. Karner, E. F. DeLong, D. M. Karl, *Nature* **409**, 507 (2001).
3. E. Blöchl *et al.*, *Extremophiles* **1**, 14 (1997).
4. M. M. M. Kuypers *et al.*, *Science* **293**, 92 (2001).
5. M. J. L. Hoefs *et al.*, *Appl. Environ. Microbiol.* **63**, 3090 (1997).
6. J. M. Hayes, K. H. Freeman, B. N. Popp, C. H. Hoham, *Org. Geochem.* **16**, 1115 (1990).
7. E. F. DeLong, C. Schleper, R. Feldman, R. V. Swanson, *Biol. Bull.* **196**, 363 (1999).
8. K. L. Hershberger *et al.*, *Nature* **384**, 420 (1996).