PERSPECTIVES: PALEONTOLOGY

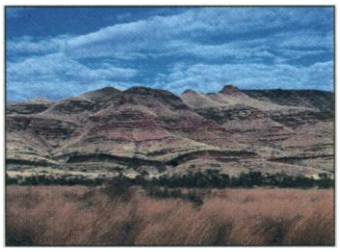
A New Molecular Window on Early Life

Andrew H. Knoll

For generations, the Precambrian-Cambrian boundary [about 544 million years ago (Ma)] formed paleontology's Great Divide, separating the tractable record of a familiar biology from an earlier Terra Incognita populated mostly out of the imagination. Although this boundary persists as an important benchmark for animal evolution (*1*), the discovery and elucidation of the Precambrian fossil record have shown it to be a Maginot line (*2*) for the history of life as a whole. The line of paleontological frustration didn't disappear—it merely receded by nearly 2 billion years to the boundary between the Archean and Proterozoic eons. Proterozoic (2500 to 544 Ma) sedimentary rocks are relatively widespread, usually little altered, and occasionally replete with morphological and chemical remnants of a familiar, if largely microscopic, biota. In contrast, the Archean (>2500 Ma) world has remained a shadow land in which "probably" and "maybe" qualify nearly all paleobiological interpretations until now, that is. On page 1033 of this issue, Brocks *et al.* (*3*) report molecular fossils that bring unprecedented clarity to the late Archean biosphere, dramatically lengthening both the geological record of eukaryotic biology and the list of questions we need to ask about early evolution.

Enhanced online at www.sciencemag.org/cgi/content/full/285/5430/1025

Biomarker compounds are geologically stable molecules, mostly lipids, of known biosynthetic origin. Biomarker geochemistry is a standard tool in petroleum exploration (*4*), but until now, biomolecules older than 1700 Ma (*5*) were unknown. Nor did conventional wisdom encourage prospects of finding earlier biomolecules, because the average Archean sedimentary rock has been heated to temperatures thought to destroy biomarkers. Brocks *et al.* wisely ignored average rocks and focused instead on exceptionally preserved 2700 Ma shales from northwestern Australia that are renowned for their high organic content (see image above). Consequently, Brocks *et al.* have extended the molecular fossil record by 1 billion years.

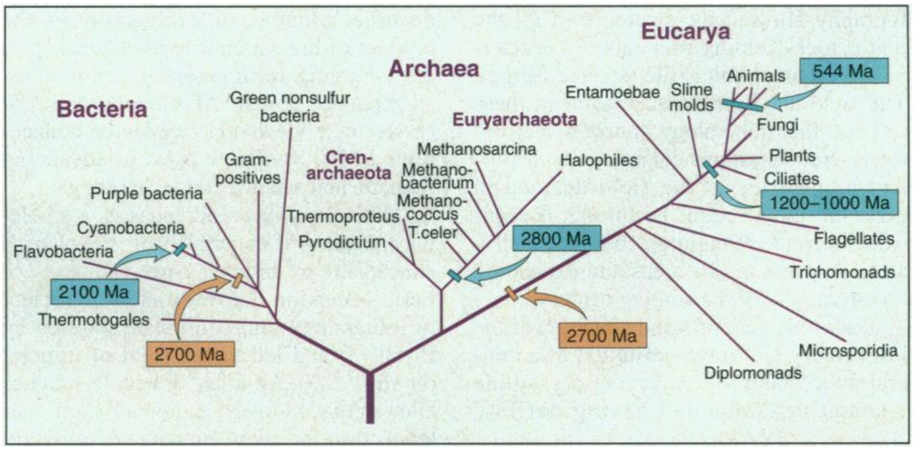


A mountain of iron. The discovery of cyanobacterial biomarker molecules in late Archean rocks in the Hamersley Range, Western Australia, bolsters the hypothesis that photosynthesis provided the oxidizing power to precipitate the ~2500 Ma Hamersley iron formation.

In molecular paleontology, contamination is an issue to be taken seriously, and so Brocks and colleagues painstakingly executed laboratory procedures designed to eliminate the possibility that younger biomarkers migrated into their Archean rocks. Room for doubt has, accordingly, been markedly reduced, and at a minimum, naysayers must go beyond curmudgeonliness to explain the complex pattern of biomarker abundance and distribution identified by Brocks and co-workers, which cannot easily be explained by fluid migration or drilling contamination.

Accepting an Archean age for the biomarkers, what do they tell us about early biology? First, they confirm that cyanobacteria lived in Archean environments. Cyanobacteria are the microscopic heroes of Earth history—primary producers, life's great ecological liberators, and source of the oxygen that transformed our planetary surface. Archean microfossils, stromatolites, and carbon isotopes have all been interpreted in terms of cyanobacterial biology (*6*), but although all of these features are consistent with a cyanobacterial origin, none requires that cyanobacteria existed in the Archean. In a recent paper in *Nature*, Summons *et al.* (*7*) show that the 2-methylhopanes found in sediments derive from 2-Me-bacteriohopanepolyols, membrane lipids synthesized in large quantities only by cyanobacteria. Therefore, the extraction of 2-methylhopanes from 2700 Ma rocks by Brocks *et al.* provides independent geochemical evidence for the antiquity of cyanobacteria and points the way toward tests of a still earlier origin. Morphological fossils show that even the shallowest branches of the cyanobacterial tree had diverged by 2100 Ma (*8*). Thus, cyanobacteria stand as prime targets for studies of molecular evolution.

Remarkably, the late Archean biomarkers also include steranes, sedimentary molecules derived from sterols. A few bacteria incorporate sterols into their membranes, and a subset of these are capable of de novo sterol biosynthesis (*9*). But no prokaryotes are known to form the more elaborate sterols that were precursors of the C28-C30 steranes extracted by Brocks *et al.* Archeae also have distinctly different membrane systems from Eucaryotes and are not known to synthesize sterols. In phylogenies based on ribosomal RNA genes, a very long branch connects eukaryotes to the Archeae (see the figure below) (*10*), and a host of phenotypic characters separate the domains. Thus, although the discovery of Brocks *et al.* indicates that a key attribute of eukaryotic physiology had evolved by 2700 Ma, we can make only limited inferences about the overall biology of the organism that synthesized the sterols.



Trimming the tree. The Universal Tree depicts the phylogenetic relationships of extant organisms, as inferred from sequence comparisons of ribosomal RNA genes (*10*). The boxed dates indicate the minimum age of selected branches, based on paleontological and biogeochemical data. New biogeochemical constraints reported by Brocks *et al.* (*3*) are shown in orange.

CREDIT: (TOP) A. H. KNOLL

The author is at the Botanical Museum, Harvard University, Cambridge, MA 02138, USA. E-mail: aknoll@oeb.harvard.edu

Nonetheless, the early appearance of eukaryotic attributes directs new attention to the immense interval between the divergence of the Eucarya and their rise to ecological and taxonomic prominence 1200 to 1000 Ma (see diagram) (*11*). Explanations based on biological innovation ("just add sex") have been favored in recent years, but these require careful rethinking, with more attention paid to possible environmental facilitation.

In a now classic model of atmospheric evolution, geochemists have postulated that oxygen concentrations grew from extremely low to nearly modern levels about 2200 to 2300 Ma (*12*). But molecular oxygen is required for sterol synthesis, and independent isotopic evidence connects methanotrophic bacteria that depend on oxygen to late Archean ecosystems (*13*). Thus, regardless of the circumstances of early Archean Earth, biogeochemical observations suggest that by the late Archean, oxygen had begun to accumulate in the atmosphere, perhaps reaching levels sufficient for aerobic respiration by single cells (about 1% of present-day values), although probably not much more (*12*, *14*). Recent models of Proterozoic ocean chemistry also suggest that the partial pressure of oxygen, P_{O_2}, approached modern levels only near the end of the Archean (*1*, *15*), further emphasizing the need to consider a protracted, multistage history of atmospheric chemistry.

Knowledge of Archean life and environments remains sketchy, but the discoveries of Brocks *et al.* bolster confidence that, like the Precambrian-Cambrian boundary before it, the paleontological barrier at the Proterozoic-Archean boundary is destined to fall. This time the advance will be driven by innovative biogeochemistry tied to careful field studies of Archean sedimentary rocks (*16*).

References and Notes

1. A. H. Knoll and S. B. Carroll, *Science* **284**, 2129 (1999).
2. The Maginot line was the line of defense built before World War II to keep the Germans from invading France. Claimed to be impenetrable, it quickly proved ineffectual when invasion began.
3. J. J. Brocks, G. A. Logan, R. Buick, R. E. Summons, *Science* **285**, 1033 (1999).
4. K. E. Peters and J. M. Moldowan, *The Biomarker Guide* (Prentice-Hall, Englewood Cliffs, NJ, 1993).
5. R. E. Summons, T. G. Powell, C. J. Boreham, *Geochim. Cosmochim. Acta* **52**, 1747 (1988).
6. J. W. Schopf, in *Early Life on Earth*, S. Bengtson, Ed. (Columbia Univ. Press, New York, 1994), pp. 193–206.
7. R. E. Summons, L. L. Janke, J. M. Hope, G. A. Logan, *Nature* **400**, 554 (1999).
8. S. Golubic, V. N. Sergeev, A. H. Knoll, *Lethaia* **28**, 285 (1995).
9. G. Ourisson, M. Rohmer, K. Poralla, *Annu. Rev. Microbiol.* **41**, 301 (1987).
10. C. R. Woese, O. Kandler, M. Wheeler, *Proc. Natl. Acad. Sci. U.S.A.* **87**, 4576 (1990).
11. A. H. Knoll, *Science* **256**, 622 (1992).
12. R. Rye and H. D. Holland, *Am. J. Sci.* **298**, 621 (1998). For a contrasting view, see H. Ohmoto [*Geology* **24**, 1135 (1996)].
13. J. M. Hayes, in *Early Life on Earth*, S. Bengtson, Ed. (Columbia Univ. Press, New York, 1994), pp. 220–236.
14. B. Rasmussen and R. Buick, *Geology* **27**, 115 (1999).
15. D. E. Canfield, *Nature* **396**, 450 (1998).
16. R. Buick, B. Rasmussen, B. Krapez, *Am. Assoc. Petrol. Geol. Bull.* **82**, 50 (1998).

PERSPECTIVES: MINERALOGY

Mineralogy at a Crossroads

Russell J. Hemley

When Theophrastus described 16 minerals in his textbook "De Lapidibus" around 300 B.C., he laid the foundation for the science of mineralogy and provided the basis for understanding a panoply of natural phenomena. The minerals he described provided the raw material that led to the discovery of many of the chemical elements, and their study was essential in establishing the disciplines of chemistry and physics. Advances within these disciplines in this century brought minerology into the modern era. In particular, the use of x-ray crystallography allowed the structure of all the major rock-forming minerals to be determined on an atomic scale (see the figure). The field has been so successful in these respects that mineralogy in now at a crossroads. New questions cut across the historical boundaries of the field defined in even the most recent textbooks. Recent workshops (*1*–*3*) highlighted both accelerating progress in key areas and expanding opportunities for the coming century.

Dana's System of Mineralogy (*4*) of the last century led to the definition of a mineral as a "naturally occurring crystalline element or compound having definite chemical composition, and formed as a product of inorganic processes." This view is now considered too restrictive: The synthesis of new "minerals" at high pressures and temperatures; the discovery of new amorphous forms; and investigations of nanoscopic to mesoscopic materials, melt structures and fluid-rock interactions, biologically precipitated minerals, and organic-inorganic interactions relevant to the origin of life have considerably broadened the purview of this science. Materials are no longer compartmentalized according to whether they are found naturally in Earth, on other planets, or exclusively as the product of human endeavors. Four themes are emerging from recent developments: an expanded domain of materials and processes, new views of complexity, connections to life, and new roles in advancing fundamental science and technology.

Mineralogy now encompasses a whole-Earth catalog of materials from the planet's atmosphere to its inner core. The study of Earth's deep interior was cast as a problem in mineralogy and solid-state physics by Birch (*5*) and led to the field of mineral physics (*6*, *7*). An array of new techniques allows detailed investigations of Earth materials over the complete range of pressure-temperature conditions that prevail within the planet. The materials of the planet's interior exhibit physical and chemical properties that can be far different from what is observed near the surface. For example, the discovery that hydrogen can be bound in dense silicates and metals has given rise to the possibility of oceans of water locked up within Earth's interior. Minerals and rocks can now be subjected to well-controlled stress conditions, providing critical information for understanding phenomena from deep earthquakes to the movement of continents, the atomic-scale underpinning of plate tectonics (*8*). With a more interdisciplinary outlook, mineral physics is evolving into the wider field of condensed-matter geophysics.

This new scope extends outward to the solar system and beyond, with the discovery of extrasolar system planets. New materials, from fullerenes to dense silicates originally synthesized only in the laboratory, are now documented in extraterrestrial samples, demonstrating the need for laboratory studies and the cross fertilization of chemistry and physics with conventional mineralogy. Future space missions will return samples from other planets, comets, and asteroids; as with the lunar samples of the Apollo era, this presents new opportunities for detailed materials characterization and improved understanding of the processes responsible for planet formation and differentiation. Advances in high pressure temperature experiments provide the prospect for a new experimental mineralogy of ultradense environments at the extreme conditions approaching those found within brown dwarfs and a connection to atmospheric science (*8*).

A distinguishing feature of natural systems is their complexity. Mineral thermo-

---

The author is at the Geophysical Laboratory and Center for High Pressure Research, Carnegie Institution of Washington, 5251 Broad Branch Rd. N.W., Washington, DC 20015, USA.