

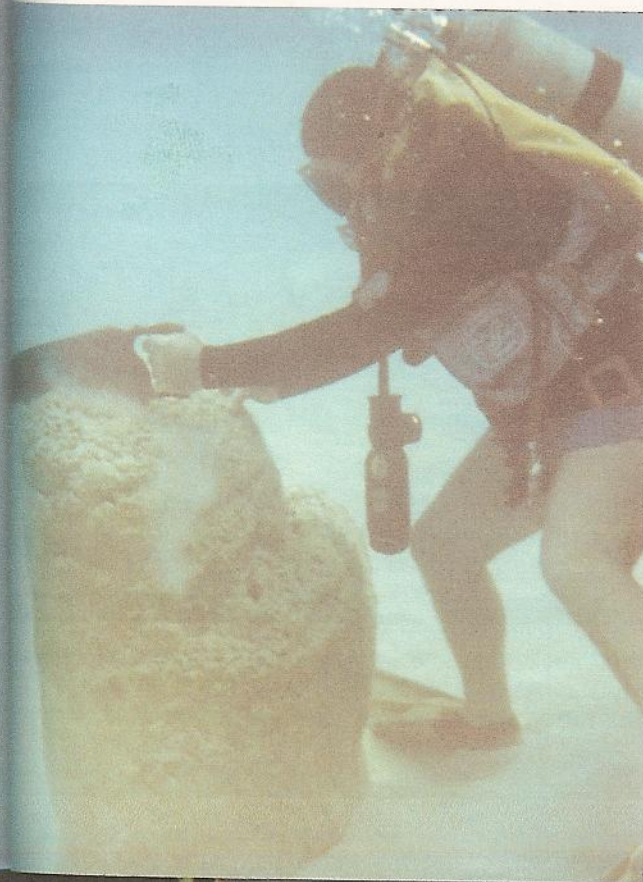
Chapter 17

Origins and Evolution

- 17.1 Origins of Life
- 17.2 Models for Early Life
- 17.3 Microbial Taxonomy
- 17.4 Microbial Divergence and Phylogeny
- 17.5 Horizontal Gene Transfer
- 17.6 Symbiosis and the Origin of Mitochondria and Chloroplasts

Microbial life may have appeared as early as 3.8 billion years ago, soon after our planet Earth formed out of dust from the young sun. Since then, microbes have diverged into new forms adapted to diverse ways of life, from psychrophiles beneath the ice of Antarctica to anaerobes in the human colon. Descendants of early microbes include all living plants and animals, including ourselves. How did microbes originate on Earth? How did their metabolism shape the chemistry of Earth's crust and atmosphere?

DNA sequence-based taxonomy has revealed vast numbers of previously unknown microbial species. How do we classify them? Some evidence, particularly the sequences of rRNA genes, support a traditional branched tree of life. Other gene sequences, however, support a more complex picture, including gene transfer between distant branches of the tree. Many microbes have evolved mutualistic partnerships with other living things, such as bacteria that fix nitrogen within plant cells. Still other microbes evolve as pathogens whose adaptations enable them to live at the expense of their host and cause disease.



A diver is sectioning a stromatolite, a layered community of cyanobacteria in a tidal pool in the Bahamas. Fossil stromatolites have been dated at 3.4 billion years ago, among the earliest forms of life on Earth. Source: Abigail C. Allwood, et al. 2006. *Nature* 441:714.

For centuries, observers of the natural world have wondered where life came from. As early as 1802, the naturalist Erasmus Darwin, grandfather of Charles Darwin, wrote:

Organic life beneath the shoreless waves
Was born and nurs'd in ocean's pearly caves;
First forms minute, unseen by spheric glass,
Move on the mud, or pierce the watery mass;
These, as successive generations bloom,
New powers acquire and larger limbs assume . . .

Thus, nineteenth-century biologists developed the idea that all living organisms had evolved from microbes, perhaps even from cells too small to be seen with the "spheric glass" of a microscope. Even without modern tools of isotope analysis and genetics, thoughtful observers recognized the overwhelming commonalities among all living cells, such as the membrane-bound compartment of cytoplasm and common metabolic pathways such as sugar metabolism. Today, lines of evidence from geology, biochemistry, and genetics overwhelmingly support the microbial origin of life.

What did early life look like? The earliest forms of life for which we have clear fossil evidence are bacterial communities called **stromatolites** (Fig. 17.1A). A stromatolite is a bulbous mass of sedimentary layers of limestone (calcium carbonate, CaCO_3) accreted by microbes over years, even centuries. Within the outer layers, microbes grow as a "microbial mat," a kind of biofilm. The outermost layers of the mat contain oxygenic phototrophs, such as diatoms and filamentous cyanobacteria, that exude bubbles of oxygen. A few millimeters below the surface, red light supports bacteria photolyzing H_2S

to sulfate, which is then reduced by still lower layers of sulfate-reducing bacteria. Stromatolites today survive mainly in isolated pools whose high salt concentration excludes predators, as in Hamlyn Bay, Australia. But 3 billion years ago, in the absence of predators, stromatolites covered shallow seas all over Earth. Fossil stromatolites appear in ancient rock formations such as the 3.4-billion-year-old Strelley Pool Chert, a sedimentary formation in Pilbara Craton, Australia (Fig. 17.1B). Their layers preserve the wavy form of the microbial mats, remarkably similar to living stromatolites. Stromatolites are studied by NASA for clues as to how life may appear on other planets.

Questions about life's origin have long sparked controversy. In eighteenth-century Europe, the idea of "spontaneous generation" of microbes was considered so dangerous that priests and monks performed scientific experiments to disprove it (described in Chapter 1). The priests ultimately won their scientific point: All microbes today have "parents"—that is, preexisting microbes. But these experiments did not address the origin of the first living cells or how early life gave rise to modern species. This concept was so controversial that in the early twentieth century, laws forbade teaching it in American public schools. In 1929, such a law in Tennessee was put to the test by high school teacher John Scopes in what became the famous Scopes trial (Fig. 17.2). According to a 14-year-old student who testified at the trial, Scopes taught that "there was a little germ of one cell organism formed, and this organism kept evolving . . . and from this was man." A large body of evidence now supports the view that microbes living more than 3 billion years ago gave rise to all animals and plants as well as to all modern microbes.

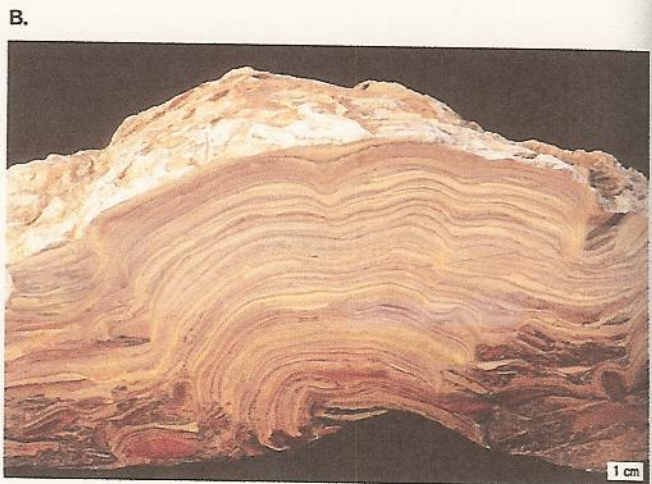


Figure 17.1 Stromatolites: an ancient life-form. **A.** Cyanobacteria form colonial stromatolites, the present-day structures believed to resemble most closely the earliest forms of life on Earth. Hamlyn Bay, Western Australia. **B.** Section through a 3.4-billion-year-old stromatolite from the Strelley Pool Chert. Pilbara Craton, Australia.



Hulton-Deutsch Collection/Corbis

Figure 17.2 **Objection to microbial ancestry.** In 1925, outside the Scopes trial in Dayton, Tennessee, demonstrators opposed the teaching that all life—including humans—evolved from a microbe.

Chapter 17 explores the evidence from geochemistry and molecular biology for the nature of the earliest cells, as well as the challenges in interpreting data from so long ago. We explore how molecular techniques reveal deep similarities among all life-forms: the core macromolecular apparatus of DNA, RNA, and proteins, expressed by genomes that share a common set of ancestral genes. We focus on three major concerns of microbial evolution:

- The origin of life on Earth and the nature of the earliest cells.
- The divergence of microbes from common ancestors.
- Gene transfer and symbiosis as agents of evolution.

17.1 Origins of Life

Before the first cells could evolve, several fundamental conditions were required. These conditions included:

- **Essential elements.** Because all life on Earth is composed of molecules, the origin of life required the fundamental elements that compose organic molecules.
- **Continual source of energy.** The generation of life requires continual input of energy, which ultimately is dissipated as heat. The main source of energy for life is the sun.
- **Temperature range permitting liquid water.** Above 150°C, life's macromolecules fall apart; below the freezing point of water, metabolic reactions cease. Maintaining the relatively narrow temperature range conducive to life depends on the nature of our sun,

our planet's distance from the sun, and the heat-trapping capacity of our atmosphere.

Elements of Life

For life to arise and grow, elements such as carbon and oxygen needed to be available on Earth. The planet Earth coalesced during formation of the solar system 4.5 Gyr (gigayears, or billions of years) ago. Central to the solar system is our sun, a “yellow” star of medium size and surface temperature (5,770 K). The sun's surface temperature generates electromagnetic radiation across the spectrum, peaking in the range of visible light. As we learned in Chapter 13, the photon energies of visible light are sufficient to drive photosynthesis but not so energetic that they destroy biomolecules. Thus, the stellar class of our sun makes organic life possible.

NOTE: A billion means the number 10^9 in American English; but in British English, a billion is 10^{12} . For clarity, we designate 10^9 years as a gigayear, or **Gyr**. A million years (10^6) is a “megayear,” or **Myr**.

The sun's surface temperature and luminosity are generated by nuclear fusion reactions in which hydrogen nuclei fuse to form helium. Yet 2% of the solar mass consists of heavier elements, such as carbon, nitrogen, and oxygen, as well as traces of iron and other metals—elements that compose Earth, including its living organisms. Where did these heavier elements come from? To answer this question, we must look to other stars in the universe at different stages of their development (**Fig. 17.3**).

Elements of life formed within stars. Throughout the universe, young stars such as our sun fuse hydrogen to form helium. As stars age, they use up all their hydrogen. With hydrogen gone, the aging star contracts and its temperature rises, enabling helium nuclei to fuse forming carbon (see **Fig. 17.3**). Carbon drives a cyclic nuclear reaction, the CNO cycle, to form isotopes of nitrogen and oxygen. Further nuclear reactions generate heavier elements through iron (Fe). Thus, the major elements of biomolecules were formed within stars that aged before the birth of our solar system.

The later nuclear reactions of aging stars generate heavier nuclei up to iron. The aging star expands, forming a red giant (see **Fig. 17.3**). When a star of sufficient mass expands (a supergiant), it explodes as a **supernova** (**Fig. 17.4**). The explosion of a supernova generates in a brief time all the heaviest elements and ejects the entire contents of the star at near-light speed. Billions of years before our sun was born, the first stars aged and died, spreading

Life cycle of a massive star

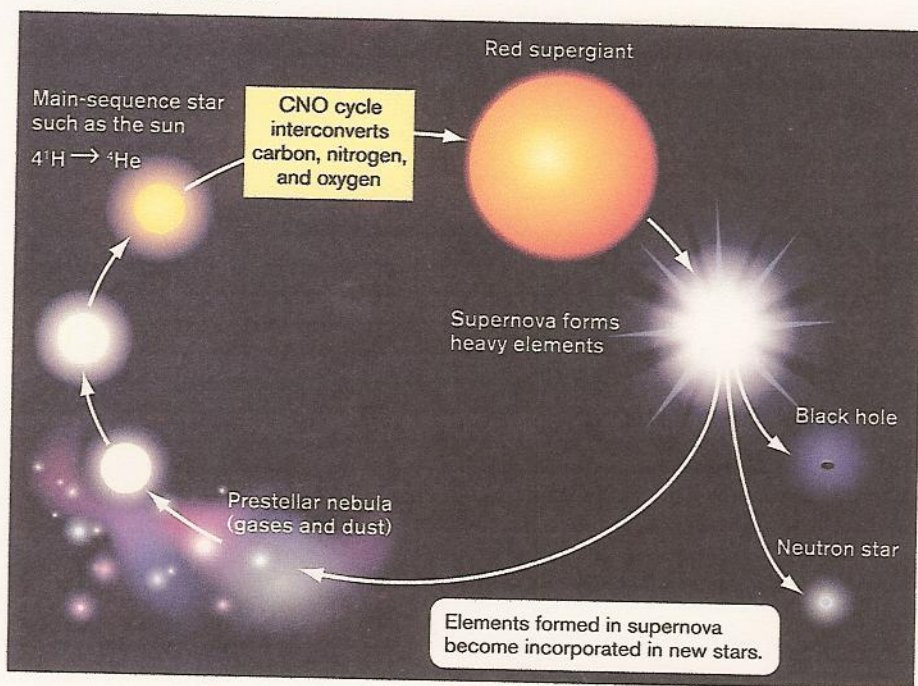
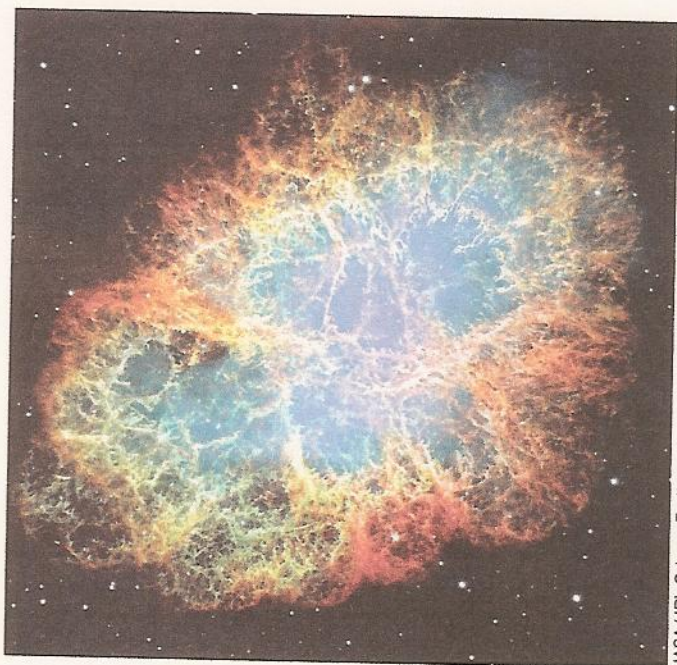


Figure 17.3 Stellar origin of atomic nuclei that form living organisms. In young stars, hydrogen nuclei fuse to form helium. In older stars, fusion of helium forms carbon, nitrogen, oxygen, and all the heavier elements up to iron. Massive stars explode as supernovae, spreading all the elements of the periodic table across space. These elements are picked up by newly forming stars, such as our own sun.



NASA/JPL-Science Faction

Figure 17.4 Crab Nebula, the remnant of a supernova. Observed by radioastronomy.

THOUGHT QUESTION 17.1 What would have happened to life on Earth if the sun were a different stellar class, substantially hotter or colder than it is now?

Elemental composition of Earth. When our solar system formed, individual planets coalesced out of matter attracted by the force of gravity. Because of Earth's small size, most of the hydrogen gas escaped Earth's gravity very early. The most abundant dense component of Earth was iron (Fig. 17.5). Much of Earth's iron sank to the center to form the core. The core is surrounded by a mantle, composed primarily of iron combined with less dense crystalline minerals such as silicates of iron and magnesium, $(\text{Fe, Mg})_2\text{SiO}_4$. The mantle is coated by Earth's thin outer crust. The crust is composed primarily of silicon dioxide, SiO_2 , also known as quartz or chert. Crustal rock includes smaller amounts of numerous minerals, including the carbonates and nitrates that provided the essential elements for life. Overall, the crust shows a redox gradient, reducing in the interior and oxidizing at the surface.

The crust, also called the lithosphere, provides a habitat for microbes down to surprising depths, such as within gold mines excavated to 3 kilometer (km). Some **endolithic** microbes (microbes living within rock) metabolize by oxidizing electron donors generated through decay of radioactive metals. The discovery of endolithic organisms deep in the crust was of great interest to NASA scientists

all the elements of the periodic table across the universe. Some of these elements coalesced with our sun and formed the planets of our solar system. In effect, all life on Earth is made of stardust, the remains of stars long gone.

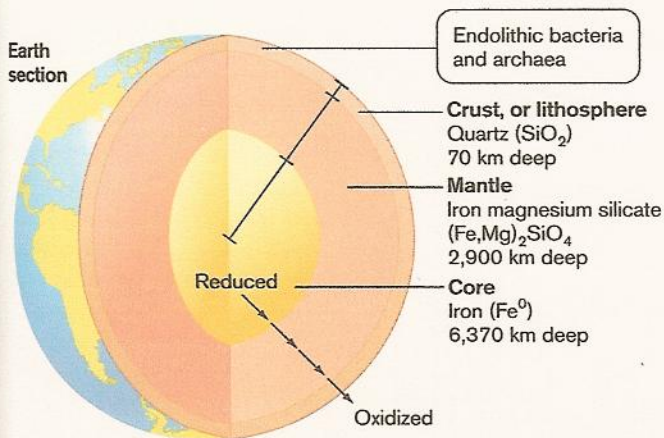


Figure 17.5 Geological composition of Earth. The cross section of Earth shows the core, the mantle, and the thin outer crust. The core and mantle are rich in iron; oxygen content increases toward the crust. The crust is composed primarily of silicates such as quartz (SiO_2). Crustal rock supports endolithic prokaryotes.

seeking life on Mars, whose crust might provide a similar habitat to Earth's.

The outer surface of the crust supports the remainder of the **biosphere**, the sum total of all life on Earth. The biosphere generates oxidants (electron acceptors), most notably O_2 . Oxygen-breathing organisms can live only on the outer surface, where O_2 is produced by photosynthesis.

Earth's atmosphere. From the crust and the mantle of early Earth, volcanic activity released gases such as carbon dioxide and nitrogen, which formed Earth's first atmosphere, while volcanic water vapor formed the ocean. The composition of this first atmosphere, before life evolved, looked much like that of Mars: thin, about 1% as dense as that of Earth today, consisting primarily of CO_2 . But unlike Mars, Earth developed living organisms that filled the atmosphere with gaseous N_2 and O_2 and that continue to produce these gases today. Organisms also produce CO_2 , as well as fixing it into biomass. Some CO_2 and N_2 arise from geological sources such as volcanoes, but their contribution is small compared to that of biological cycles (discussed in Chapter 22). The overall composition of Earth's atmosphere is determined by living organisms, primarily microbes.

Temperature. Another important aspect of Earth's habitat, determined by the atmospheric density and composition, is temperature. Atmospheric gases absorb light and convert the energy to heat, raising the temperature of the surface and atmosphere. This rise in temperature is known as the **greenhouse effect**. Because car-

bon dioxide is an especially potent greenhouse gas, the CO_2 -rich atmosphere of early Earth could have heated the planet to temperatures approaching that of Venus, eliminating the possibility of life. Instead, microbial consumption of CO_2 and generation of nitrogen and oxygen gases limited Earth's surface temperature to an average of 13°C . The cooling effect may have led to an ice age, possibly forestalled by rising methane from methanogens. One way or another, the history of Earth's atmosphere is intimately related to the history of microbial evolution.

Geological Evidence for Early Life

The first period of Earth's existence, ranging 4.5–3.8 Gyr ago, is designated the **Hadean eon** (Fig. 17.6), named for Hades, the ancient Greek world of the dead. During the Hadean eon, repeated bombardment by meteorites vaporized the oceans, which then cooled and recondensed. Meteor bombardment may have killed off incipient life more than once before living microbes finally became established. Still, scientists speculate whether some forms of life might have survived Hadean conditions, perhaps growing 3 km below the Earth's surface. Like the dead spirits imagined by the Greeks to have populated Hades, Earth's earliest cells might have reached deep enough within the crust that they were protected from the heat and vaporization at the surface. As of this writing, however, no geological evidence supports the existence of life earlier than 3.8 Gyr ago.

The Archaean era. The earliest geological evidence for life dates to 3.8–2.5 Gyr ago, in the **Archaean eon** (Fig. 17.6). In the Archaean, meteor bombardment was less frequent, and the Earth's crust had become solid. The Archaean marked the first period with stable oceans containing the key ingredient of life: liquid water. Water is a key medium for life because it remains liquid over a wide range of temperatures and because it dissolves a wide range of inorganic and organic chemicals. Rock strata dating to the Archaean era reveal the first evidence of living organisms and their metabolic processes.

NOTE: The term *Archaean* refers to the earliest eon in which life existed, whereas *archaeal* is the adjective referring to the taxonomic domain Archaea. The domain Archaea (originally, Archaeobacteria) was named by Carl Woese based on his theory that the species of this domain most closely resembled the earliest life-forms of the Archaean eon. In fact, early life may have encompassed diverse traits later associated with archaea, bacteria, and eukaryotes.

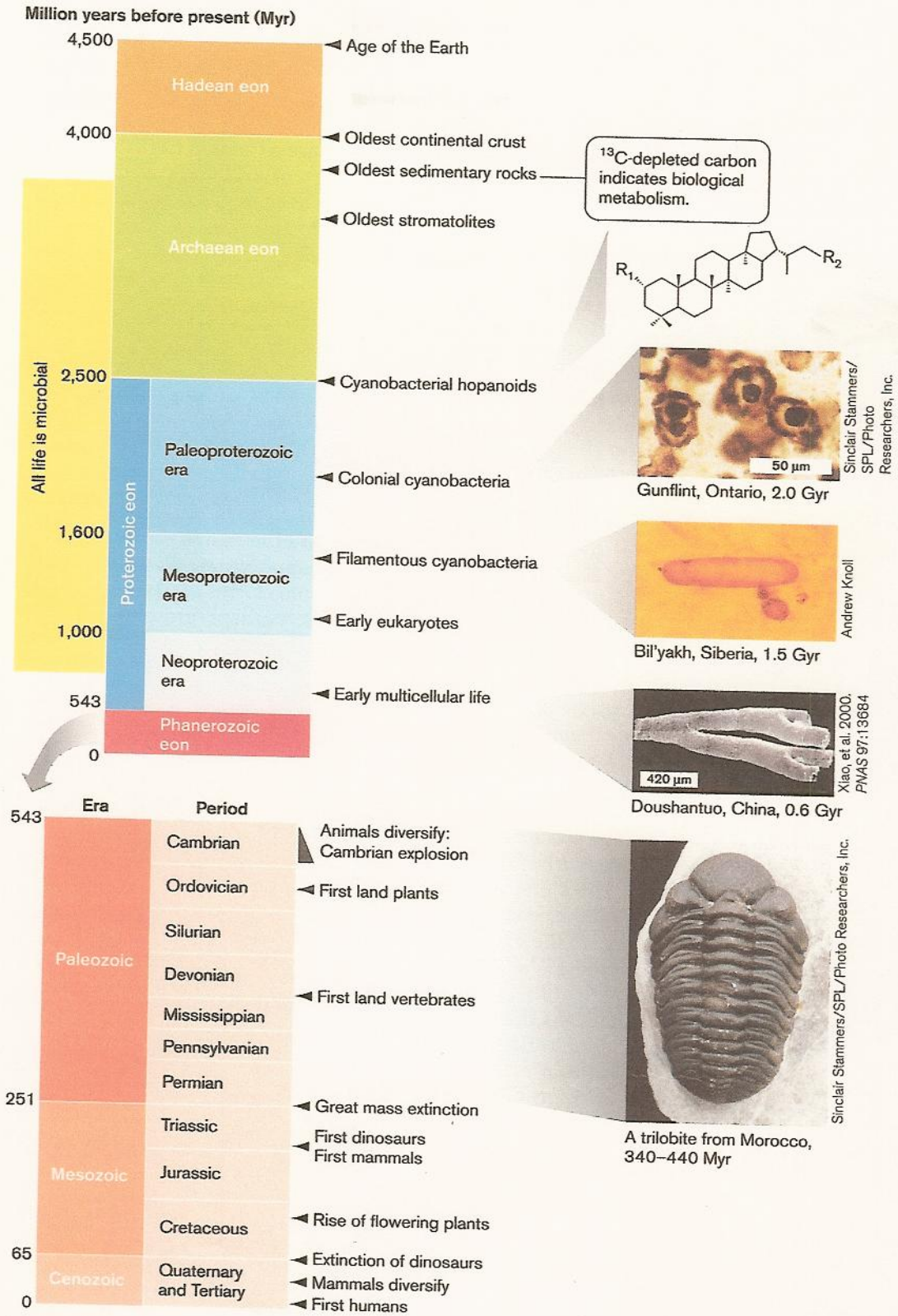


Figure 17.6 Geological evidence for early life. The geological record shows evidence of microbial life early in Earth's history, 3 Gyr before the first multicellular forms.

How and when did living cells arise out of inert materials? Without a time machine to take us back 4 Gyr, we must rely on evidence from Earth's geology. Interpreting geology is a challenge because most forms of evidence for early life are indirect and subject to multiple interpretations. The farther back in time, the more change has occurred to the rock strata and the greater the difficulties. One way to meet this challenge, however, is to compare the results from different kinds of evidence (Table 17.1). If two or more kinds of evidence (such as microfossils and isotope ratios) point to life in the same location, the conclusion is strengthened.

Stromatolites. Fossil stromatolites are layers of carbonate or silicate rock that resemble modern living stromatolites. Presumably, the fossils formed as layers of phototrophic microbial communities grew and died, their

form filled in by calcium carbonate or silica. Fossil stromatolites accepted by geologists date as early as 3.4 Gyr ago (see Fig. 17.1). These rock formations appear remarkably similar to the layered forms of stromatolites today. The ancient rock, however, is too deformed to reveal the detailed structure of cells, and the biological origin of such fossils is questioned by some researchers.

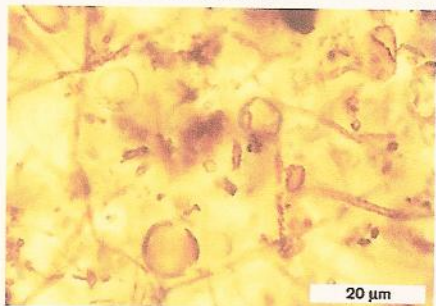
Microfossils. The most convincing evidence is the visual appearance of **microfossils**, microscopic fossils in which calcium carbonate deposits have filled in the form of ancient microbial cells (Fig. 17.7). Microfossils are dated based on the age of the rock formation in which they are found, which in turn is based on evidence such as radioisotope decay. Convincing microfossils need to show regular three-dimensional patterns of cells that cannot be ascribed to abiotic (nonbiological) causes.

Table 17.1 Geological evidence of early life.

Type of evidence	Advantages	Limitations
Stromatolites. Layers of phototrophic microbial communities grew and died, their form filled in by calcium carbonate or silica.	Fossil stromatolites can be observed in the oldest rock of the Archaean eon. Their distinctive shapes resemble those of modern living stromatolites.	Some layered formations attributed to stromatolites have been shown to be generated by abiotic (nonbiological) processes.
Microfossils. Early microbial cells decayed, and their form was filled in by calcium carbonate or silica. The size and shape of microfossils resemble that of modern cells.	Microfossils are visible and measurable under a microscope, offering direct evidence of cellular form.	Microscopic rock formations require subjective interpretation. Some formations may result from abiotic processes.
Isotope ratios. Microbes fix $^{12}\text{CO}_2$ more readily than $^{13}\text{CO}_2$. Thus, limestone depleted of ^{13}C must have come from living cells. Similarly, sulfate reduced by sulfate-respiring bacteria shows depletion of ^{34}S compared with ^{32}S .	Isotope ratios offer objective measurement of a highly reproducible physical quantity. They provide the best evidence for dating the earliest life. Isotope ratios generated by key biochemical reactions can calibrate the timeline of phylogenetic trees.	We cannot prove absolutely that no abiotic process could generate a given isotope ratio. Isotope ratios tell us nothing about the form of early life or how it evolved.
Biosignatures. Certain organic molecules found in sedimentary rock are known to be formed only by microbes. These molecules are used as biosignatures.	Biosignatures such as hopanoids are complex molecules and highly specific to different life-forms.	In the oldest of rocks, organic molecules are eliminated by metamorphic processes.
Oxidation state. The oxidation state of metals such as iron and uranium indicates the level of O_2 available when the rock formed. Banded iron formations (BIF) suggest oxidation by microbial phototrophs that intermittently produced oxygen.	Oxidized metals offer evidence of microbial processes even in highly deformed rock.	It is hard to rule out abiotic causes of oxidation. If biological processes were responsible, the kind of metabolism is not revealed.

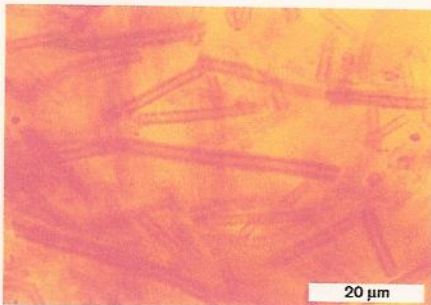
Microfossils

A. Filamentous prokaryotes



Andrew Knoll

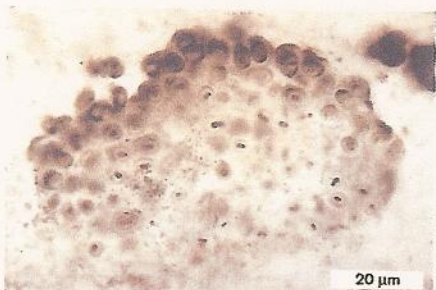
Modern species

B. *Leptothrix* sp.

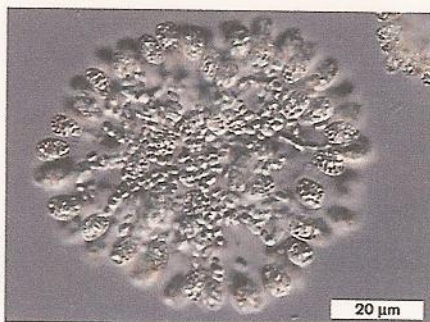
Victor Cruz

Figure 17.7 Microfossils compared with modern bacteria. **A.** Filamentous prokaryotes, 2.0 Gyr, from Gunflint formation, Ontario, Canada. **B.** Modern *Leptothrix* sp. filamentous bacteria. **C.** Colonial cyanobacteria, about 2.0 Gyr, from Belcher Islands, Canada. **D.** Modern *Entophysalis* cyanobacteria. **E.** Filamentous algae, 1.2 Gyr, from arctic Canada. **F.** Modern red algae, a eukaryote, *Bangia* species.

C. Colonial cyanobacteria



© Hans Hofmann, McGill University, Montreal

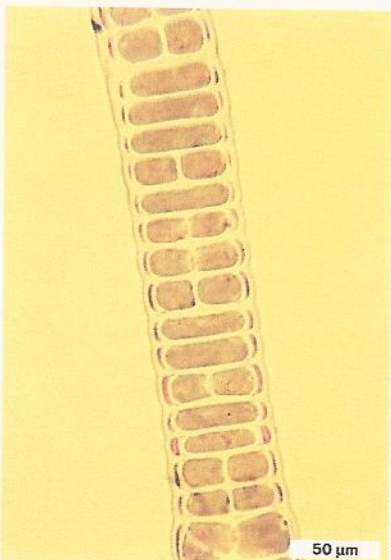
D. *Entophysalis* sp.

Laboratory of Phytoplankton Ecology

E. Algae (eukaryote)



Nicholas Butterfield, UK

F. *Bangia* sp., red algae

Nicholas Butterfield, UK

The earliest convincing microfossils are dated at 2.0 Gyr. Microfossils dated to 2.0 Gyr include filamentous prokaryotes in the Gunflint formation, Ontario, Canada (Fig. 17.7A). The Gunflint outcrops consist of chert, a kind of silicate formed by precipitation from an ancient sea. The sea was rich in carbonates and reduced iron, a good combination for redox metabolism. Some of the fossils resemble the form of filamentous iron-metabolizing bacteria today, such as *Leptothrix* species (Fig. 17.7B). Other microfossils

dated at 2.0 Gyr resemble colonial cyanobacteria (compare Fig. 17.7C with 17.7D). More recent strata, dated at 1.2 Gyr, contain larger fossil cells comparable to those of modern eukaryotes such as algae (Figs. 17.7E and F).

If life existed in more ancient times, such as the Archaean eon, where are the microfossils? Archaean rock is metamorphic, greatly modified by temperature and pressure. The macroscopic contours of stromatolites can be identified, but microfossil interpretation is highly

Brazier, et al. 2002. *Nature* 416: 76

Figure 17.8 Microfossils or artifacts? Structures originally identified as cyanobacterial microfossils from western Australia, dated to 3.85 Gyr. Further testing indicates that the structures are nonbiological artifacts.

controversial. For example, microfossils of cyanobacteria dated to 3.85 Gyr by William Schopf in the early 1990s were accepted and described in many textbooks (Fig. 17.8). The 3.85-Gyr fossils have since been reinterpreted by Martin Brazier and colleagues as nonbiogenic artifacts (caused by abiotic processes). The form of the proposed Archaean microfossils is less regular and convincing than the form of later specimens, particularly when observed at different angles not shown in the original publication.

Another kind of evidence is that of a **biosignature** or **biological signature**, a chemical indicator of life. Biosignatures have been found that are even earlier than the oldest fossils. Their significance is limited, however, as it

A. Minik Rosing



BBC

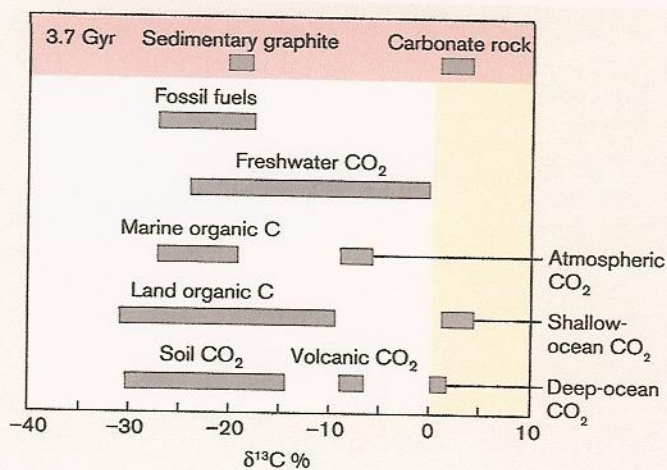
Figure 17.9 Biosignatures of early life. **A.** Minik Rosing (left), in Greenland, shows the Isua rocks whose carbon isotope ratios indicate photosynthesis at 3.8 Gyr. **B.** ^{13}C isotope depletion (negative $\delta^{13}\text{C}$) occurs in biomass as a result of the Calvin-Benson cycle. Negative $\delta^{13}\text{C}$ is observed at 3.7 Gyr in sedimentary graphite, which may derive from sedimented phototrophs. Little or no isotope depletion is seen in carbonate rock, which has no biological origin. **C.** 2-methylhopane, a biological signature of cyanobacteria, is found in rock strata dated at 2.5 Gyr. The 2-methyl group is highlighted.

is hard to rule out nonbiogenic explanations, so researchers seek additional, corroborating evidence based on independent principles.

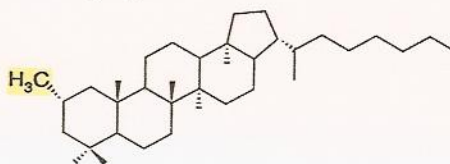
Isotope ratios. An **isotope ratio** may serve as a biosignature if the ratio between certain isotopes of a given element is altered by biological activity. Enzymatic reactions, unlike abiotic processes, are so selective for their substrates that their rates may differ for molecules containing different isotopes. For example, the carbon-fixing enzyme rubisco, found in chloroplasts, preferentially fixes CO_2 containing ^{12}C rather than ^{13}C . The carbon dioxide fixed into microbial cells eventually is converted to calcium carbonate in sedimentary rock. Thus, the calcium carbonate deposited by CO_2 -fixing autotrophs (such as cyanobacteria) shows lower ^{13}C content than calcium carbonate deposited by abiotic processes (Fig. 17.9B). The difference, $\delta^{13}\text{C}$, is defined by the fractional difference (in parts per thousand) between the $^{13}\text{C}/^{12}\text{C}$ ratios in a sample versus a standard inorganic rock:

$$\delta^{13}\text{C} = \frac{^{13}\text{C}/^{12}\text{C} (\text{experimental}) - ^{13}\text{C}/^{12}\text{C} (\text{standard})}{^{13}\text{C}/^{12}\text{C} (\text{standard})} \times 1,000$$

Typical $\delta^{13}\text{C}$ values are shown in Figure 17.9B. Organisms on land and sea show $\delta^{13}\text{C}$ values of -10 to -30 parts per thousand, a significant ^{13}C depletion through carbon fixation. A comparable $\delta^{13}\text{C}$ is observed in fossil fuels, which formed from plant and animal bodies decomposed by bacteria.

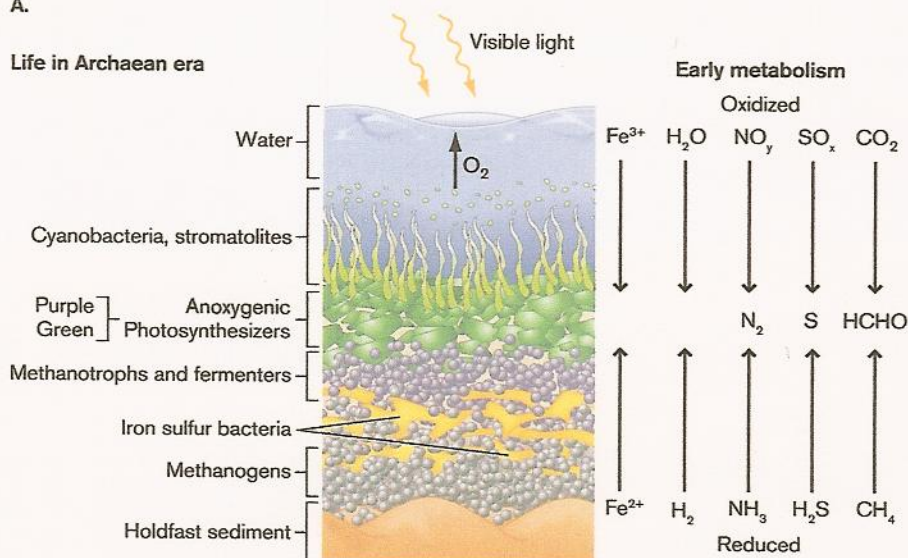
B. ^{13}C isotope depletion

C. 2-Methylhopane



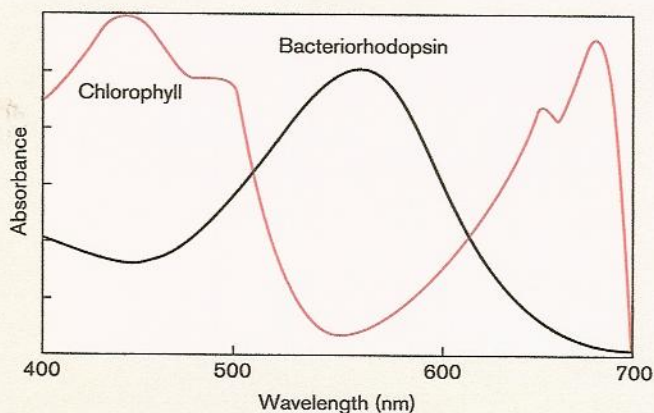
A.

Life in Archaean era

**Figure 17.10** Early metabolism.

A. Early metabolism could have been based on various reactions between oxidized minerals that diffuse down from the air and water and reduced minerals in the sediment, upwelling from hydrothermal vents. **B.** Early photosynthesis may have resembled that of haloarchaea, whose bacteriorhodopsin absorbs light in the central range of sunlight (yellow-green, 500–600 nm), in contrast to the chlorophyll of cyanobacteria and plants, which absorbs blue and red. Source: B. Shil DasSarma, U. Maryland.

B.



The most ancient mineral samples showing a substantial $\delta^{13}\text{C}$ (about -18 parts per thousand) are graphite granules in the Isua rock bed of West Greenland, dated at 3.7 Gyr. The graphite granules were analyzed by Minik Rosing, a native Greenlander at the Danish Lithosphere Center (Fig. 17.9A). The graphite grains derive from microbial remains buried within sediment that subsequently metamorphosed, driving out the water content but leaving behind the telltale carbon. By contrast, carbonate rock of nonbiogenic origin from the same formation shows a $\delta^{13}\text{C}$ near zero.

Cyanobacterial hopanoids. A different kind of biosignature is given by organic molecules specific to a particular life form. Certain organic molecules may last within rock for hundreds of millions of years. A particularly durable class of molecules are membrane lipids. Recall from Chapter 3 that bacterial cell membranes contain steroid-like molecules called hopanoids (Fig. 17.9C). A hopanoid consists of four or five fused rings of hydrocarbon with variable side groups, depending on the bacterial species.

The 2-methylhopanoids, containing a methyl side chain are highly specific to cyanobacteria and are found in no other class of organism today. They are considered a biosignature of cyanobacteria.

The hopanoid derivative 2-methylhopane is found in sedimentary rock of the Hamersley Basin of Western Australia, dated to 2.5 Gyr. This highly specific biosignature is strong evidence that cyanobacteria existed by the end of the Archaean eon. Furthermore, because cyanobacterial photosynthesis is a relatively advanced form of metabolism, the finding suggests that more primitive microbes must have evolved earlier.

Metabolism of the First Cells

How did the earliest life-forms metabolize without oxygen gas to respire and without the complex machinery of photosynthesis? The nature of the first metabolism is unknown, but geochemistry and modern metabolism suggest several possibilities (Fig. 17.10A).

- Oxidation-reduction reactions.** The early oceans contained oxidized forms of nitrogen, sulfur, and iron that could interact with reduced minerals from the crust. For example, nitrate (NO_3^-) or sulfate (SO_4^{2-}) could be reduced by hydrogen gas to yield energy (hydrogenotrophy, discussed in Chapter 14). The oxidized molecules were generated by reactions driven by ultraviolet radiation, which penetrated the atmosphere in the absence of the ozone layer. Sulfur isotope ratios ($^{34}\text{S}/^{32}\text{S}$) suggest the growth of sulfate-reducing bacteria as early as 3.47 Gyr ago.
- Light-driven ion pumps.** A simple light-driven pump, such as the bacteriorhodopsin of haloarchaea (halophilic archaea), could have conducted the first kind of phototrophy. The absorption spectrum of

bacteriorhodopsin matches the peak of solar radiation reaching the upper layers of ocean (Fig. 17.10B), in contrast to the chlorophylls of cyanobacteria and plants, which absorb the outer ranges of blue and red. Perhaps cyanobacteria evolved in the presence of haloarchaea, filling the unexploited photochemical niches.

- **Methanogenesis.** Climate models of early Earth suggest a methane atmosphere, produced by methanogenic archaea. Methanogenesis involves reaction of H_2 and CO_2 producing CH_4 and H_2O . Methanogens show highly divergent genomes, a finding that suggests early evolution of their common ancestor. Their biochemistry and evolution (discussed in Chapter 19) are consistent with proposed models of ancient life.

Oxygen from Cyanobacteria Appeared Gradually

An extraordinary event in the planet's history was the evolution of the first oxygenic phototrophs, cyanobacteria that split water to form O_2 . The entry of O_2 into Earth's biosphere is often portrayed as a sudden event that would have been disastrous to microbial populations that lacked defenses against its toxicity. In fact, geological evidence shows that oxygen arose gradually in the oceans, starting about 2 Gyr ago, and may have arisen and disappeared numerous times before reaching a high steady-state level in our atmosphere.

Banded iron formations. Evidence for oxygen in the biosphere comes from the oxidation state of minerals, particularly those containing iron. The bulk of crustal iron is in the reduced form (Fe^{2+}), which is soluble in water and reached high concentrations in the anoxic early oceans. Sedimentary rock, however, contains many fine layers of oxidized iron (Fe^{3+}), which is insoluble and forms a precipitate, such as iron oxide (Fe_2O_3). The layers of iron oxide suggest periods of alternating oxygen-rich and anoxic conditions. These layered iron minerals are called **banded iron formations (BIFs)** (Fig. 17.11A). A common form of banded iron consists of gray layers of silica oxide (SiO_2) alternating with layers colored red by iron

oxides and iron oxyhydroxides [$FeO_x(OH)_y$]. Banded iron formations are widespread around the world and provide our major sources of iron ore (Fig. 17.11B).

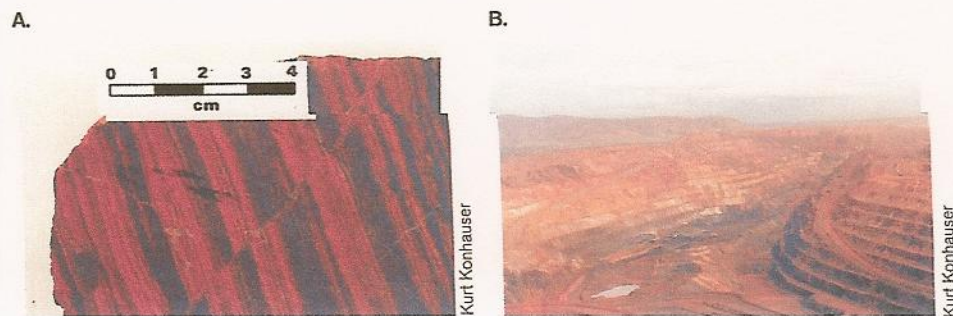
Banded iron formations are often found in rock strata containing signs of past life such as ^{13}C depletion and other biomarkers. For example, the Isua formations (Greenland) and Hamersley formations (western Australia), which both show ^{13}C depletion, also contain extensive banded iron. Calculations show that the layers of oxidized iron could result from biological metabolism involving iron oxidation. One possibility is that the iron was oxidized by chemolithotrophs, using molecular oxygen produced by cyanobacteria. The Archaean and early Proterozoic eons experienced fluctuating levels of molecular oxygen in the atmosphere. These fluctuations could have led to oscillating levels of iron oxide thus producing bands in the sediment, as microbes used up all the oxygen.

Alternatively, Dianne Newman, at the California Institute of Technology, proposes that the iron oxides arose directly from anaerobic photosynthesis, in which the reduced iron served as the electron donor (Fig. 17.12). Photosynthetic oxidation of Fe^{2+} to Fe^{3+} , or "photoferrotrophy," could have occurred in cycles until the marine iron was all oxidized, generating sedimentary layers of iron oxides and iron oxyhydroxides. This argument was supported by Newman's discovery of iron phototrophy by modern purple bacteria such as *Rhodospseudomonas palustris*.

By 2.3 Gyr ago, the prevalence of oxidized iron and other minerals indicates the steady rise of oxygen from photosynthesis in Earth's atmosphere. All the dissolved Fe^{2+} from the ocean floor was oxidized, leaving the oceans in the iron-poor state that persists today. Oxygen as the most efficient electron acceptor enabled the evolution of aerobic respiratory bacteria. Aerobic bacteria gave rise to mitochondria, which enabled the evolution of eukaryotes and ultimately multicellular organisms (Fig. 17.13).

Remarkably, modern cells are still composed primarily of reduced molecules, highly reactive with oxygen, a relic of the time when our ancestral cells evolved in the absence of oxygen. The conditions under which such cells may have evolved can be simulated in the laboratory—conditions under which some of life's most common

Figure 17.11 Banded iron formations. **A.** Banded iron formation in ancient sedimentary rock. Its main component is chert, a form of quartz (silica oxide, SiO_2) with layers colored red by iron oxide (Fe_2O_3). **B.** The BHP Iron Ore Mine at Newman, western Australia.



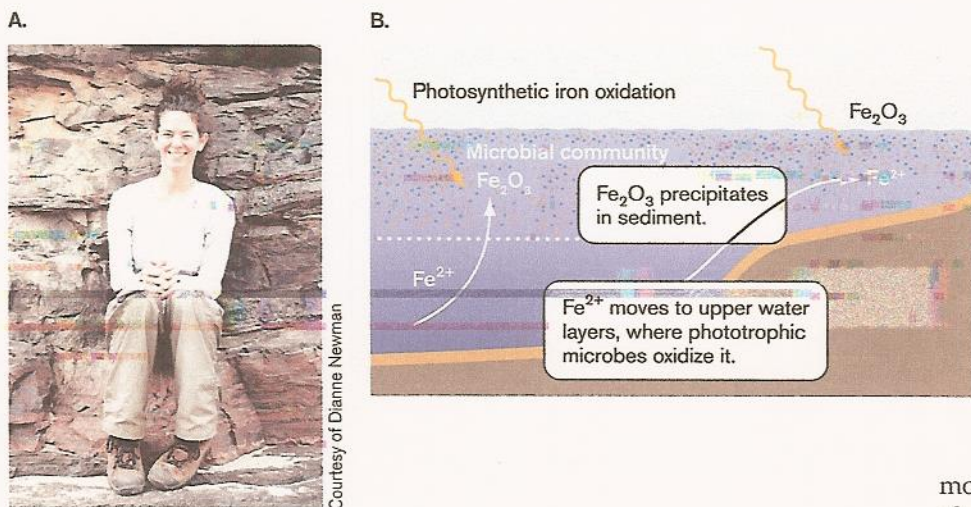


Figure 17.12 Iron phototrophy. **A.** Dianne Newman at the California Institute of Technology proposes that early iron phototrophs caused the iron oxide deposition generating banded iron formations. **B.** Photosynthetic oxidation of Fe^{2+} to Fe^{3+} may have generated sedimentary layers of Fe_2O_3 and $FeO_x(OH)_4$.

molecules, such as adenine and simple amino acids, form spontaneously. These early-Earth simulation experiments can never prove the actual conditions under which life began, but they can suggest testable models with intriguing implications.

Origin and evolution of life on Earth

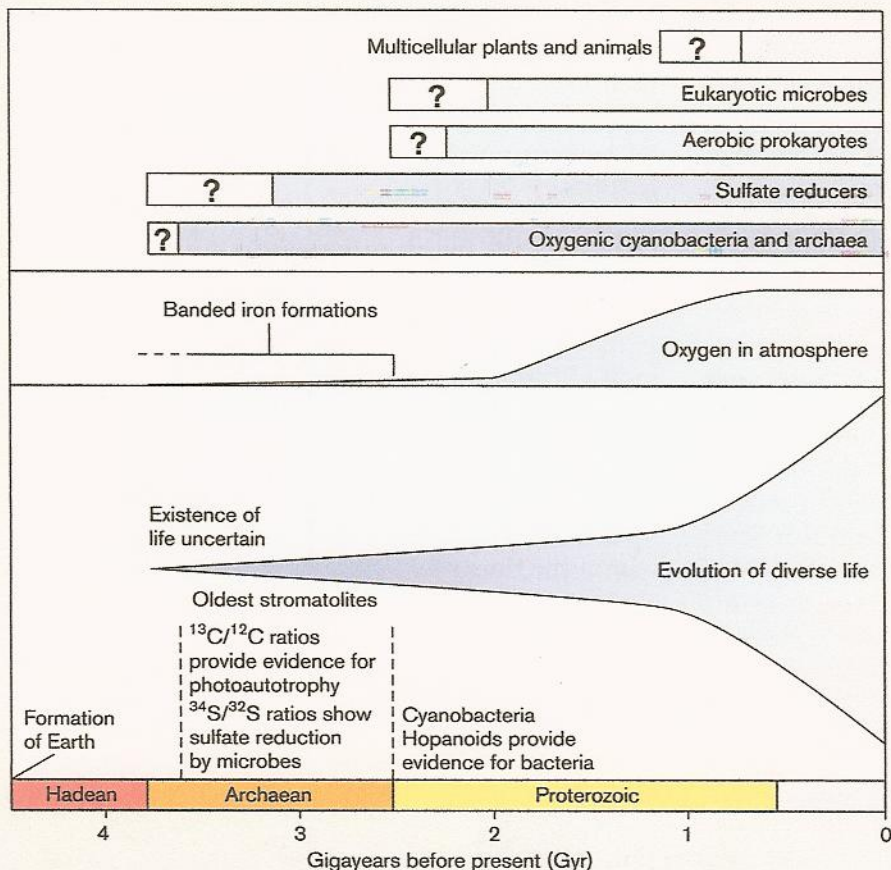


Figure 17.13 Proposed timeline for the origin and evolution of life. The planet Earth formed during the Hadean eon (about 4.5 Gyr ago). The environment was largely reducing until cyanobacteria pumped O_2 into the atmosphere. When the O_2 level reached sufficient levels (about 0.6 Gyr ago), multicellular animals and plants evolved. Question marks designate periods when evidence for given life-forms is uncertain.

TO SUMMARIZE:

- **Elements of life** were formed through nuclear reactions within stars that exploded into supernovae before the birth of our own sun.
- **Reduced molecules** compose Earth's interior. Oxidized minerals are found only near the surface. Early Earth had no molecular oxygen (O_2).
- **Archaean rocks show evidence for life** based on fossil stromatolites, isotope ratios, and chemical biosignatures. Fossil stromatolites appear in chert formations formed 3.4 Gyr ago. Isotope ratios for carbon indicate photosynthesis at 3.7 Gyr ago and sulfate reduction at 3.47 Gyr. Cyanobacterial hopanoids appear at 2.5 Gyr ago.
- **Microfossils of filamentous and colonial prokaryotes** date to 2.0 Gyr ago. At 1.2 Gyr, larger fossil cells resemble those of modern eukaryotes.
- **Early metabolism** involved anaerobic oxidation-reduction reactions. Likely forms of early metabolism include sulfate respiration, light-driven ion pumps, iron phototrophy, and methanogenesis.

■ **Banded iron formations** reflect the cyclic increase and decrease of oxygen produced by cyanobacteria and consumed through reaction with reduced iron. After all the ocean's iron was oxidized, oxygen increased gradually in the atmosphere.

17.2 Models for Early Life

Various models have been proposed to explain how the first life-forms originated from nonliving materials and how they replicated and evolved. Models for early life attempt to address the following questions: In what kind of environment did the first cells form? What kind of metabolism did the first cells use to generate energy? What was their hereditary material?

Models for Origin of the First Cells

Models for early life include:

- **The prebiotic soup.** Organic building blocks of life could arise **abiotically** (in the absence of life) out of simple reduced chemicals such as ammonia and methane. This "prebiotic soup" could have generated complex macromolecules that eventually acquired the apparatus needed for self-replication and membrane compartmentalization.
- **Metabolist models.** The central components of intermediary metabolism, including the TCA cycle to generate amino acids, arose from self-sustaining chemical reactions based on inorganic chemicals. These abiotic reactions then acquired self-replicating macromolecules and membranes.
- **The RNA world.** Proposed by Francis Crick in the 1960s, the **RNA world** is a model of early life in which RNA performed all the informational and catalytic roles of today's DNA and proteins. The concept of an RNA world derives support from the emerging sequences of genomes, which reveal thousands of catalytic and structural RNAs.

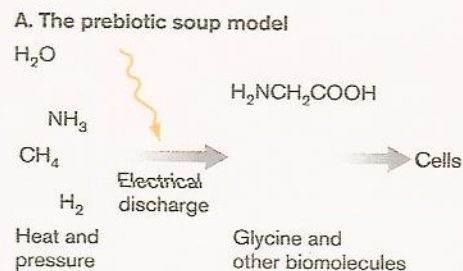
The prebiotic soup. In the mid-twentieth century, biochemists Aleksandr Oparin, at Moscow University, and Stanley Miller and Harold Urey, at the University of Chicago, showed that organic building blocks of life could arise abiotically out of a mixture of water and reduced chemicals, including CH_4 , NH_3 , and H_2 (Fig. 17.14). The mixture was subjected to an electrical discharge, similar to the lightning discharges that arise from volcanic eruptions, which would have been common in the late Hadean or early Archaean eons. The chemical reaction produced fundamental amino acids such as glycine and alanine. Similar experiments by Juan Oró, at the University of Houston, showed the formation of adenine by condensation of ammonia and methane. The same amino acids and nucleic bases are found in meteorites, which are believed to retain the chemistry of the early solar system "frozen" in time.

The original model conditions for the prebiotic soup assumed that molecules in the early Archaean ocean were largely reduced, with little or no oxygen present in the atmosphere. More recent geochemical evidence suggests that the early ocean actually included oxidized forms of nitrogen, sulfur, and iron that arose through reactions driven by ultraviolet radiation, which penetrated the atmosphere in the absence of the ozone layer. These oxidized minerals could have reacted with the reduced crustal minerals, releasing energy to drive production of more complex biomolecules.

Forming the first cell, or "proto-cell," must have required enclosing the first biochemical reactants within a membrane-like compartment. Such compartments can arise spontaneously from fatty acid derivatives such as fatty acid glycerol esters. The fatty acid derivatives are "amphipathic," that is, they possess both hydrophobic portions that associate together as well as hydrophilic portions that associate with water. In water, the fatty acid derivatives collect in "micelles," small round aggregates in which the hydrophobic portions associate in the interior and the hydrophilic portions associate with water. Under certain conditions, micelles can aggregate to form hollow spheres of membrane. The membrane spheres can

Figure 17.14 The prebiotic soup model for the origin of life.

A. In the prebiotic soup, inorganic molecules could have reacted to form complex macromolecules that eventually acquired the apparatus for self-replication and membrane compartmentalization. B. Lightning accompanies eruption of the Galunggung volcano in West Java, Indonesia, 1982. The first biomolecules may have formed as a result of lightning triggered by volcanic eruption.



R. Hadian, U.S. Geological Survey

be made to enclose molecules such as RNA, suggesting a primitive cell-like form. These spontaneous processes of membrane formation suggest models for how the first living cells may have arisen.

Metabolist model. Other models attempt to explain the origin of biosynthesis based on CO_2 fixation, the fundamental metabolism of all life today. Proponents of a **metabolist model**, including Harold Morowitz and Günter Wächterhäuser, at George Mason University, propose that CO_2 -based metabolism originated through self-sustaining reactions (Fig. 17.15A). Simulation experiments suggest that such premetabolic reactions could have been catalyzed by metal sulfides prevalent in the early ocean. For example, abiotic polymerization of CO_2 into TCA cycle intermediates may be catalyzed by FeS.

How did simple inorganic reactions lead to biochemical cycles involving more complex biopolymers such as nucleic acids and proteins? A major challenge is to explain the genetic code by which nucleic acid codons are assigned to unique amino acids. The genetic code may have arisen from an earlier pretranslational mechanism of amino acid biosynthesis (Fig. 17.15B). In this mechanism, proposed by Morowitz and colleagues, amino acids were originally synthesized from TCA cycle acids complexed to a dinucleotide. The dinucleotide later evolved into the first two nucleotides of the codon specifying the amino acid. The proposed dinucleotide association explains certain features of the genetic code, such as the fact that most amino acids specified by a codon starting with the same

nucleotide are synthesized from the same TCA cycle acid (discussed in Chapter 15).

The RNA world. Neither the prebiotic soup model nor the **metabolist models** account for the evolution of macromolecules that encode complex information, such as nucleic acids and proteins. A candidate for life's first "informational molecule" is RNA. RNA is a relatively simple biomolecule, with only 4 different "letters," compared to the 20 standard amino acids of proteins. Its purine bases, especially adenine, have been shown to arise spontaneously from ammonia and carbon dioxide under conditions believed to resemble those of the Archaean eon. Its ribose sugar is a fundamental building block of living cells, with key roles in numerous biochemical pathways, including the Calvin-Benson cycle and the synthesis of deoxyribose for DNA. Compared to DNA, RNA is easier to form and degrade, and its pyrimidine base uracil is formed early by biochemical pathways; only later is it transformed to the thymine used by DNA.

Most importantly, RNA molecules have been shown to possess catalytic properties analogous to those of proteins. Catalytic RNA molecules are called **ribozymes**. The first ribozyme, discovered by Nobel laureate Tom Cech in the protist *Tetrahymena*, can splice introns in mRNA. Other ribozymes actually catalyze synthesis of complementary strands of RNA, suggesting a model for early replication of RNA chromosomes. The most elaborate example of catalytic RNA is found in the ribosome. In the ribosome, X-ray crystallography reveals that the

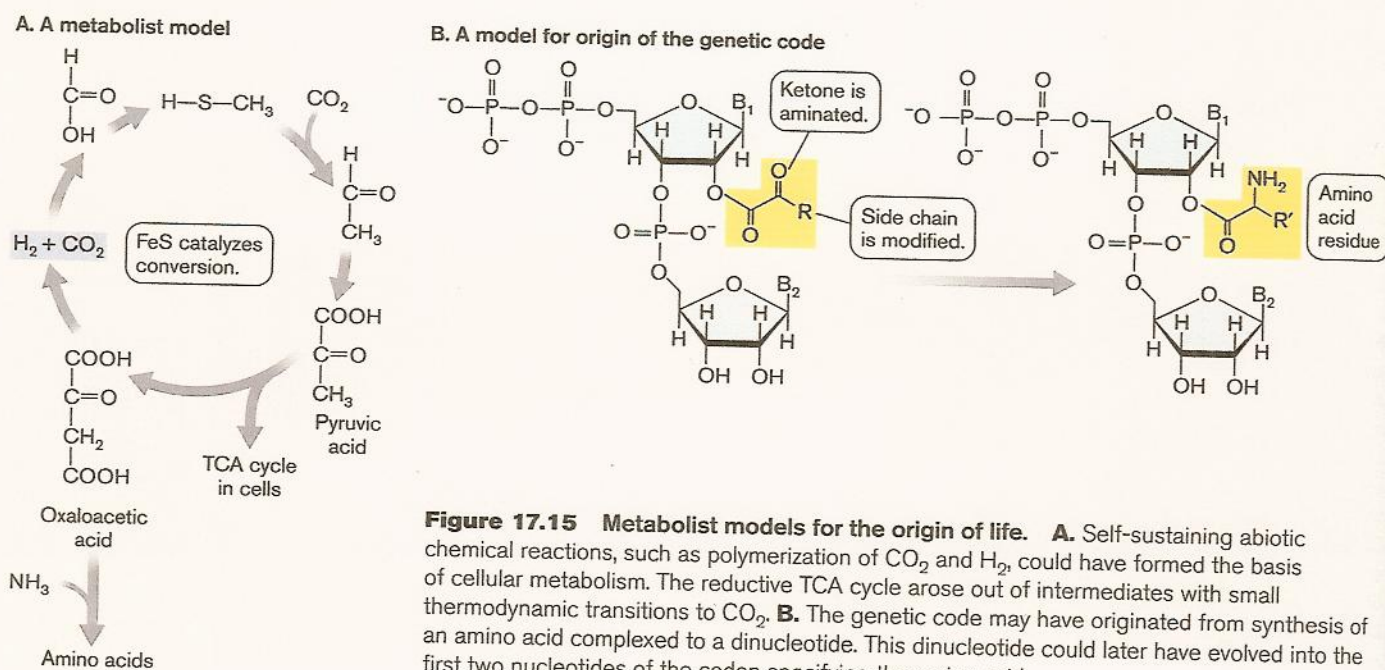


Figure 17.15 Metabolist models for the origin of life. **A.** Self-sustaining abiotic chemical reactions, such as polymerization of CO_2 and H_2 , could have formed the basis of cellular metabolism. The reductive TCA cycle arose out of intermediates with small thermodynamic transitions to CO_2 . **B.** The genetic code may have originated from synthesis of an amino acid complexed to a dinucleotide. This dinucleotide could later have evolved into the first two nucleotides of the codon specifying the amino acid.

key steps of protein synthesis, such as peptide bond formation, are actually catalyzed by the RNA components, not proteins (discussed in Chapter 8). The ribosomal proteins possess relatively little catalytic function; their main role seems to be protection and structural support of the RNA.

Thus, in the earliest cells, RNA might have fulfilled all the functions today filled by DNA and proteins, including information storage, replication, and catalysis (Fig. 17.16). This model is known as the “RNA world.” The prominent function of RNA in the ribosome, one of life’s most ancient and conserved molecular machines, leads to a model for the transition from an RNA world to the modern cell, with unexpected relevance for modern medicine (Special Topic 17.1).

The RNA world model explains the central role of RNA throughout the history of living cells. Yet the role of RNA offers little clue as to the origins of cell compartmentalization and metabolism. No one model of life’s origin yet addresses all the requirements for a living cell—metabolism, membrane compartmentalization, and hereditary material. Each model does, however, offer important insights into the evolutionary history and mechanisms of life today.

THOUGHT QUESTION 17.2 Outline the strengths and limitations of each model of the origin of living cells. Which aspects of living cells does each model explain?

Unresolved Questions about Early Life

Overall, geology and biochemistry provide compelling evidence that organisms resembling today’s cyanobacteria lived on Earth at least 2.5 Gyr ago, possibly 3.7 Gyr ago, and that bacteria with anaerobic metabolism evolved as early or earlier. Many intriguing questions remain. We outline here three unresolved questions regarding the

temperature of early Earth, the role of methane in the early atmosphere, and the actual source of Earth’s first cells.

Thermophile or psychrophile? The apparent existence of life so soon after Earth cooled suggests a thermophilic origin. Thermophily is supported by the fact that in the domains Bacteria and Archaea, the deepest-branching species (that is, species that diverged the earliest from others in the domain) are thermophiles. Such organisms could have thrived at hydrothermal vents, which offer a continual supply of H_2S and carbonates.

On the other hand, after meteoric bombardment abated, early Earth should have become glacially cold. In the Archaean, solar radiation was 20–30% less intense than it is today, and the thin CO_2 atmosphere was insufficient to increase the temperature by a greenhouse effect. A colder habitat would support psychrophiles. Psychrophiles might have had an advantage in an “RNA world,” given the thermal instability of RNA compared to DNA and proteins.

A world of methane? Among Earth’s earliest life-forms were methanogens (methane producers). Methanogens are one of the most widely divergent groups of organisms and persist today in environments ranging from anaerobic sediment to the human intestine. Methanogenesis requires only carbon dioxide and hydrogen gas, which would have been plentiful in early anoxic sediment. The production of methane, an extremely potent greenhouse gas, could have greatly increased Earth’s temperature during the Archaean. Thus, methanogenesis could explain how Earth escaped the permanent freeze of Mars. Overheating would have been halted when the oxygen gas produced by cyanobacteria enabled growth of methanotrophs, bacteria that oxidize methane. The decline of methane and the rise of CO_2 then brought about relative thermal stability.

The debate over temperature and climate of early Earth has interesting implications for Earth today when we again face the prospect of massive global climate change. Human agriculture favors explosive growth of methanogens, which threaten to accelerate global warming faster than the biosphere can moderate it. Understanding the climate of early Earth may help us better understand and manage our own climate, as discussed in Chapter 22.

Origin on Earth or elsewhere? Twenty years ago, the accepted picture of life’s origin was still one of anaerobic early metabolism that gave rise much later to oxygenic and aerobic metabolism. But emerging evidence from fossils and geochemistry has inexorably pushed back the earliest known dates for several kinds of metabolism closer to 3.7 Gyr. This implies that as soon as Earth cooled to a temperature suitable for life, all the fundamental components of cells evolved almost immediately. How could

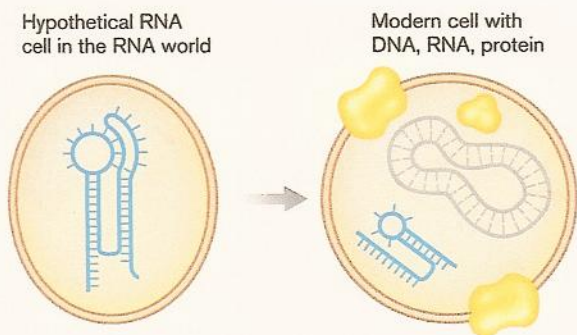


Figure 17.16 The RNA world model for the origin of life. In the RNA world, RNA molecules performed all the structural and catalytic functions performed today by proteins and DNA.

life, with all its diverse kinds of metabolism, have arisen so quickly?

The mystery deepens as we combine geochemistry with **phylogeny**, the measurement of genetic relatedness (discussed in the next section). Australian geochemist Roger Buick and colleagues at the University of Washington discovered early evidence of sulfate respiration based on isotope ratios of sulfur (**Fig. 17.17A**). Sulfate reducers use sulfate (SO_4^{2-}) as an electron acceptor to catabolize organic compounds in the absence of O_2 (as discussed in Chapter 14). The sulfate reductase enzyme preferentially acts on ^{32}S , generating sulfide depleted for ^{34}S . Buick discovered ^{34}S -depleted sulfides trapped in rock crystals of formations in western Australia dated to 3.47 Gyr.

The early date was surprising because sulfate respiration is performed by a class of bacteria that evolved relatively late, based on DNA sequence analysis (**Fig. 17.17B**). Sequence similarity data show that sulfate respirers diverged from other bacteria well after bacteria diverged from archaea and eukaryotes. So if the sulfate respirers had already diverged by 3.47 Gyr ago, when did bacteria diverge from archaea?

DNA sequence analysis shows that the common ancestor of bacteria, eukaryotes, and archaea already possessed most of the complexity of the organisms that diverged from it. Furthermore, data from Buick's laboratory in 2006 indicates biosignatures of eukaryotes as early as 2.4 Gyr ago, far earlier than was thought possible.

If the rate of evolution were constant, the three major domains would have diverged before the formation of Earth. In other words, life would have evolved elsewhere, and then come to Earth.

The idea that life-forms originated elsewhere and "seeded" life on Earth is called **panspermia**. Theories of panspermia remain highly speculative. One hypothesis is that microbial life originated on Mars and was then carried to Earth on meteorites. As the solar system formed, Mars would have cooled sooner than Earth, and as a smaller planet, its weaker gravity would have generated less bombardment by meteorites. Martian rocks ejected into space by meteor impact have reached the Earth, and calculations based on simulated space habitats show that microbes could survive such a journey. A Martian origin, however, only gains us about half a billion years; it does not really explain the origin of life's complexity and diversity. Did life-forms come from still farther away, perhaps borne on interstellar dust from some other solar system?

An alternative possibility is that early evolution on Earth occurred much faster than later evolution. Simpler reproductive entities such as viruses mutate and evolve much faster than modern cells. If early cells mutated as fast as viruses, they would have evolved faster than indicated by molecular clock molecules such as small-subunit ribosomal RNA (a method discussed in Section 17.3). Thus, for example, the common ancestor of Buick's sulfate reducers and cyanobacteria may have arisen on Earth but evolved much faster than later bacteria. The answers are unknown.

THOUGHT QUESTION 17.3 Suppose living organisms were to be found on Mars. How might such a find shed light on the origin and evolution of life on Earth?

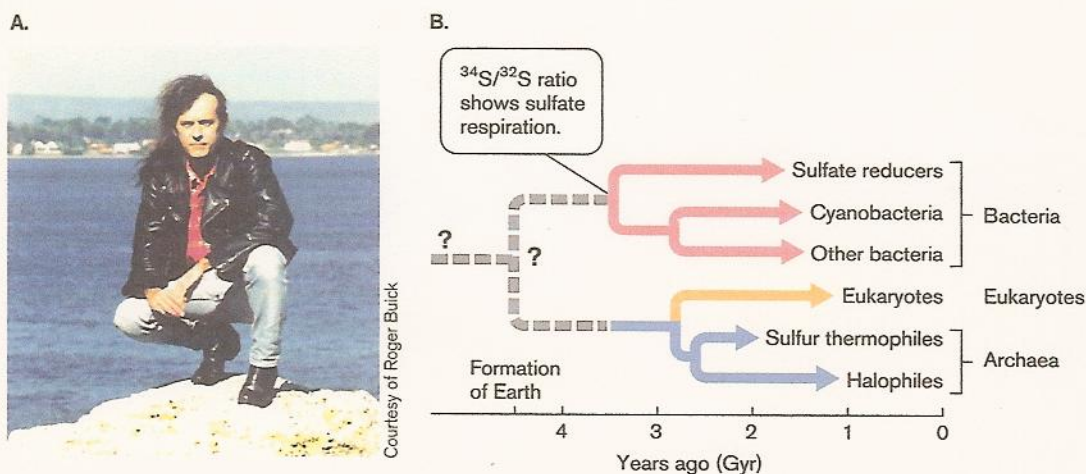


Figure 17.17 Chemical biosignatures calibrate microbial divergence. **A.** Roger Buick, Australian geochemist, explores isotope ratios and fossil evidence for early microbial life. Besides science, he likes "listening to punk bands, reading interminable Russian novels and arguing politics ferociously." **B.** The divergence of major life-forms is based on comparing sequences of small-subunit rRNA. Discovery of ^{34}S -depleted rock formations 3.5 Gyr old suggests that sulfate respirers evolved by that time. Other biosignatures calibrate the divergence of eukaryotes at 2.70 Gyr. *Source:* B. Based on Shen, et al. 2001. *Nature* 410:77–81.