20 LIFE'S ORIGIN AND EARLY EVOLUTION

Looking for Life in All the Odd Places

In the 1960s, microbiologist Thomas Brock was looking for signs of life in the hot springs and pools in Yellowstone National Park (Figure 20.1). He found a simple ecosystem of microscopically small cells, including *Thermus aquaticus*. This prokaryote uses simple carbon compounds dissolved in the water as its energy source. It is known as one of the thermophiles, or "heat lovers," for good reason. *T. aquaticus* withstands temperatures on the order of 80°C (176°F)!

Brock's work had two unexpected results. First, it put researchers on paths that led them to a great domain of life, the Archaea. Second, it led to a faster way to copy DNA and end up with useful amounts of it. *T. aquaticus* happens to make a heat-resistant enzyme, and it can catalyze the polymerase chain reaction—PCR. Synthetic forms of the enzyme helped trigger a revolution in biotechnology.

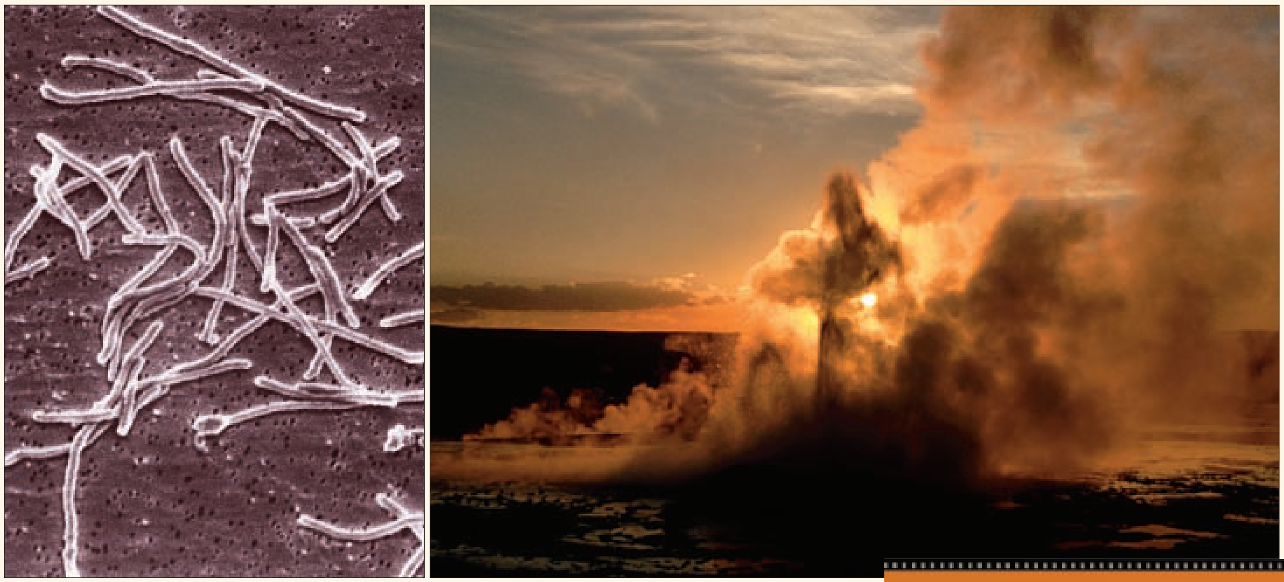
Bioprospecting became the new game in town. Many companies started to look closely at thermal pools and other extreme environments for species that might yield valuable products. They found forms of life adapted to extraordinary levels of temperature, acidity, alkalinity, salinity, and pressure.

To extreme thermophiles on the seafloor, Yellowstone's hot water would be too cool. They live in the superheated, mineral-rich water near hydrothermal vents. One kind even grows and reproduces at 121°C (249°F). Different species live in acidic springs, where the pH approaches zero, and in highly alkaline soda lakes. In Earth's polar regions, some types cling to life in salt ponds that never freeze and in glacial ice that never melts.

Extreme environments also support some eukaryotic species of ancient lineages. Populations of snow algae tint mountain glaciers red. Another red alga, *Cyanidium caldarium,* is a resident of acidic hot springs. Free-living photosynthetic cells called diatoms live in extremely salty lakes, where the hypertonicity would make cells of most organisms shrivel and die.

What could top that? Nanobes. Australian researchers found nanobes growing 3.8 kilometers (3 miles) below Earth's surface in truly hot rocks—170°C (338°F). Being one-tenth the size of most bacteria, nanobes cannot be observed without electron microscopes. Outwardly, they look something like the simplest fungi (Figure 20.2).

Nanobes are probably too small to be alive. They do not seem to be big enough to hold all of the metabolic machinery that now runs life processes. Even so, nanobes do contain DNA. And they appear to grow. Are they like proto-cells, which preceded the origin of the first living cells? Maybe.



Watch the video online!

Figure 20.1 From a thermal pool in Yellowstone National Park, cells of *Thermus aquaticus*, a prokaryotic species that is immensely admired by recombinant DNA researchers for its heat-resistant enzymes.

IMPACTS, ISSUES

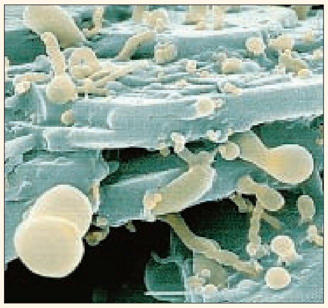


Figure 20.2 Nanobes, possibly like proto-cells. Australian researchers found them in hot rocks far beneath Earth's surface. They are only fifteen to twenty nanometers across; this image has been magnified 20,000 times. However, they do have DNA and other organic compounds enclosed within a membrane, and they grow.

What is the point of these examples? Simply this: *Life can take hold in almost any environment that has sources of carbon and energy.*

This chapter is your introduction to a sweeping slice through time, one that cuts back to Earth's formation and to life's chemical origins. The picture it paints sets the stage for the next unit, which will take you along lines of descent that led to the present range of biodiversity.

The picture is incomplete. Even so, evidence from many avenues of research points to a concept that can help us organize information about an immense journey: *Life is a magnificent continuation of the physical and chemical evolution of the universe, and of the planet Earth.*

How Would You Vote?

Private companies make millions of dollars selling an enzyme first isolated from cells in Yellowstone National Park. Should the federal government let private companies bioprospect within the boundaries of national parks, as long as it shares in the profits from any discoveries? See BiologyNow for details, then vote online.

Key Concepts

ABIOTIC SYNTHESIS OF ORGANIC COMPOUNDS

The origin and early evolution of life correlate with the physical and chemical evolution of the universe, the stars, and Earth. The first step toward life was the spontaneous formation of complex organic compounds from simpler substances present on the early Earth. Section 20.1

ORIGIN AND EARLY EVOLUTION OF CELLS

Laboratory studies and computer simulations yield indirect evidence that self-assembly of membranes, combined with chemical and molecular evolution, gave rise to the structural and functional forerunners of cells.

The first cells were anaerobic prokaryotes. Some gave rise to bacteria, others to archaeans and to the ancestors of eukaryotic cells. Evolution of the noncyclic pathway of photosynthesis added oxygen to the atmosphere, which became a major selection pressure. Sections 20.2, 20.3

HOW THE FIRST EUKARYOTIC CELLS EVOLVED

Organelles help define eukaryotic cells. The nucleus and ER membranes may have evolved through infoldings of the plasma membrane. Mitochondria and chloroplasts may be descended from bacterial parasites or prey that took up permanent residence in host cells. Section 20.4

VISUAL PREVIEW OF THE HISTORY OF LIFE

A timeline for milestones in the history of life highlights the shared connections among all organisms. Section 20.5

Links to Earlier Concepts

This chapter starts your survey of the sweep of biodiversity, as introduced in Section 1.3. This is where all of those details of cell metabolism, genetics, and evolutionary theory start to converge and help you make sense of life's fabulous journey. Now you can correlate prokaryotes (4.3) and eukaryotes (4.4) with a timeline of Earth history (17.5).

You will use your knowledge of how organic compounds are assembled (3.2), and of amino acids (3.5), membranes (5.1), enzymes (6.3), and the link between photosynthesis and aerobic respiration (Chapter 7). You may find yourself referring to the sections on DNA replication (13.3), RNAs and protein synthesis (14.1), and the genetic code (14.2). You will consider how the nucleus, ER, mitochondria, and chloroplasts (4.5–4.8) may have originated.

ABIOTIC SYNTHESIS OF ORGANIC COMPOUNDS

20.1 In the Beginning . . .

LINKS TO SECTIONS 3.2, 3.5

Life originated when Earth was a thin-crusted inferno, so we may never find evidence of the first cells. Still, answers to three questions can yield clues to their origins. What were conditions like? Did cells emerge as a result of chemical and molecular evolution? Can experimental tests disprove that they did? Let's take a look.

Some clear evening, look up at the moon. *Five billion trillion times* the distance between it and you are the systems of stars, or galaxies, at the edge of the known universe. Light energy travels far faster than anything else, millions of meters a second, yet wavelengths of light that originated from faraway galaxies billions of years ago are just now reaching Earth. By all known measures, all near and distant galaxies in the space of the universe are moving away from one another. The entire universe, it seems, is expanding. One theory of how the colossal expansion started might account for every bit of matter in every living thing.

Figure 20.3 Part of the Eagle nebula, a hotbed of star formation. Each pillar is wider than our solar system. New stars shine on the tips of gaseous streamers.

Think about how you can rewind a videotape on a VCR, then imagine "rewinding" the universe. As you do, the galaxies start moving closer together. After 12 to 15 billion years of rewinding, all galaxies, all matter and space are compressed into a hot, dense volume at one single point. You have arrived at time zero.

That incredibly hot, dense state lasted only for an instant. What happened next is called the **big bang**, the nearly instantaneous distribution of all matter and energy throughout the universe. Within minutes, the temperature dropped a billion degrees. Nuclear fusion reactions created most of the simplest elements, such as helium, which still are the most abundant kinds in the universe. Radio telescopes have detected a relic of the big bang—cooled, diluted background radiation left over from the beginning of time.

Over the next billion years, uncountable numbers of gaseous particles collided, and gravitational forces condensed them into the first stars. When stars were massive enough, nuclear reactions ignited inside them and gave off tremendous light and heat as the heavier elements formed. Stars have a life history, from birth to an often explosive death. In what might be called the original stardust memories, the heavier elements released from dying stars were swept up when new stars formed and helped form even heavier elements.

When explosions of dying stars ripped through our galaxy, they left behind a dense cloud of dust and gas that extended trillions of kilometers in space. As the cloud cooled, countless bits of matter gravitated toward one another. By 5 billion years ago, the shining star of our solar system—the sun—was born.

CONDITIONS ON THE EARLY EARTH

Figure 20.3 shows part of one of the vast clouds in the universe. It is mostly hydrogen gas, along with water, iron, silicates, hydrogen cyanide, ammonia, methane, formaldehyde, and other small inorganic and organic substances. Between 4.6 billion and 4.5 billion years ago, the cloud that became our solar system probably had a similar composition. Clumps of minerals and ice at the cloud's perimeter grew more massive. They became planets; one was the early Earth.

By four billion years ago, gases blanketed the first patches of Earth's thin, fiery crust (Figure 20.4). Most likely, this first atmosphere was a mixture of gaseous hydrogen, nitrogen, carbon monoxide, carbon dioxide. There was little free oxygen. How can we tell? When free oxygen is present, some binds to iron in rocks. However, geologists have discovered that such "rust" did not form until fairly recently in Earth's history.

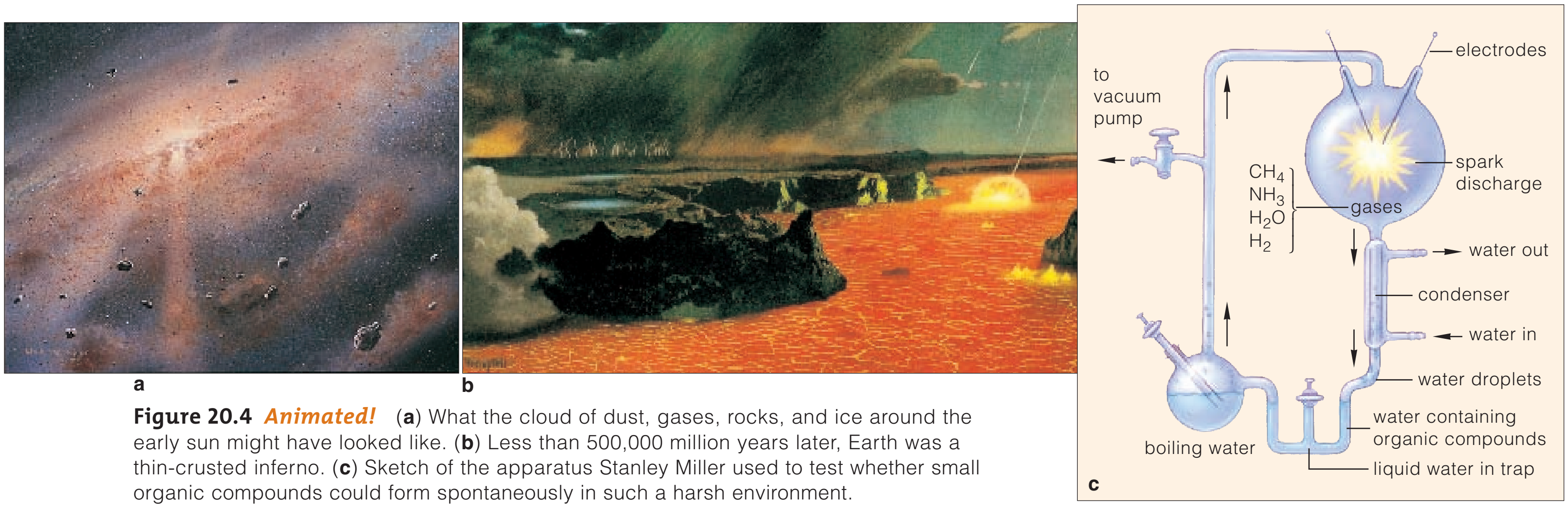


Figure 20.4 ***Animated!*** (**a**) What the cloud of dust, gases, rocks, and ice around the early sun might have looked like. (**b**) Less than 500,000 million years later, Earth was a thin-crusted inferno. (**c**) Sketch of the apparatus Stanley Miller used to test whether small organic compounds could form spontaneously in such a harsh environment.

The relatively low oxygen levels on the early Earth probably made the origin of life possible. Free oxygen is highly reactive. If it had been present, the organic compounds characteristic of life would not have been able to form and persist. Oxygen radicals would have attacked and destroyed compounds as they formed.

What about water? All of the water that fell on the molten surface would have evaporated at once. After the crust cooled and became solid, however, rainfall and runoff eroded mineral salts from rocks. Over many millions of years, salty water collected in crustal depressions and formed early seas. If liquid water had not accumulated, membranes could not have formed, because they take on their bilayer structure in water. No membrane, no cell, and no life.

ABIOTIC SYNTHESIS OF ORGANIC COMPOUNDS

Cells appeared less than 200 million years after the crust solidified, so complex carbohydrates and lipids, proteins, and nucleic acids must have formed by then. We know that meteorites, Mars, and Earth all formed at the same time, from the same cosmic cloud. Their rocks contain simple sugars, fatty acids, amino acids, and nucleotides, so we can expect that the precursors of biological molecules were on the early Earth, too.

Synthesizing organic compounds requires energy. On the early Earth, lightning, sunlight, or heat from hydrothermal vents might have fueled the reactions. Stanley Miller was the first to test the hypothesis that the simple compounds that now serve as the building blocks of life can form by chemical processes. He put water, methane, hydrogen, and ammonia in a reaction chamber. He kept circulating the mixture and zapping it with sparks to simulate lightning (Figure 20.4*c*). In less than a week, amino acids and other small organic compounds had formed in the chemical brew.

Recent geologic evidence suggests that Earth's early atmosphere was not quite like the Miller mixture. But in simulations that used other gases, different organic compounds formed—including certain types that can act as nucleotide precursors of nucleic acids.

By another hypothesis, simple organic compounds formed in outer space. Researchers detect amino acids in interstellar clouds and in some of the carbon-rich meteorites that have landed on Earth. One meteorite found in Australia contains eight amino acids that are identical with those in living organisms.

What about proteins, DNA, and the other *complex* organic compounds? Where could they form? In open water, hydrolysis reactions would have broken them apart as fast as they assembled. By one hypothesis, the clay of tidal flats bound and protected the newly forming polymers. Certain clays contain mineral ions that attract amino acids or nucleotides. Experiments show that once some of these molecules stick to clay, other molecules bond to them and form chains that resemble the proteins or nucleic acids in living cells.

Another hypothesis that is currently getting a lot of attention is this: The first biological molecules were synthesized near hydrothermal vents. Certainly the ancient seafloor was oxygen-poor. Experiments show that amino acids, at least, will condense into protein-like structures when heated in water.

Experiments provide indirect evidence that the complex organic molecules characteristic of life could have formed under conditions that probably prevailed on the early Earth.

20.2 How Did Cells Emerge?

LINKS TO SECTIONS 5.1, 6.3,13.4, 14.1, 14.3

Metabolism and reproduction are defining characteristics of life. In the first 600 million years or so of Earth history, enzymes, ATP, and other essential organic compounds assembled spontaneously. If they did so in the same places, their close association might have promoted the start of metabolic pathways and self-replicating systems.

ORIGIN OF AGENTS OF METABOLISM

Before cells appeared, chemical processes may have favored the formation of proteins and other complex organic compounds (Figure 20.5). However proteins originated, their molecular structure dictated their behavior. If some promoted reactions by acting like weak enzymes, they could interact with more amino acids and enzyme helpers, such as metal ions.

Visualize an early estuary, where seawater mixed with mineral-rich water that drained from the land. Beneath the sun's rays, organic molecules got stuck to clay in the mud (Figure 20.6*a*). At first, there were quantities of an amino acid; call it **D**. Molecules of **D** became incorporated into proteins—until **D** started to run out. Close by, however, was a weakly catalytic protein. This protein could speed the formation of **D** from a plentiful, simpler substance **C**.

By chance, clumps of organic molecules included the enzyme-like protein. Such clumps had an edge in the acquisition of starting materials. Suppose that the **C** molecules became scarce. The advantage tilted to molecular clumps that promoted the formation of **C** from simpler substances **B** and **A**. Suppose that **B** and **A** were carbon dioxide and water. The atmosphere and seas contain unlimited amounts of both. Thus, chemical selection favored a synthetic pathway:

$$A + B \longrightarrow C \longrightarrow D$$

Were some clumps better at absorbing and using energy? Think back on chlorophyll *a* (Section 7.1). A group of rings in this pigment absorbs light and gives up electrons. The same kinds of ring structures occur in electron transfer chains in all photosynthetic and aerobically respiring cells. They form spontaneously from formaldehyde (Figure 20.5)—one of the legacies of cosmic clouds. Were similar structures transferring electrons in early metabolic pathways? Probably.

The point is, long before cells emerged, a form of chemical competition was under way. Enzymes and other reactive organic compounds had the competitive edge in the acquisition of energy and materials.

ORIGIN OF THE FIRST PLASMA MEMBRANES

All living cells have an outer membrane that controls which substances enter and leave the cytoplasm in a given interval (Section 5.1). By a current hypothesis, proto-cells were transitional forms between simple organic compounds and the first living cells. These **proto-cells** were no more than membrane-bound sacs

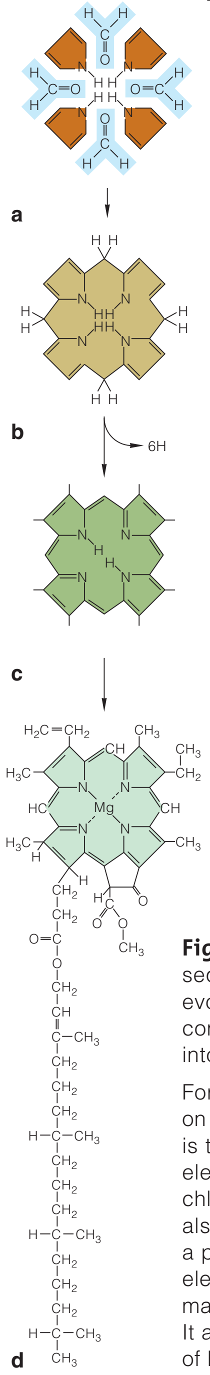


Figure 20.5 Hypothetical sequence of the chemical evolution of (**a**) an organic compound, formaldehyde, into (**c**) porphyrin.

Formaldehyde was present on the early Earth. Porphyrin is the light-absorbing and electron-donating part of chlorophyll molecules (**d**). It also is part of cytochrome, a protein component of the electron transfer chains in many metabolic pathways. It also is part of the heme of hemoglobin.

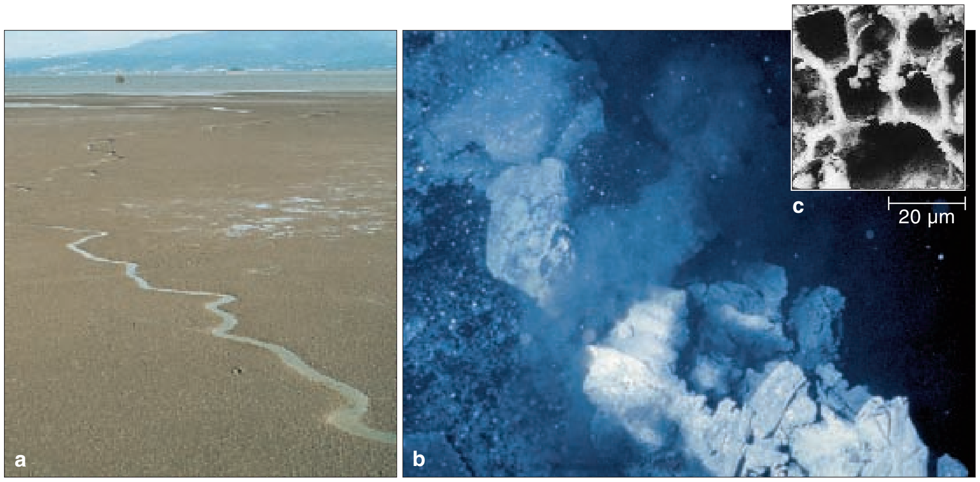
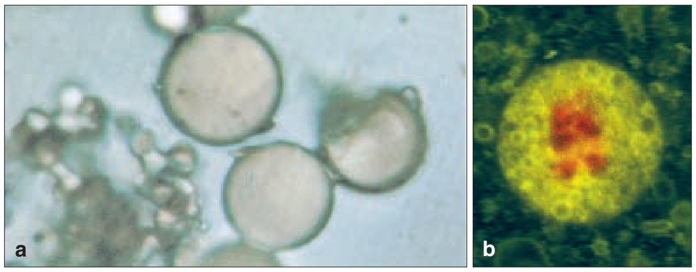


Figure 20.6 Where did the cells originate? Two likely candidates: (**a**) Clay templates in mud flats, and (**b**) iron sulfide-rich rocks at hydrothermal vents, which contain cell-sized chambers (**c**). Experiments show that such chambers are protected microenvironments in which membranes can form spontaneously. Iron sulfides projecting from the walls of such chambers catalyzed the synthesis of short peptide chains and other substances, as happens in metabolism. Many reactions in living cells use iron-sulfide cofactors. Are the cofactors a metallic legacy from a deep-sea ancestor? Perhaps.



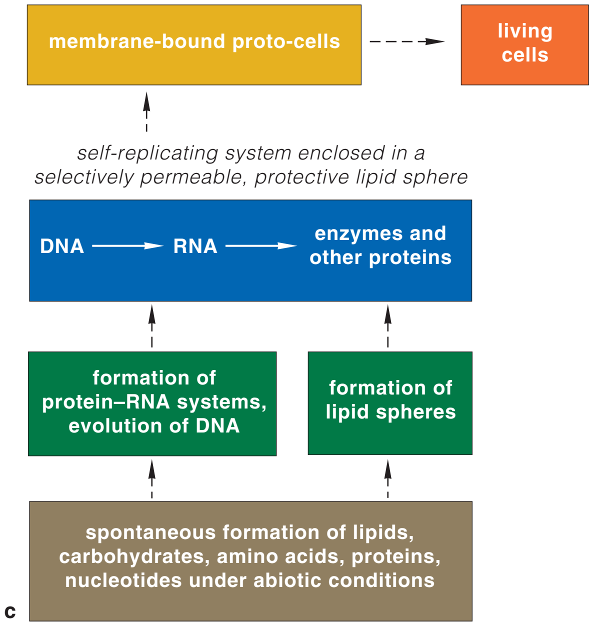


Figure 20.7 Laboratory-grown proto-cells. (**a**) Selectively permeable sacs. Heated amino acids formed protein chains. When moistened, the chains assembled into a membrane. (**b**) A membrane of fatty acids and alcohols (*green*) enclosing RNA-coated clay (*red*). The mineral-rich clay catalyzes RNA polymerization and promotes the formation of a membrane sac. (**c**) Model for steps in the chemical processes that led to the first living, self-replicating, membrane-bound cells.

that contained systems of enzymes and other agents of metabolism, and that were self-replicating.

Experiments reveal that membrane sacs can form spontaneously. Under conditions that simulate ancient sunbaked tidal flats, amino acids do form chains that surround a volume of fluid (Figure 20.7*a*). Fatty acids and alcohols spontaneously form vesicles, especially when clays rich in minerals are present (Figure 20.7*b*).

Or did proto-cells form from organic compounds at hydrothermal vents? Cell-sized chambers occur in mineral-rich rocks at existing vents (Figure 20.6*b*,*c*). Were the chamber walls replication templates for RNA, proteins, DNA, and lipids? The molecules would have accumulated inside, favoring the chemical conditions required for the emergence of living cells.

ORIGIN OF SELF-REPLICATING SYSTEMS

Life also is characterized by reproduction, which now starts with protein-building instructions in DNA. As you know from Section 14.3, it takes RNA, enzymes, and other molecules to translate DNA into proteins.

Coenzymes and metal ions assist most enzymes—and certain coenzymes are structurally identical with RNA subunits. When you mix and heat RNA subunits with very short chains of phosphate groups, they self-assemble into strands of RNA. Simple self-replicating systems of RNA, enzymes, and coenzymes have been made in laboratories. So we know RNA can serve as an information-storing template for making proteins.

Also, remember that one of the rRNA components of ribosomes catalyzes protein synthesis (Sections 14.3 and 14.4). The structure and function of ribosomes have been conserved over time; ribosomes of the most complex eukaryotes are extremely similar to those in prokaryotic cells of ancient lineages. rRNA's catalytic behavior probably evolved early in Earth history.

Did an **RNA world** *precede* the emergence of DNA? That is, were short RNA strands the first templates for protein synthesis? As you know, RNA and DNA are similar. Three of their four bases are identical. RNA's uracil differs from DNA's thymine by a single functional group. But DNA's *helically coiled, double-stranded* structure is more stable than RNA, and it can store much more protein-building information in less space. There would have been selective advantage in functionally separating the storage of protein-building information (DNA) from protein synthesis (RNA).

Until we identify chemical ancestors of RNA and DNA, the history of life's origin will not be complete. But clues are coming in. For instance, researchers fed data about inorganic compounds and energy sources into a supercomputer. They programmed the computer to simulate random chemical reactions among organic compounds, which may well have happened untold billions of times in the distant past. Then they ran the program again and again.

The outcome of their experiment was always the same. *Simple precursors evolved. Then they spontaneously organized themselves into large, complex molecules. And they began to interact as complex systems.*

There are gaps in our knowledge of life's origin. But diverse laboratory experiments and computer simulations show that chemical processes can result in all organic molecules and structures that we think of as being characteristic of life.

20.3 The First Cells

LINKS TO SECTIONS 4.3, 6.4, 7.8

The first cells apparently evolved during the Archaean, an eon that lasted from 3.8 billion to 2.5 billion years ago. Not long afterward, divergences gave rise to three great lineages that have persisted to the present.

THE GOLDEN AGE OF PROKARYOTES

Fossils indicate that the first cells were like existing prokaryotes; they had no nucleus (Section 4.3). There was very little free oxygen that could attack them. Its absence is a clue to their mode of nutrition. Anaerobic pathways would allow them to obtain energy from simple organic compounds and mineral ions that had accumulated by natural geologic processes in the seas.

Molecular comparisons of living prokaryotes tell us that some populations diverged not long after life originated. One lineage gave rise to the bacteria. The other gave rise to the shared ancestors of archaeans and eukaryotic cells.

Microscopically small fossils in 3.5-billion-year-old rocks give clues to what some of the first prokaryotes looked like (Figure 20.8*a*). Other fossils clearly show that chemoautotrophic forms had become established near deep-sea hydrothermal vents by 3.2 billion years ago. In some groups, pigments probably detected the type of weak infrared radiation (heat) that has been measured at hydrothermal vents. Pigments may have helped cells detect and avoid boiling water, as they do for some existing hydrothermal vent species.

Gene mutations arose independently in some of the prokaryotic populations. They led to modifications in radiation-sensitive pigments, electron transfer chains, and other bits of metabolic machinery that started a novel mode of nutrition. We call it the cyclic pathway of photosynthesis. Those bacterial populations were photoautotrophic; they had tapped into sunlight, an unlimited energy source (Section 7.8).

As they reproduced, those self-feeding populations of tiny cells grew on top of one another. They became flattened mats, infiltrated with calcium carbonate and other dissolved mineral ions, and fine sediments. In time, they were transformed into dome-shaped fossils known as **stromatolites**. Radiometric dating tells us that some are 3 billion years old (Figure 20.9).

When the Proterozoic dawned 2.7 billion years ago, stromatolites were abundant. By that time, a noncyclic pathway of photosynthesis had evolved in a bacterial lineage, the cyanobacteria. Cyanobacterial populations increased, and so did the pathway's waste product—free oxygen. At first, oxygen slowly accumulated in the surface waters of the seas, then in air. So now we return to events sketched out in Chapter 7.

An atmosphere enriched with free oxygen had two irreversible effects. First, *it stopped the further chemical origin of living cells*. Except in a few anaerobic habitats, complex organic compounds could no longer assemble spontaneously and stay intact; they could not escape attacks by oxygen radicals. Second, *aerobic respiration evolved and in time became the dominant energy-releasing pathway*. In many prokaryotic lineages, selection had favored this pathway, which neutralized oxygen by *using* it as an electron acceptor. Aerobic respiration was a key innovation that contributed to the rise of all complex, multicelled eukaryotes.

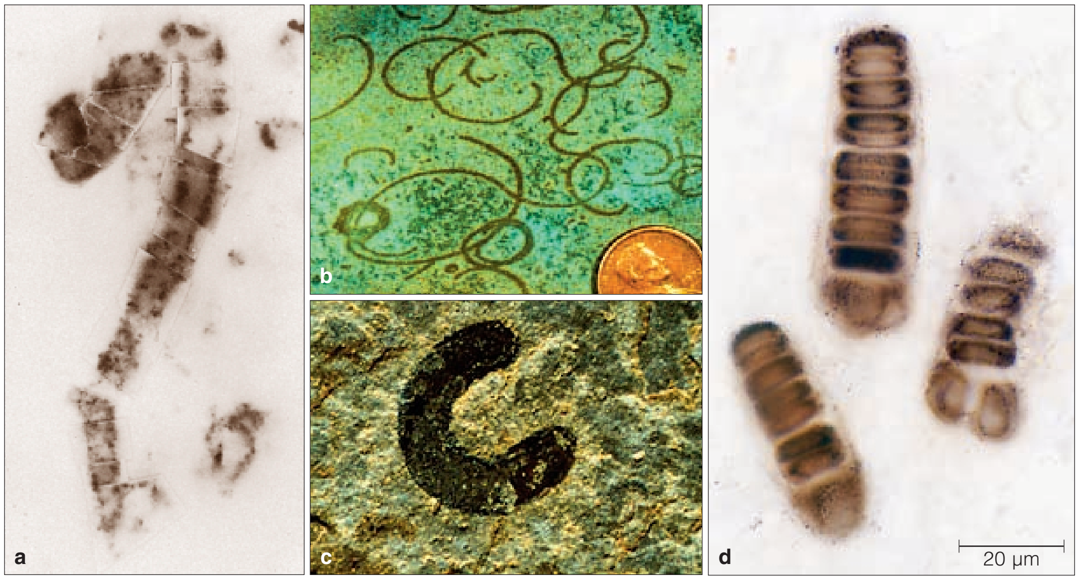


Figure 20.8 A sampling of early life. (**a**) A strand of what might be walled prokaryotic cells dates back 3.5 billion years. (**b**) One of the oldest known eukaryotic species, *Grypania spiralis*, which lived 2.1 billion years ago. Its fossilized colonies are large enough to see without a microscope. (**c**) Fossil of *Tawuia*, another early eukaryotic species that lived during the Proterozoic. (**d**) Fossils of a red alga, *Bangiomorpha pubescens*. This multicelled species lived 1.2 billion years ago, and it reproduced sexually.

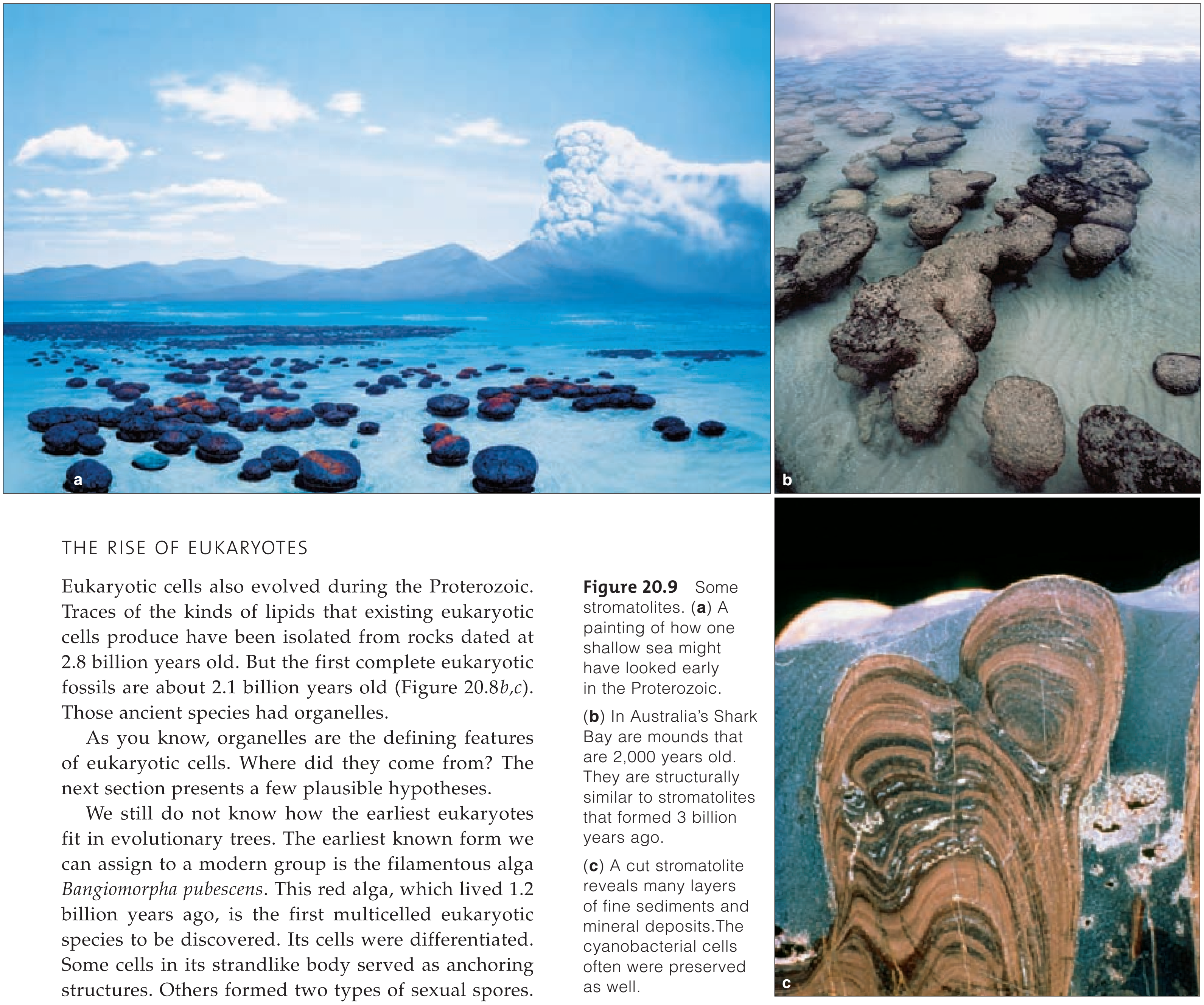


Figure 20.9 Some stromatolites. (**a**) A painting of how one shallow sea might have looked early in the Proterozoic.

(**b**) In Australia's Shark Bay are mounds that are 2,000 years old. They are structurally similar to stromatolites that formed 3 billion years ago.

(**c**) A cut stromatolite reveals many layers of fine sediments and mineral deposits.The cyanobacterial cells often were preserved as well.

THE RISE OF EUKARYOTES

Eukaryotic cells also evolved during the Proterozoic. Traces of the kinds of lipids that existing eukaryotic cells produce have been isolated from rocks dated at 2.8 billion years old. But the first complete eukaryotic fossils are about 2.1 billion years old (Figure 20.8*b,c*). Those ancient species had organelles.

As you know, organelles are the defining features of eukaryotic cells. Where did they come from? The next section presents a few plausible hypotheses.

We still do not know how the earliest eukaryotes fit in evolutionary trees. The earliest known form we can assign to a modern group is the filamentous alga *Bangiomorpha pubescens*. This red alga, which lived 1.2 billion years ago, is the first multicelled eukaryotic species to be discovered. Its cells were differentiated. Some cells in its strandlike body served as anchoring structures. Others formed two types of sexual spores. Spore production certainly makes *B. pubescens* one of the earliest practitioners of sexual reproduction.

By 1.1 billion years ago the supercontinent Rodinia had formed. Stromatolites dotted its vast shorelines, but 300 million years later, they were in decline. Were the cyanobacteria a vast food source for predators and parasites? By then, protists, fungi, animals, and the algae that would later give rise to plants were sharing the shoreline with them. Also, 570 million years ago, when oxygen in the atmosphere approached modern levels, animals began their first adaptive radiations in the Cambrian seas. A coevolutionary arms race that continues to this day was off and running.

The first living cells evolved by 3.8 billion years ago, in the Archaean eon. All were prokaryotic, and they obtained energy by anaerobic pathways. Not long afterward, the ancestors of archaeans and eukaryotic cells diverged from the lineage that led to modern bacteria.

After the noncyclic pathway of photosynthesis evolved, free oxygen accumulated in the atmosphere and ended the further spontaneous chemical origin of life. The stage was set for the evolution of eukaryotic cells.

20.4 Where Did Organelles Come From?

LINKS TO SECTIONS
4.3, 4.5–4.8, 14.2

Thanks to globe-hopping microfossil hunters, we have considerable evidence of early life, including the fossil treasures shown in Sections 4.3 and 20.3. Today, most descendant species contain a profusion of organelles. Where did the organelles come from?

ORIGIN OF THE NUCLEUS AND ER

Prokaryotic cells, recall, do not have an abundance of organelles. Some do have infoldings of their plasma membrane, which incorporates many enzymes and other components used in metabolic reactions (Figure 20.10*a*). Applying the theory of natural selection, we may hypothesize that infoldings originated among ancestors of eukaryotic cells. What advantages did the infoldings offer? They became channels that could concentrate nutrients, organic compounds, and other substances. Also, a membrane with a greater surface area could be a physical platform for more metabolic machinery as well as transport proteins. Remember the surface-to-volume ratio?

The channels of endoplasmic reticulum (ER) may have evolved this way. They also may have protected the metabolic machinery from uninvited guests. From time to time, metabolically "hungry" foreign cells do enter the cytoplasm of existing prokaryotic cells.

Some infoldings might have extended around the DNA, the start of a nuclear envelope (Figure 20.10*b*). A nuclear envelope would have been favored because it helped protect the cell's hereditary material from foreign DNA. Bacteria and the simple eukaryotic cells called yeasts can transfer plasmids among themselves. Early eukaryotic cells with a nuclear envelope could copy and use their messages of inheritance, free from metabolic competition from a potentially disruptive hodgepodge of foreign DNA.

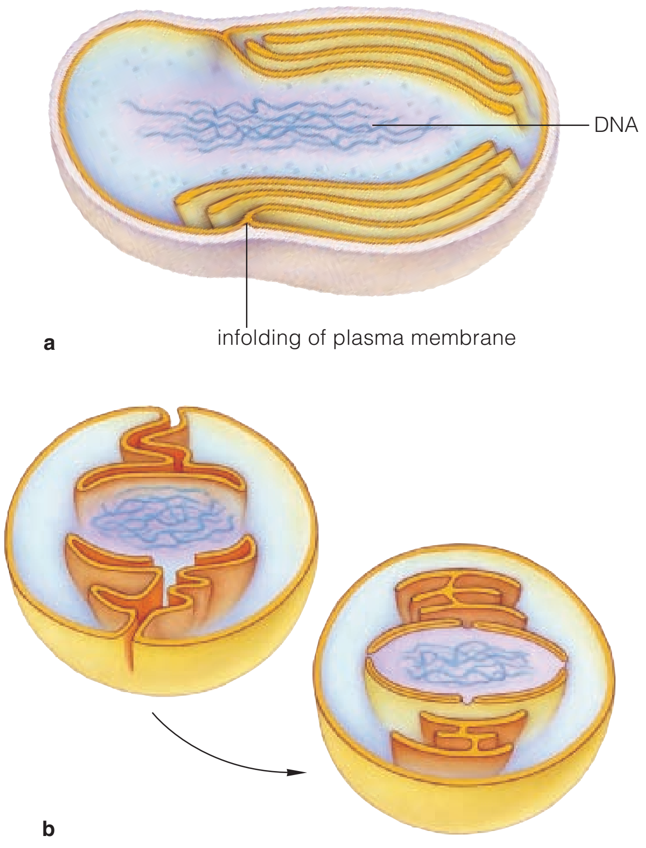


Figure 20.10 (**a**) Sketch of a bacterial cell (*Nitrobacter*) that lives in soil. Cytoplasmic fluid bathes permanent infoldings of the plasma membrane. (**b**) Model for the origin of the nuclear envelope and the endoplasmic reticulum. In prokaryotic ancestors of eukaryotic cells, infoldings of the plasma membrane may have evolved into these organelles.

ORIGIN OF MITOCHONDRIA AND CHLOROPLASTS

Early in the history of life, cells became food for one another. Heterotrophs engulfed autotrophs and other heterotrophs. Intracellular parasites dined inside their hosts. In some cases, the engulfed meals or parasites struck an uneasy balance with the host cells. They were protected, they withdrew some nutrients from the cytoplasm, and—like their hosts—they continued to divide and reproduce. Over time, they evolved into mitochondria, chloroplasts, and some other organelles.

The novel partnerships are one premise of a theory of **endosymbiosis**, as championed by Lynn Margulis and others. (*Endo–* means within and *symbiosis* means living together.) The symbiont species lives out its life inside a host species, and the interaction benefits one or both of them.

By this theory, eukaryotic cells evolved after the noncyclic pathway of photosynthesis emerged and permanently changed the atmosphere. By 2.1 billion years ago, remember, certain prokaryotic cells had adapted to the concentration of free oxygen and were already engaged in aerobic respiration. The ancestors of eukaryotic cells preyed upon some aerobic bacteria and were parasitized by others (Figure 20.11*a*). At that time, endosymbiotic interactions began.

The host began to use ATP produced by its aerobic symbiont. The aerobe no longer had to spend energy on acquiring raw materials; the host did this work for it. DNA regions that specified proteins produced by both host and symbiont were free to mutate and lose their function in one partner or the other. In time, both types of cells became incapable of independent life.

Figure 20.11 Clues to ancient endosymbiotic interactions. (**a**) What the ancestors of mitochondria may have looked like. The protist *Reclinomonas americana* has the structurally simplest mitochondria. The mitochondrial genes resemble genes of *Rickettsia prowazekii*, a parasitic bacterium that causes typhus. Like mitochondria, *R. prowazekii* divides only inside the cytoplasm of eukaryotic cells. Enzymes in the cytoplasm catalyze the partial breakdown of organic compounds—a task that is completed inside aerobically respiring mitochondria. (**b**) *Cyanophora paradoxa* is one of the flagellated protists called glaucophytes. Its mitochondria resemble aerobic bacteria in size and structure. Its photosynthetic structures resemble cyanobacteria—they even have a wall like that of cyanobacteria.

EVIDENCE OF ENDOSYMBIOSIS

Is such a theory far-fetched? A chance discovery in Jeon Kwang's laboratory suggests otherwise. In 1966, a rod-shaped bacterium had infected his culture of *Amoeba discoides*. Some infected cells died right away. Others grew more slowly, and they were smaller and vulnerable to starving to death. Kwang maintained the infected culture. Five years later, infected amoebas were harboring many bacterial cells, yet they were all thriving. Exposure to antibiotics killed the bacterial cells (but not the amoebas).

Infection-free cells were stripped of their nucleus and got a nucleus from an infected cell. They died. Yet more than 90 percent survived when a few bacteria were included with the transplant. As other studies showed, the infected amoebas had lost their ability to synthesize an essential enzyme. They depended on the bacterium to make it for them! Invading bacterial cells had become symbiotic with the amoebas.

When you think about it, mitochondria do resemble bacteria in size and structure. Each has its own DNA and divides independently of cell division. The inner membrane of a mitochondrion resembles a bacterial cell's plasma membrane. Its DNA has just a few genes (thirty-seven in human mitochondrial DNA). Also, a few of the codons are slightly different from those of the near-universal genetic code (Section 14.2).

We can predict that chloroplasts, too, originated by endosymbiosis. In one scenario, photosynthetic cells were engulfed by predatory aerobic bacteria, but they escaped digestion. They started to absorb nutrients in the host's cytoplasm and continued to function. They also released oxygen when they photosynthesized. By releasing oxygen inside the aerobically respiring hosts, they acted as agents favoring endosymbiosis.

In their metabolism and their overall nucleic acid sequence, existing chloroplasts resemble cyanobacteria. The chloroplast DNA replicates itself independently of cellular DNA. Chloroplasts and the cells in which they reside divide independently of each other.

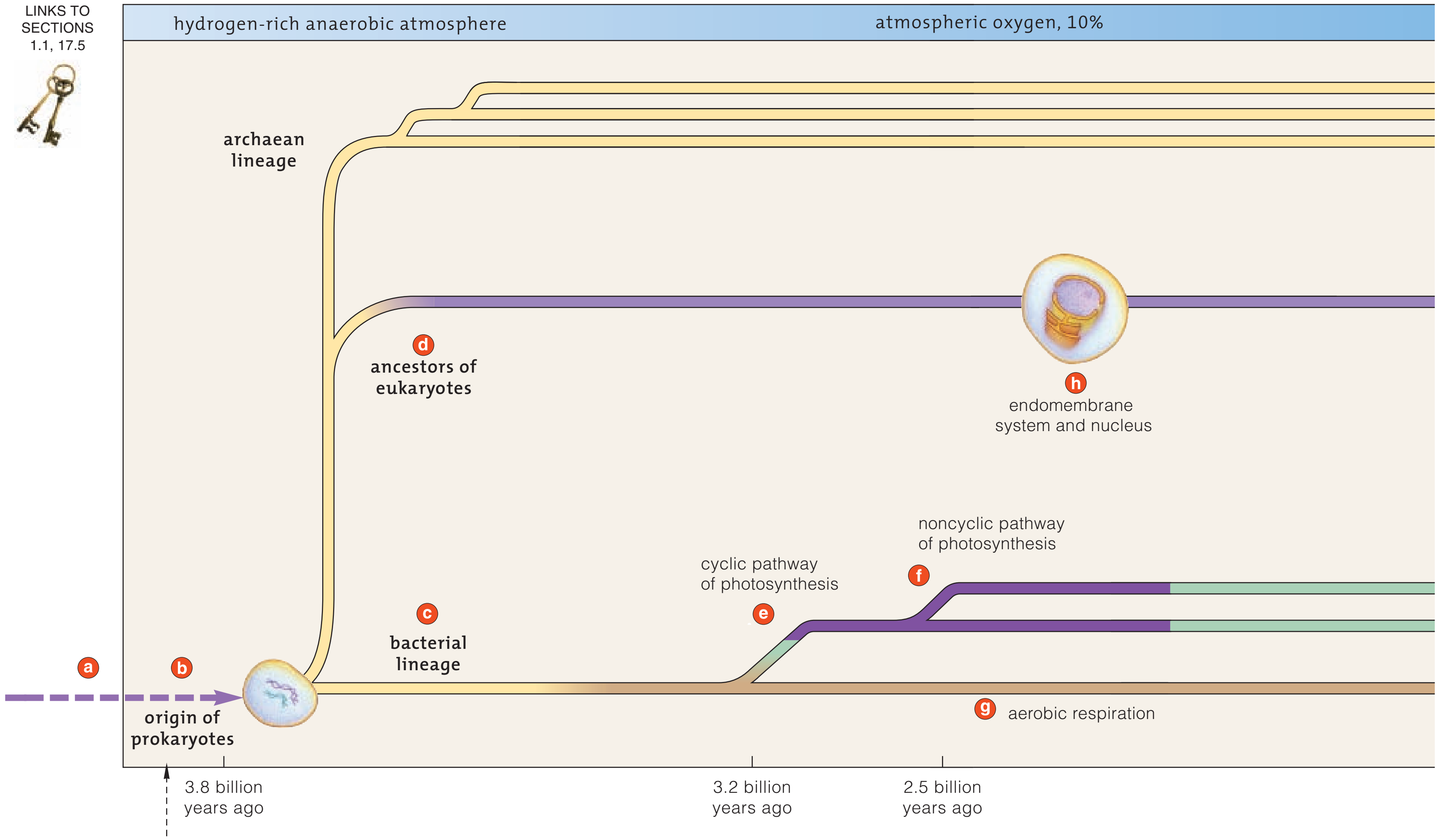
Or consider the protists called glaucophytes. They have unique photosynthetic organelles that resemble cyanobacteria. These organelles even have their own cell wall (Figure 20.11*b*).

However they arose, the first eukaryotic cells had a nucleus, an endomembrane system, mitochondria and, in some lineages, chloroplasts. They were the world's first protists. They had efficient metabolic systems, and they evolved fast. In no time at all, evolutionarily speaking, some of their descendants evolved into the plants, fungi, and animals. The next section provides a time frame for these pivotal events.

A nucleus and other organelles are defining features of eukaryotic cells. The nucleus and ER may have evolved by infoldings of the plasma membrane. Mitochondria and chloroplasts may have evolved through endosymbiosis between heterotrophic host cells and their prey or parasites.

20.5 Time Line for Life's Origin and Evolution

LINKS TO SECTIONS 1.1, 17.5



Chemical and Molecular Evolution

ⓐ Between 5 billion and 3.8 billion years ago, as an outcome of chemical and molecular evolution, complex carbohydrates, lipids, proteins, and nucleic acids formed from the simple organic compounds present on the early Earth.

Origin of Prokaryotic Cells

ⓑ The first living cells probably had evolved by 3.8 billion years ago. All were prokaryotic; they did not have a nucleus or other organelles. Atmospheric oxygen was low and the early cells made ATP by anaerobic pathways.

Three Domains of Life

ⓒ The first major divergence gave rise to bacteria and to the common ancestor of the archaeans and all eukaryotic cells.

ⓓ Not long after, the ancestors of archaeans and eukaryotic cells diverged.

Photosynthesis, Aerobic Respiration Evolve

ⓔ A cyclic pathway of photosynthesis evolved in some bacterial groups.

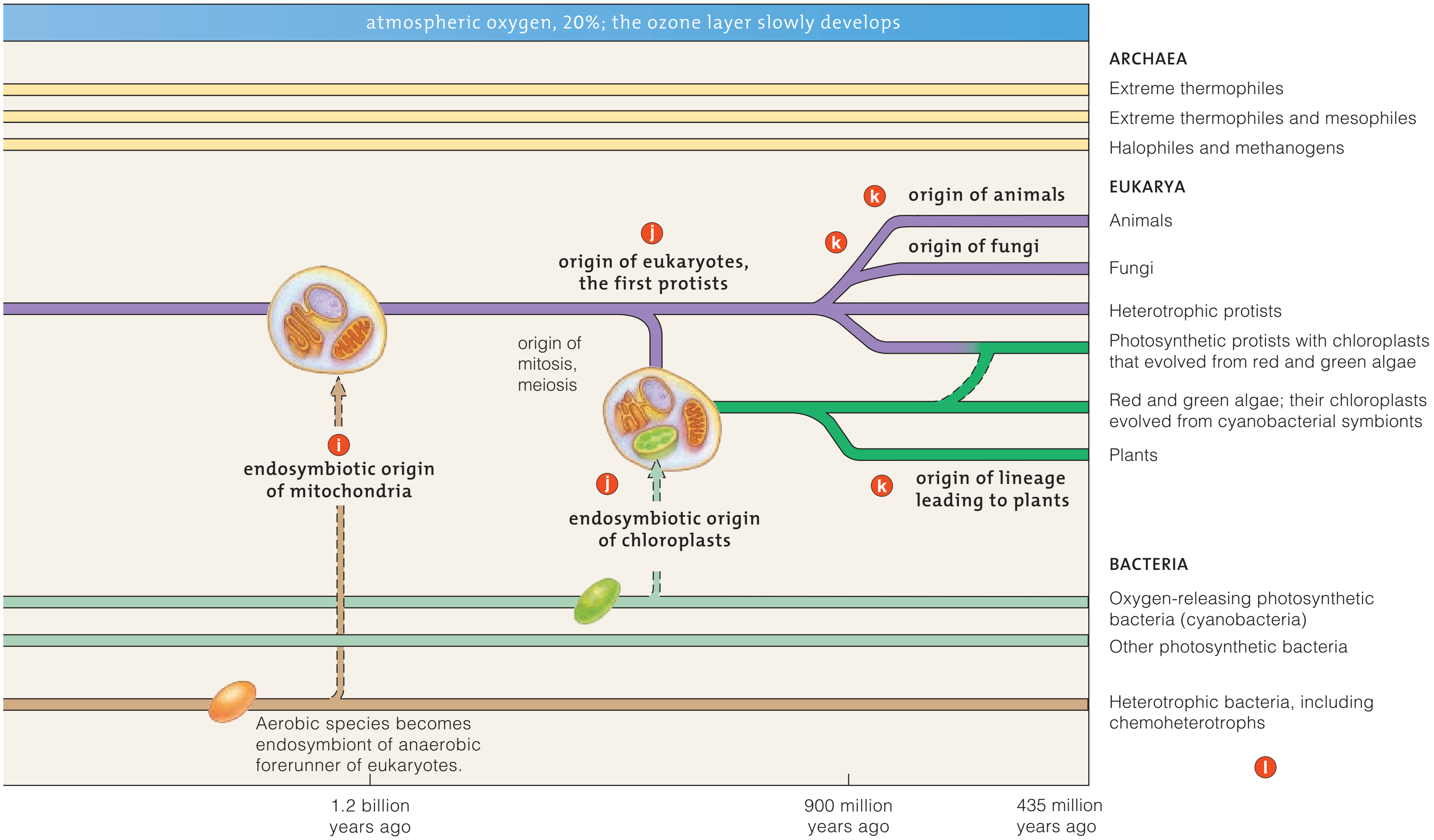
ⓕ An oxygen-releasing noncyclic pathway evolved later in the cyanobacteria and, over time, changed the atmosphere.

ⓖ Aerobic respiration evolved independently in many bacterial groups.

Origin of Endomembrane System, Nucleus

ⓗ Cell sizes and the amount of genetic information continued increasing in ancestors of what would become the eukaryotic cells. The endomembrane system, including the nuclear envelope, arose through the modification of cell membranes.

Figure 20.12 ***Animated!*** Milestones in the history of life. As you read the next unit on life's past and present diversity, refer to this visual overview. It can serve as a simple reminder of the evolutionary connections among all groups of organisms, from the structurally simple to the most complex.



Endosymbiotic Origin of Mitochondria

ⓘ Before about 1.2 billion years ago, aerobic bacterial species and an anaerobic ancestor of eukaryotic cells entered into close symbiotic interaction. The endosymbiont evolved into the mitochondrion.

Endosymbiotic Origin of Chloroplasts

ⓙ Cyanobacteria entered into a close symbiotic interaction with early protists and evolved into chloroplasts. Later, photosynthetic protists would evolve into chloroplasts inside other protist hosts.

Plants, Fungi, and Animals Evolve

ⓚ By 900 million years ago, all major lineages—including fungi, animals, and the algae that would give rise to plants—had evolved along shorelines of the first supercontinent.

Lineages That Have Endured to the Present

ⓛ Today, organisms live in all regions of Earth's waters, crust, and atmosphere. They are related by descent and share certain traits. However, each lineage encountered different selective pressures, and each has evolved its own characteristic traits.

Summary

Section 20.1 Earth formed more than 4 billion years ago. Experimental tests, information on the formation of stars and planets, and other lines of research offer indirect evidence that the complex organic compounds characteristic of life could have formed spontaneously under the conditions that prevailed on the early Earth.

Biology Now

See experiments on how organic compounds can form spontaneously with the animation on BiologyNow.

Section 20.2 The emergence of the first cells was preceded by chemical evolution that led to enzymes and other agents of metabolism, the self-assembly of membranes on environmental templates, and a self-replicating system. RNA probably was the template for protein synthesis before DNA evolved as an efficient way to store protein-building information.

Biology Now

Read the InfoTrac article "Transitions from Nonliving to Living Matter," Steen Rasmussen et al., Science, *February 2004. Also "First Cell," David Deamer,* Discover, *November 1995.*

Section 20.3 The first cells may have originated 3.8 billion years ago. They were anaerobic prokaryotes. An early divergence separated bacteria from the ancestors of archaeans and eukaryotes. Evolution of the noncyclic pathway of photosynthesis in cyanobacteria resulted in an accumulation of free oxygen in the atmosphere, which favored aerobic respiration. This pathway was a key innovation in the evolution of eukaryotic cells.

Biology Now

Explore levels of biological organization with the interaction on BiologyNow.

Section 20.4 The internal membranes of eukaryotic cells may have evolved through infoldings of the cell membrane. Mitochondria and chloroplasts most likely evolved by endosymbiosis, at the times indicated in the Section 20.5 visual summary.

Section 20.5 Key events in life's origin and early evolution can be correlated with the geologic time scale.

Biology Now

Investigate the history of life with the animated interaction on BiologyNow.

Self-Quiz

Answers in Appendix II

1. An abundance of ______ in the atmosphere would have prevented the spontaneous (abiotic) assembly of organic compounds on the early Earth.
   a. hydrogen b. methane c. oxygen d. nitrogen

2. The prevalence of iron-sulfide cofactors in living organisms may be evidence that life arose ______ .
   a. in outer space c. near deep-sea vents
   b. on tidal flats d. in the upper atmosphere

3. The evolution of ______ resulted in an increase in the levels of atmospheric oxygen.
   a. sexual reproduction
   b. aerobic respiration
   c. the noncyclic pathway of photosynthesis
   d. the cyclic pathway of photosynthesis

4. Mitochondria may have evolved from ______ .
   a. chloroplasts c. early protists
   b. bacteria d. archaeans

5. Infoldings of the plasma membrane into the cytoplasm of some prokaryotes may have evolved into the ______ .
   a. nuclear envelope c. primary cell wall
   b. ER membranes d. both a and b

6. Chronologically arrange the evolutionary events, with 1 being the earliest and 6 the most recent.

____ 1
____ 2
____ 3
____ 4
____ 5
____ 6

a. emergence of the noncyclic pathway of photosynthesis
b. origin of mitochondria
c. origin of proto-cells
d. emergence of the cyclic pathway of photosynthesis
e. origin of chloroplasts
f. the big bang

Additional questions are available on **Biology Now™**

Critical Thinking

1. Mars formed about 5 million years earlier than Earth, and it has a similar composition but is far richer in iron. It is farther from the sun and much chillier, with an average surface temperature of −63° C. Today, nearly all of the water on Mars is permanently frozen in soil. To some researchers, photographs of certain geological features indicate that liquid water might have flowed across the planet's surface during an earlier and warmer time. The Martian atmophere is now richer in carbon dioxide than Earth's, but very low in nitrogen and oxygen. Based on this information, would you rule out the possibility that life could have existed on Mars or that simple life forms could currently exist there? Explain your reasoning.

2. What if it were possible to create life in test tubes? That is the idea behind modeling and perhaps creating minimal organisms: living cells having the smallest set of genes required to survive and reproduce.

Craig Venter and Claire Fraser found that *Mycoplasma genitalium*, a bacterium that has only 517 genes (and 2,209 transposons), is a good candidate for such an experiment. By disabling its genes one at a time, they discovered it may have only 265–350 essential protein-coding genes.

What if those genes were synthesized one at a time and inserted into an engineered cell consisting only of a plasma membrane and cytoplasm? Would the cell come to life? The possibility that it might prompted Venter and Fraser to seek advice from a panel of bioethicists and theologians. No one on the panel objected to synthetic life research. They said that much good might come of it, provided scientists did not claim to have found "the secret of life." The December 10, 1999, issue of *Science* includes an essay from the panel and an article on *M. genitalium* research. Read both, then write down your thoughts about "creating" life in a test tube.

IV Evolution and Biodiversity

From the Green River formation near Lincoln, Wyoming, the stunning fossilized remains of a bird trapped in time. During the Eocene, some 50 million years ago, sediments that had been slowly deposited in layers at the bottom of a large inland lake became its tomb. In this same formation, fossils of palms, cattails, sycamore, and other plants tell us that the climate was warm and moist. Fossils from places all around the world yield major clues to life's early history.