Black smoker hydrothermal vents on the ocean floor. Many scientists support the theory that life developed near hydrothermal vents, where superheated, mineral-rich water is found.

Dr. Ken Macdonald/SPL/Photo Researchers, Inc.

24 The Origin of Life

STUDY PLAN

24.1 The Formation of Molecules Necessary for Life

- Conditions on primordial Earth led to the formation of organic molecules
- The Oparin-Haldane hypothesis initiated scientific investigations into the origin of life
- Chemistry simulation experiments support the Oparin-Haldane hypothesis
- Scientists have new theories about the sites for the origin of life

24.2 The Origin of Cells

- Protocells formed with some of the properties of life
- Living cells may have developed from protocells
- Prokaryotic cells were the first living cells
- Subsequent events increased the oxidizing nature of the atmosphere

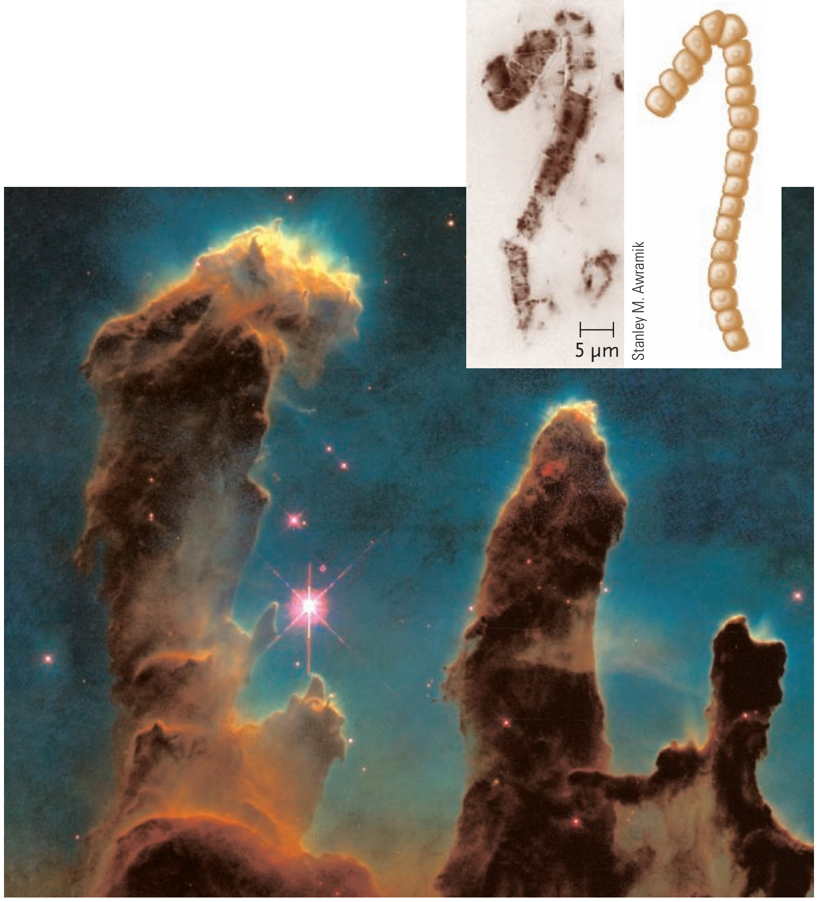
24.3 The Origins of Eukaryotic Cells

- The endosymbiont hypothesis proposes that mitochondria and chloroplasts evolved from ingested prokaryotes
- Several lines of evidence support the endosymbiont hypothesis
- Eukaryotic cells may have evolved from a common ancestral line shared with archaeans
- Multicellular eukaryotes probably evolved in colonies of cells
- Life may have been the inevitable consequence of the physical conditions of the primitive Earth

WHY IT MATTERS

In 1927, Belgian priest and astronomer George Lemaître proposed the Big Bang Theory, which is now the dominant scientific theory about the origin of the universe. According to this theory, an incomprehensibly vast explosion about 14 billion years ago produced the matter and energy of our universe. Most of the matter was initially distributed in clouds of gas and dust; some of these clouds still exist today **(Figure 24.1).** As the universe expanded, gravitational attraction caused the dust clouds to condense in some regions into more concentrated collections of matter. In our small corner of the early universe, the dust clouds condensed into the sun and its surrounding planets, including Earth.

Earth is estimated to have formed approximately 4.6 billion years ago, when it condensed out of cosmic dust and began its long transition into the environment we know today. There is no record of the time when life first formed, but microscopic deposits resembling bacteria have been found in Australia, in rocks laid down as sediments about 3.5 billion years ago during the Archaean era (inset to Figure 24.1). If these deposits are actually fossil prokaryotes, then life may have appeared during the first billion years or so of Earth's existence.



Stanley M. Awramik

Jeff Hester and Paul Scowen, Arizona State University, and NASA

Figure 24.1
The Eagle nebula, a cloud of gas and dust particles some 7000 light years from Earth. Gas is condensing and forming stars, and perhaps planets, in this nebula. The inset shows structures that are believed to be a strand of fossil prokaryote cells in a rock sample 3.5 billion years old.

Figure 24.2 outlines the key events in the early evolution of life, which we will examine in this chapter. The earliest events are uncertain, but probably include the formation of organic molecules and the development of **protocells**, primitive cell-like structures that have some of the properties of life and that might have been the precursors of cells. Prokaryotic cells arose during the first billion years or so after the formation of Earth, and about 500 million years later some of them developed the capacity to perform photosynthesis, which released oxygen into the atmosphere. The oxygen-enriched environment was probably essential to the development of the first eukaryotic cells, which may have occurred as long as 2.2 billion years ago.

24.1 The Formation of Molecules Necessary for Life

All present-day living cells are complex; they have (1) a boundary membrane separating the cell interior from the exterior; (2) one or more nucleic acid coding molecules located in a nuclear region (a nucleus in eukaryotes and a nucleoid region in prokaryotes); (3) a system using the coded information to make proteins and, through them, other biological molecules; and (4) a metabolic system providing energy for these activities. Because these systems are so complex, it is highly unlikely that living cells appeared suddenly from nonliving matter. Rather, there must have been a transition from nonliving to living matter.

No fossils or other records exist to inform us about this transition, but much evidence supports the idea that life did emerge from the nonliving world. Living organisms are composed entirely of elements common in the nonliving, physical world on Earth and throughout the universe. Moreover, all of the reactions that sustain life are elaborations of those in the physical world. Most scientists study the origin of life by assuming that it originated from nonliving matter on Earth, through chemical and physical processes no different from those operating today. Hypotheses made under these assumptions are testable to the extent that the chemical and physical processes can be duplicated in the laboratory.

But some scientists have not ruled out an extraterrestrial origin of life. Analysis of meteorites has shown that they contain some organic molecules characteristic of living organisms. Could a living cell or organism have arrived in such a way? Most scientists believe it is unlikely that a cell or an organism could have survived a long journey in space, even if protected from radiation, or that it could have survived intense heating while traveling through Earth's atmosphere and the actual impact with Earth. However, other scientists argue that conditions inside some meteorites might have been less extreme and allowed "life" to continue. At this point the hypothesis that life arrived on Earth by interplanetary transport cannot be ruled out. Nonetheless, even if a living organism arrived from space and

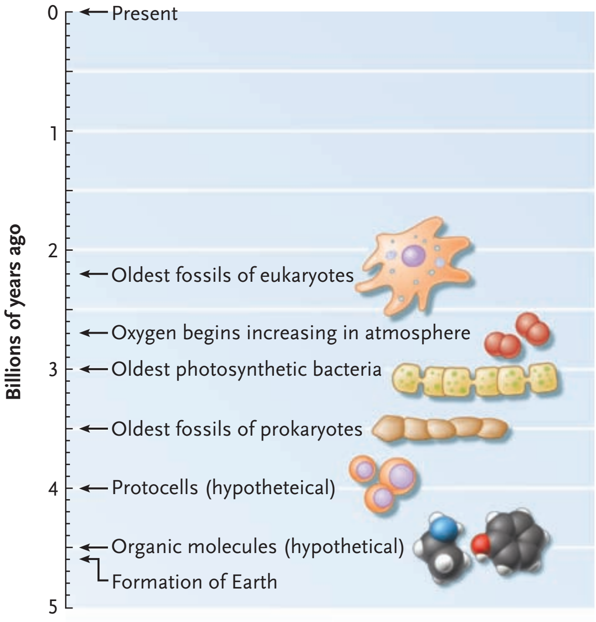


Figure 24.2
A timeline for the evolution of cellular life.

spawned a population on this planet, life would still have had to arise from nonliving matter in a similar way on the organism's home planet.

Conditions on Primordial Earth Led to the Formation of Organic Molecules

As we noted in the introduction, astronomers estimate that our solar system condensed from an interstellar dust cloud some 4.6 billion years ago. Intense heat and pressure generated in the central region of the cloud by the condensation set off a thermonuclear reaction that established the star of our solar system, the sun. The remainder of the spiraling dust and gas condensed into the planets and other bodies orbiting the sun.

Gravitational compression caused internal temperatures in our planet to rise to 1000° to 3000°C, causing its matter to melt and stratify into layers. Metallic elements sank to the core and lighter substances, such as silicates, carbides, and sulfides of the metallic elements, floated to the surface **(Figure 24.3).** As the planet radiated away some of its heat, the surface layers cooled and solidified into the rocks of the crust. Earth's gravitational pull was strong enough to hold an atmosphere around the planet, derived partly from the original dust cloud and partly from gases released from the planet's interior as it cooled.

Primordial Earth met several basic conditions necessary for life to begin. Although its gravitational pull was strong enough to retain an atmosphere, it was not strong enough to compress the atmospheric gases into liquid form. Earth's distance from the sun was such that, on average, sunlight warmed the surface enough to keep much of the liquid water (much of which may have come from icy objects from the main asteroid belt colliding with Earth) from freezing, but not enough to boil the water. This allowed liquid water to accumulate in rivers, lakes, and seas. *Liquid water is essential for the chemistry of biological systems* (see Chapter 2).

Evaporation of water at the surface would have contributed water vapor to the atmosphere. Besides water vapor, the primordial atmosphere probably contained hydrogen and nitrogen molecules. Erupting volcanoes probably released large quantities of hydrogen sulfide, carbon dioxide, and carbon monoxide. Any molecular oxygen would have reacted with elements of the crust and atmosphere to form oxides. Spontaneous reactions of hydrogen, nitrogen, and carbon would have produced ammonia (NH_3) and methane (CH_4).

As Earth's surface cooled, natural sources of energy caused chemical bonds to break and reform, leading to the formation of organic molecules. In addition to sunlight and electrical discharges during storms, radioactivity from atomic decay and heat from volcanoes, geysers, and hydrothermal (hot water) vents in the sea floor all acted on the primordial atmosphere and crust—as they still do today. As many as a half-billion years may have passed before the concentrations of organic molecules reached levels where their interactions formed more complex organic substances. We now consider the current thinking about how simple molecules were converted into the key molecules of life.

Photo by Chesley Bonestell

Figure 24.3
An artist's depiction of Earth during its early cooling stage, still too hot to support life.

The Oparin-Haldane Hypothesis Initiated Scientific Investigations into the Origin of Life

Scientific efforts to explain the origin of life began with a major hypothesis proposed independently in the 1920s by two investigators, Aleksandr I. Oparin, a Russian plant biochemist at Moscow State University in Russia, and J. B. S. Haldane, a Scottish geneticist and evolutionary biologist at Cambridge University in England. Their hypothesis rested on the critical assumption that Earth's primordial atmosphere was radically different from today's atmosphere. They proposed that, rather than being an oxygen-rich (oxidizing) atmosphere as it is now, the early atmosphere was composed of substances such as hydrogen (H_2), methane (CH_4), ammonia (NH_3), and water, which are *fully reduced*—they contain the maximum possible number of electrons and hydrogens (see Section 8.1). These substances, they concluded, would have given the primordial atmosphere a *reducing* character; it contained an abundance of electrons and hydrogens available for reduction reactions, which could create organic molecules from inorganic elements and compounds. Energy to drive the reductions, according to the hypothesis, came from solar energy and other natural sources such as the electrical energy of lightning in atmospheric storms.

The absence of oxygen in the primitive atmosphere is essential to the Oparin-Haldane hypothesis. Oxygen can reverse reductions by removing electrons and hydrogens from organic molecules (see Section 8.1). In other words, if oxygen was present, the newly formed molecules would have been broken down quickly by oxidation.

Oparin and Haldane proposed that reductions occurring on the primordial Earth produced great quantities of organic molecules. The molecules accumulated because the two main routes by which such substances break down today, chemical attack by oxygen and decay by microorganisms, could not take place. According to Oparin and Haldane's hypothesis, the organic substances would have became so concentrated that the oceans and other bodies of water resembled a "prebiotic soup."

Oparin and Haldane assumed that these highly concentrated organic molecules would tend to aggregate in random combinations and that, by chance, some of the combinations were able to carry out one or more primitive reactions characteristic of life, such as increasing in mass by adding new materials. Later, scientists reasoned that these combinations were able to compete successfully against less efficient combinations for space and materials in the organic soup. As a result, they persisted and became more numerous.

Chemistry Simulation Experiments Support the Oparin-Haldane Hypothesis

In the 1950s, new discoveries in chemistry provided direct support for the most basic proposals of Oparin and Haldane's hypothesis. In 1953, Stanley L. Miller, a graduate student in Harold Urey's laboratory at the University of Chicago, tested the hypothesis by creating a laboratory simulation of conditions Oparin and Haldane believed existed on early Earth. Miller placed components of a reducing atmosphere—hydrogen, methane, ammonia, and water vapor—in a closed apparatus and exposed the gases to an energy source in the form of continuously sparking electrodes **(Figure 24.4).** Water vapor was added to the "atmosphere" by boiling water in one part of the apparatus, and it was removed by cooling and condensation in another part. After running the apparatus for only a week, Miller found a large assortment of organic compounds in the water, including urea, amino acids, and lactic, formic, and acetic acids. In fact, as much as 15% of the carbon was now in the form of organic compounds. Two percent of the carbon was in the form of amino acids, which form easily under sufficiently reducing conditions. The significance of the finding at the time was enormous: amino acids, which are essential to cellular life, could be made under the conditions scientists believed existed on early Earth.

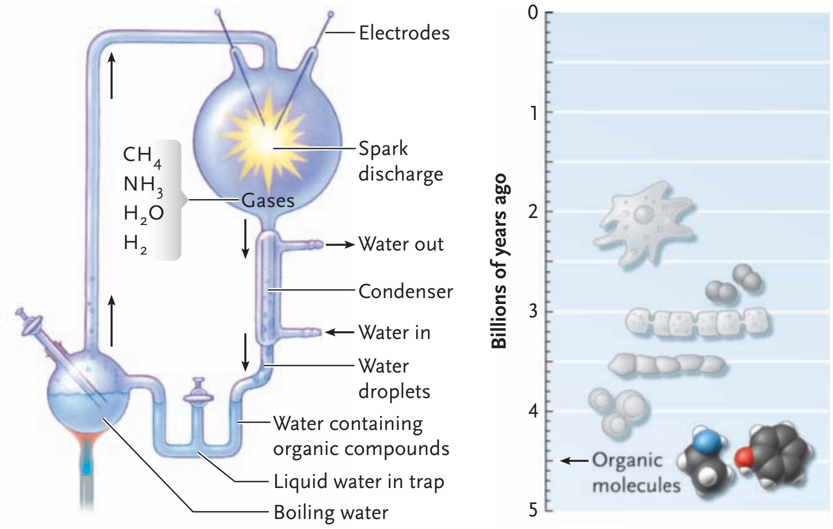


Figure 24.4
The Miller-Urey apparatus demonstrating that organic molecules can be synthesized spontaneously under conditions simulating the primordial Earth. Operation for 1 week converted 15% of the carbon in the "atmosphere" inside the apparatus into a surprising variety of organic compounds.
(Redrawn from an original courtesy of S. L. Miller. Copyright 1955 by the American Chemical Society.)

Other chemicals have been tested in the Miller-Urey apparatus. For example, hydrogen cyanide (HCN) and formaldehyde (CH_2O) were considered likely to have been among the earliest substances formed in the primitive atmosphere. When HCN and CH_2O molecules were added to the simulated primitive atmosphere in Miller's apparatus, all the building blocks of complex biological molecules were produced. Among the products were amino acids; fatty acids; the purine and pyrimidine building blocks of nucleic acids; sugars such as glyceraldehyde, ribose, deoxyribose, glucose, fructose, mannose, and xylose; and phospholipids, which form the lipid bilayers of biological membranes.

The synthesis of complex biological molecules in a reducing atmosphere in the Miller-Urey experiment supported the Oparin-Haldane hypothesis. However, it is only a conjecture that a reducing atmosphere was present at the time key organic molecules were formed on early Earth. Indeed, current thinking is that early Earth's atmosphere was not reducing but that it contained large amounts of oxidants such as CO_2 and N_2. In such an oxidizing atmosphere, any organic molecules generated spontaneously in the environment would be oxidized quickly back to inorganic forms by combination with the oxygen in the atmosphere. This is supported experimentally: running the Miller-Urey experiment in the presence of oxygen results in essentially no organic molecules. Moreover, amino acids cannot be produced in such an atmosphere, making the origin of life impossible.

In addition, the Miller-Urey experiment required the input of a large amount of energy. In the experiment, energy was provided continuously, but in the atmosphere of early Earth it would have been delivered, at best, intermittently from lightning storms. Scientists think that amino acids and other organic compounds may well have formed under these conditions, but not in the amounts seen in the laboratory experiment.

Scientists Have New Theories about the Sites for the Origin of Life

If organic compounds were not generated in a reducing atmosphere, how else could they have arisen? Scientists have developed a number of theories. All of them assume the presence of liquid water, which is a reasonable assumption. Remember that water is essential for the chemistry of biological systems (see Chapter 2). Two of the more reasonable theories are described here.

One current theory for the origin of life, which has significant support among scientists, is that life developed near hydrothermal vents in the sea floor. Many such vents exist in today's oceans, emitting bursts of mineral-rich water superheated to up to 400°C by submarine volcanoes. Scientists exploring hydrothermal vents find complex ecosystems associated with them.

Life might have originated near oceanic hydrothermal vents because reducing conditions existed there along with an abundance of the chemicals essential for life. Even now, there are high levels of hydrogen gas, methane, and ammonia around the vents. Indeed, based on simulation experiments, scientists believe that hydrothermal vents could have produced a lot more organic material than that generated in the Miller-Urey experiment. However, if life did evolve near hydrothermal vents, we would expect many present hydrothermal-vent life forms to be ancient. This is not the case: in most cases these organisms are closely related to modern nonvent organisms. Critics of the hydrothermal-vent origin of life theory also argue that the temperature at the vents is too high to permit the origin of life. The critics argue that, at the high temperature found at vents, the organic molecules are too unstable and would be destroyed as soon as they form. Supporters of the theory counter that the necessary organic molecules for life are formed not at the vent itself, but somewhere in the gradient between the hot water at the vent and the near-freezing water surrounding the vent.

Scientists debate whether organic molecules could be produced in the temperature gradient in the amounts needed. Recently, Koichiro Matsuno and his colleagues at Nagaoka University of Technology in Japan assembled an artificial system simulating the environment of ocean bottom hydrothermal vents, and added the feature of cycling materials between heat and cold. This feature accommodated the possibility that chemical products made near the vents were quenched in the surrounding colder water and then reentered the vent area where they could undergo further reactions. Their experiments demonstrated that amino acids are formed and that they can polymerize into short polypeptides under these conditions. They argue that the amounts are sufficient to form complicated molecules.

Another theory is that some organic compounds had an extraterrestrial origin. Interestingly, many of the compounds made in the Miller-Urey experiment exist in outer space. For example, a meteorite that fell on Murchison, Australia, in 1969 contained more than 90 amino acids, only 19 of which are found on Earth. Since amino acids appear to be able to survive in outer space, they could potentially have been present when Earth was formed. And perhaps other organic compounds arrived by meteor or comet impact.

STUDY BREAK

1. Why is the issue of the reducing nature of early Earth's atmosphere key to the origin of molecules necessary for life?
2. How do the theories about the sites for the origin of life differ?

24.2 The Origin of Cells

Whether organic molecules originated in the atmosphere, in hydrothermal vents, or in outer space, they still do not qualify as life. In this section, we discuss the key stage in the origin of life, the formation of the first cells.

Protocells Formed with Some of the Properties of Life

How did organic building blocks such as amino acids assemble into macromolecules such as proteins and nucleic acids? To answer this question, researchers have proposed and tested several processes. One process is the concentration of subunits by the evaporation of water. Another is *dehydration synthesis (condensations)*, in which subunits assemble into larger molecules through removal of the elements of a molecule of water (see Section 3.1). Experiments with these processes under simulated conditions showed that both evaporation and condensation reactions can produce polypeptide chains from amino acids, polysaccharides from glucose and other monosaccharides, and nucleotides and nucleic acids from nitrogenous bases, ribose, and phosphates.

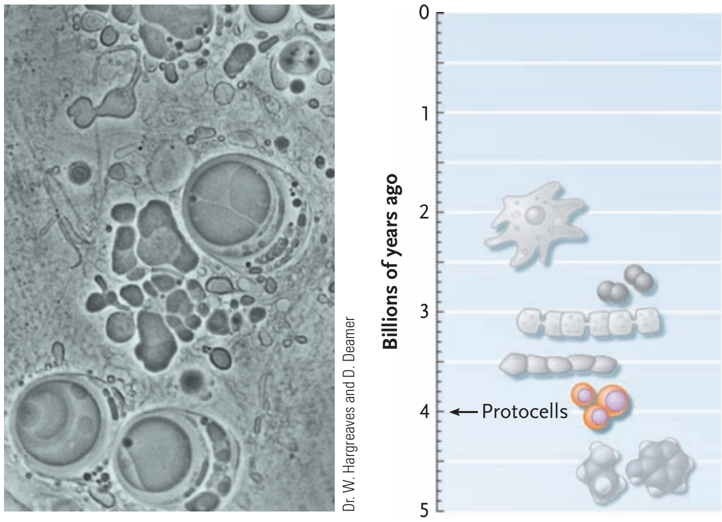
Scientists reason that spontaneous condensations and other reactions produced significant quantities of all the major biological molecules over the hundreds of millions of years following the initial formation of Earth. They hypothesize that the accumulation of organic matter set up the conditions necessary for the next stage, the chance assembly of molecules into aggregations that became membrane-bound to form primitive protocells. Protocells are key to the origin of life, because life depends upon reactions occurring in a controlled and sequestered environment, the cell. Researchers have proposed several mechanisms for the assembly of organic molecules into aggregates, each of which has been successfully duplicated in laboratory experiments simulating primordial conditions. Two of those mechanisms are absorption into clays and lipid bilayer assembly.

Absorption into Clays. Could clays have provided an ideal environment for molecular aggregation and interaction on the primitive Earth? Clays consist of very thin layers of minerals separated by layers of water only a few nanometers thick. The layered structure readily absorbs ions and organic molecules and promotes their interactions, including condensations and other assembly reactions. Clays can also store potential energy, and therefore could have channeled some of the energy into reactions taking place inside them.

Several experiments have supported these proposals. For example, Noam Lahav at the Hebrew University in Israel and Sherwood Chang of NASA's Ames Research Center added amino acids to clays and exposed the mixtures to water-content changes and fluctuating temperatures, as they might be in a tidal flat. After several cycles of the fluctuating conditions, polypeptides were detected in the clays. Other researchers found that RNA nucleotides linked to phosphate chains could combine into RNA-like molecules in clays. Accumulation of these and other macromolecules in the clays could have provided an environment in which they could react to carry out the first reactions of life.

However, even if molecules became organized in clay and some of the reactions of life commenced, it is not clear how a lipid bilayer membrane could have formed around them. Such a membrane is necessary to organize the molecules into protocells, the presumed precursors of cells. (The biological importance of lipid bilayers and membranes are discussed in Sections 2.4, 3.4, and 6.1.)

Lipid Bilayer Assembly. In the 1950s, R. J. Goldacre at Chester Beatty Research Institute, London, hypothesized that protocells could have formed starting with lipid bilayers that had assembled spontaneously. In the 1970s, David W. Deamer at the University of California at Davis and other investigators tested this hypothesis, finding that phospholipids and some other types of lipid molecules could form under simulated conditions. The phospholipids self-assembled readily into bilayers when suspended in water (see Section 6.1). Often, the bilayers rounded up into stable, closed vesicles consisting of a continuous-boundary "membrane" surrounding an inner space **(Figure 24.5).**



Dr. W. Hargreaves and D. Deamer

Figure 24.5
An electron micrograph of vesicles of various sizes and shapes assembled from phospholipids synthesized under simulated primordial conditions. When the vesicles are more highly magnified than in this micrograph, their walls can be seen to consist of a lipid bilayer.

Further tests showed that the bilayers formed in these experiments have many properties of living membranes. For example, they can incorporate proteins onto their surfaces or into the hydrophobic membrane interior, and they form vesicles that can trap other substances in the fluid enclosed by the membrane. Potentially, on early Earth, the concentration of organic molecules in such vesicles could have stimulated their growth and eventual fragmentation into smaller vesicles, providing a primitive form of reproduction. These mechanisms of aggregation, as well as others, may have worked separately or together to form protocells.

Living Cells May Have Developed from Protocells

Eventually the chemical reactions taking place in the primitive protocells became organized enough to make the transition to living cells. Of the several critical events necessary for this transition, we will look closely at two: the development of pathways that captured and harnessed the energy required to drive molecular synthesis and the development of a system for the storage, replication, and translation of information for protein synthesis. Remember that proteins are the catalysts for most cellular reactions.

Development of Energy-Harnessing Reaction Pathways. Oxidation-reduction reactions (see Section 8.1) were probably among the initial energy-releasing reactions of the primitive protocells. In an oxidation, electrons are removed from a substance; the removal releases free energy that can be used to drive synthesis and other reactions. In a reduction, electrons are added to a substance; the added electrons provide energy that can contribute to the formation of complex molecules from simpler building blocks.

At first the electrons removed in an oxidation would have been transferred directly to the substances being reduced, in a one-step process. However, the greater efficiency of stepwise energy release would have favored development of intermediate carriers and opened the way for primitive electron transfer systems. Evolved from those primitive systems are the present-day electron transfer systems of mitochondria and chloroplasts (see Sections 8.4 and 9.2).

As part of the energy-harnessing reactions, ATP became established as the coupling agent that links energy-releasing reactions to those requiring energy. ATP may first have entered protocells as one of many organic molecules absorbed from the primitive environment. Initially, it was probably simply hydrolyzed into ADP and phosphate as an energy source. Later, as protocells developed, some of the free energy released during electron transfer was probably used to synthesize ATP directly from ADP and inorganic phosphate. Because of the efficiency and versatility of energy transfer by ATP, it gradually became the primary substance connecting energy-releasing and energy-requiring reactions in early cells.

Origin of the Information System. A system that could store, reproduce, and translate the information required for protein synthesis was a second critical event for the transition from protocells to living cells. How the information system developed is crucial to the understanding of the origin of life.

In contemporary organisms, information flows from DNA to RNA to protein. This nucleic acid–based information system depends mostly on enzymatic proteins for replication, transcription, and translation of the nucleic acids. However, the specificity of enzymatic proteins depends on their amino acid sequences, which are determined by the sequences of nucleotides in nucleic acids. Thus, proteins depend on nucleic acids for their structure, and nucleic acids depend on proteins to catalyze their activities. How could one have appeared before the other? Scientists believe the information system developed in stages, although the order of the steps is a subject of debate. There are two main hypotheses: the RNA-first hypothesis and the protein-first hypothesis.

The *RNA-first hypothesis* states that the first genes and enzymes were RNA molecules. That is, *ribozymes*—RNA molecules capable of catalyzing biochemical reactions—may have functioned both as informational molecules and as catalysts in protocells, without requiring protein enzymes for catalytic reactions (ribozymes are discussed in Section 4.6). Thus, a self-catalyzed "RNA world" may have been the first step in the development of an information system.

Ribozymes may have originally developed by the chance assembly of RNA nucleotides taking part in oxidative and other metabolic reactions in protocells (RNA nucleotides such as ATP, NAD, and coenzyme A form important parts of many metabolic pathways, including glycolysis, respiration, and photosynthesis; see Chapters 8 and 9). The RNA molecules then developed the capacity to replicate themselves and other RNA molecules. That is, these RNA molecules acted both as templates—like mRNA—and as catalysts—like ribosomal RNA (see Section 15.4). Then ribozymes could replicate ribozymes, with no need for protein enzymes. Such self-replicating systems may have provided the basis of an RNA-based informational system, and founded the RNA world. *Insights from the Molecular Revolution* describes an experiment in which ribozymes that can replicate RNA were generated in a test tube.

In the RNA world, DNA would have developed as a subsequent step. At first, DNA nucleotides may have been produced by random removal of an oxygen atom from the ribose subunits of the RNA nucleotides. At some point, the DNA nucleotides paired with the RNA informational molecules, and were assembled into complementary copies of the RNA sequences. Some modern day viruses carry out this RNA-to-DNA reaction using the enzyme reverse transcriptase (see Section 18.1). Once the DNA copies were made, selection may have favored DNA as the informational storage molecule because it has greater chemical stability and can be assembled into much longer coding sequences than RNA. RNA was left to function at intermediate steps between the stored information in DNA and protein synthesis, as it still does today.

As the RNA-based information system evolved, some RNAs may have acted as tRNA-like molecules, linking to amino acids and pairing with the RNA informational molecules. These associations could have led to the assembly of polypeptides of ordered sequence—the development of an RNA genetic code. When DNA took over information storage from RNA, the code would have been transferred to DNA.

Modern analysis of the ribosome, the organelle responsible for translation of mRNA (see Section 15.4) has shown that the enzyme that catalyzes the formation of a peptide bond between amino acids is a property of one of the RNA molecules of the ribosome. This finding supports the proposal that, in addition to replicating themselves, RNA molecules also generated the first proteins.

The second hypothesis, the *protein-first hypothesis,* states that proteins were the first informational molecules to arise. Then, once complex enzymes developed within protocells, nucleic acids—both DNA and RNA—were assembled enzymatically from small molecules, and replication and transcription processes developed.

Of course, we have no way of knowing exactly how life originated. Sifting through the various models and theories we can perhaps agree that there were some basic steps: (1) the abiotic (nonliving) synthesis of organic molecules such as amino acids; (2) the assembly of complex organic molecules from simple molecules, including protein or RNA or both; and (3) the aggregation of complex organic molecules inside membrane-bound protocells. Once the information system had developed in the protocells, and the protocells could divide, they had become true living cells. The advent of living cells marked the beginning of biological evolution, which depends on cells that can reproduce and pass on information to their descendants.

Prokaryotic Cells Were the First Living Cells

The change to biological evolution set the stage for the appearance of all the features of cellular life. One of these features was a nuclear region that contained the DNA of the coding system and the mechanisms replicating the DNA and transcribing it into RNA. Another feature was a cytoplasmic region containing ribosomes and the enzymes required to translate RNA informa-

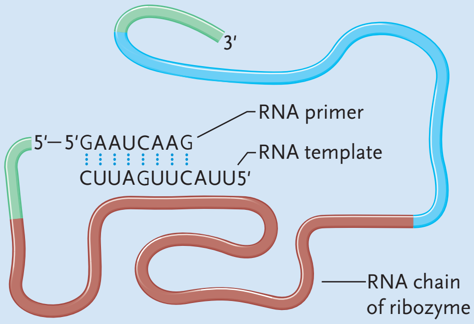
Insights from the Molecular Revolution

Replicating the RNA World

The discovery of ribozymes led to the proposal that an RNA world was the first step in the evolution of a molecular information system that could store, reproduce, and translate the information required for protein synthesis. In an RNA world, RNA molecules would have to act both as templates for their own replication and as catalysts to carry out the replication. The catalytic ability of RNA molecules has been amply demonstrated, but could they carry out RNA replication?

Wendy K. Johnston and her coworkers at the Massachusetts Institute of Technology decided to answer this question by using a ribozyme (a catalytic RNA) as the starting point for developing an RNA molecule that could replicate itself, as might have happened during the evolution of cellular life. The ribozyme they chose is an RNA ligase, which can catalyze one of the most fundamental reactions of replication, linking together short chains of nucleotides.

To achieve their feat, Johnston and her coworkers used a technique that accomplishes molecular evolution in a test tube (the RNA ligase used to start their experiments was the product of an earlier test-tube experiment). They assembled a reaction mixture containing the RNA ligase with an added a 76-nucleotide RNA strand of random sequence to serve as a template for self-replication. They then generated 1×10^{15} versions (a quintillion!) of the ligase with different sequences concentrated in the added strand. To the mutated versions in a test tube they added RNA nucleoside triphosphates (NTPs), an RNA template chain, and an RNA primer, with the RNA primer linked covalently to the ribozyme (see **figure**).



The general arrangement of sequences in the ribozymes used by Johnston and her coworkers. The blue and green portions are sequences added to provide raw materials for test-tube evolution. The template shown is three nucleotides longer than the primer and would require a ribozyme to add two nucleotides to the primer to be selected as successful (the last nucleotide in the template cannot be copied).

In the initial run, the template was only two bases longer than the primer, so to be successful a ribozyme had only to add two nucleotides to the primer. To detect the successful ribozymes, the investigators used RNA nucleoside triphosphates that were tagged with a chemical label. Any ribozymes that added the nucleotides to the primer would become labeled and thus be identifiable among the unsuccessful ribozymes in the test tube.

After the first round of selection, the investigators selected the labeled ribozyme variants, which had added nucleotides to the primer, and multiplied them using PCR (the polymerase chain reaction; see Section 18.1). They then added all the elements to the test tube for another round of replication and selection. This cycle of replication and selection was repeated through 18 successive rounds. As part of the process, additional mutations were induced in the ribozymes after round 10, and the selection pressure was increased by several methods. One was to make the template longer in successive rounds, so that the ribozymes had to add more nucleotides to the primer to be successful. Another was to alter the sequence of the template chain, so that the ribozymes had to be able to copy a template of any sequence to be successful. Also, the investigators shortened the time allowed for replication in successive runs, so that ribozymes had to work faster to be successful.

By the 18th round of replication, the selection process had produced a ribozyme that could replicate an RNA template 14 nucleotides longer than the primer. The template could be of any sequence. In addition, the template did not have to be covalently linked to the ribozyme for replication to occur.

To check on the accuracy of replication, the investigators gave the 18th-round ribozyme a template chain that was 11 nucleotides longer than the primer and then sequenced 100 of the complementary chains produced by the ribozyme. Of the replication products, 89 of 100 were precise complementary copies, all matched exactly to the template. In the remaining 11 products, only 12 base mismatches were found, slightly more than one base mismatch per copy.

Thus, the selected ribozyme was able to work as an RNA polymerase, faithfully replicating an RNA template into a complementary copy and thereby meeting a major requirement for an RNA world. The research continues, with further test-tube selection experiments designed to increase the accuracy of replication, the length of the template, and the rate of replication. These are small steps compared to the enormous task involved in the evolution of a full-fledged information system, but it is likely that life evolved in the same pattern, through the accumulation of small changes over hundreds of millions of years of molecular trial and error.

tion into sequences of amino acids in proteins. The cytoplasm also contained an oxidative system supplying chemical energy for protein synthesis and assembly of other required molecules. A mechanism of cell division also evolved, allowing replicated DNA to be distributed equally between daughter cells. All these systems were enclosed by a membrane controlling the flow of molecules and ions in and out of the cell. The stages leading to this level may have taken more than a billion years, occupying the period from Earth's formation 4.6 billion years ago to the earliest known prokaryotic fossils, dated as 3.5 billion years old.

Bill Bachmann/Photo Researchers, Inc.

Figure 24.6
Stromatolites exposed at low tide in Western Australia's Shark Bay. These mounds, which consist of mineral deposits made by photosynthetic cyanobacteria, are about 2000 years old; they are highly similar in structure to fossil stromatolites that formed more than 3.0 billion years ago. As a result of photosynthesis by cyanobacteria, oxygen began to accumulate in the atmosphere.

Subsequent Events Increased the Oxidizing Nature of the Atmosphere

According to Richard E. Dickerson of UCLA and others, the earliest form of photosynthesis evolved about 3.5 billion years ago in the early prokaryotes. This form of photosynthesis probably used electron donors such as hydrogen sulfide (H_2S) that do not release oxygen. However, at some point, an enzymatic system evolved that could use the most abundant molecule of the environment, water (H_2O), as the electron donor for photosynthesis. This reaction split water into protons, electrons, and oxygen, which was released into the atmosphere.

The oxygen released by the water-splitting reaction accumulated in the atmosphere and set the stage for the development of electron transfer systems using oxygen as the final electron acceptor. These transfer systems arose when some cells developed cytochromes that could deliver low-energy electrons to oxygen (see Section 8.4). These cells were able to tap the greatest possible amount of energy from the electrons before releasing them from electron transfer, making the cells highly successful in their environment.

When might water-splitting photosynthesizers have appeared? A possible answer to this question has been found in rock formations laid down at least 3 billion years ago. These rocks contain **stromatolites,** fossils of ancient prokaryotes (cyanobacteria) that carried out photosynthesis by the water-splitting reaction **(Figure 24.6).** Thus, oxygen-producing bacteria were present at least 3 billion years ago and perhaps evolved soon after the first prokaryotes appeared. Scientists believe that it may have taken another billion years for oxygen to accumulate to significant quantities in the atmosphere.

These major events established the preconditions for the evolution of eukaryotic cells. The next section traces this evolution, which was pivotal to the later evolution of large-scale multicellularity and the plants, animals, and the other organisms of the domain Eukarya.

STUDY BREAK

Several mechanisms have been proposed for the assembly of organic molecules into protocells. Why is the model involving a lipid bilayer membrane a particularly attractive one?

24.3 The Origins of Eukaryotic Cells

Present-day eukaryotic cells have several interrelated characteristics that distinguish them from prokaryotes: (1) the separation of DNA and cytoplasm by a nuclear envelope; (2) the presence in the cytoplasm of membrane-bound compartments with specialized metabolic and synthetic functions—mitochondria, chloroplasts, the endoplasmic reticulum (ER), and the Golgi complex, among others; and (3) highly specialized motor (contractile) proteins that move cells and internal cell parts. In this section we discuss how eukaryotes most probably evolved from associations of prokaryotes.

The Endosymbiont Hypothesis Proposes that Mitochondria and Chloroplasts Evolved from Ingested Prokaryotes

The **endosymbiont hypothesis,** put forward by Lynn Margulis at the University of Massachusetts, Amherst, proposes that the membranous organelles of eukaryotic cells, the mitochondria and chloroplasts, may each have originated from symbiotic (mutually advantageous) relationships between two prokaryotic cells **(Figure 24.7).**

Mitochondria began to develop when photosynthetic and nonphotosynthetic prokaryotes coexisted in an oxygen-rich atmosphere. The nonphotosynthetic prokaryotes fed themselves by ingesting organic molecules from their environment. These prokaryotes included both anaerobes, unable to use oxygen as the final acceptor for electron transfer, and aerobes, fully

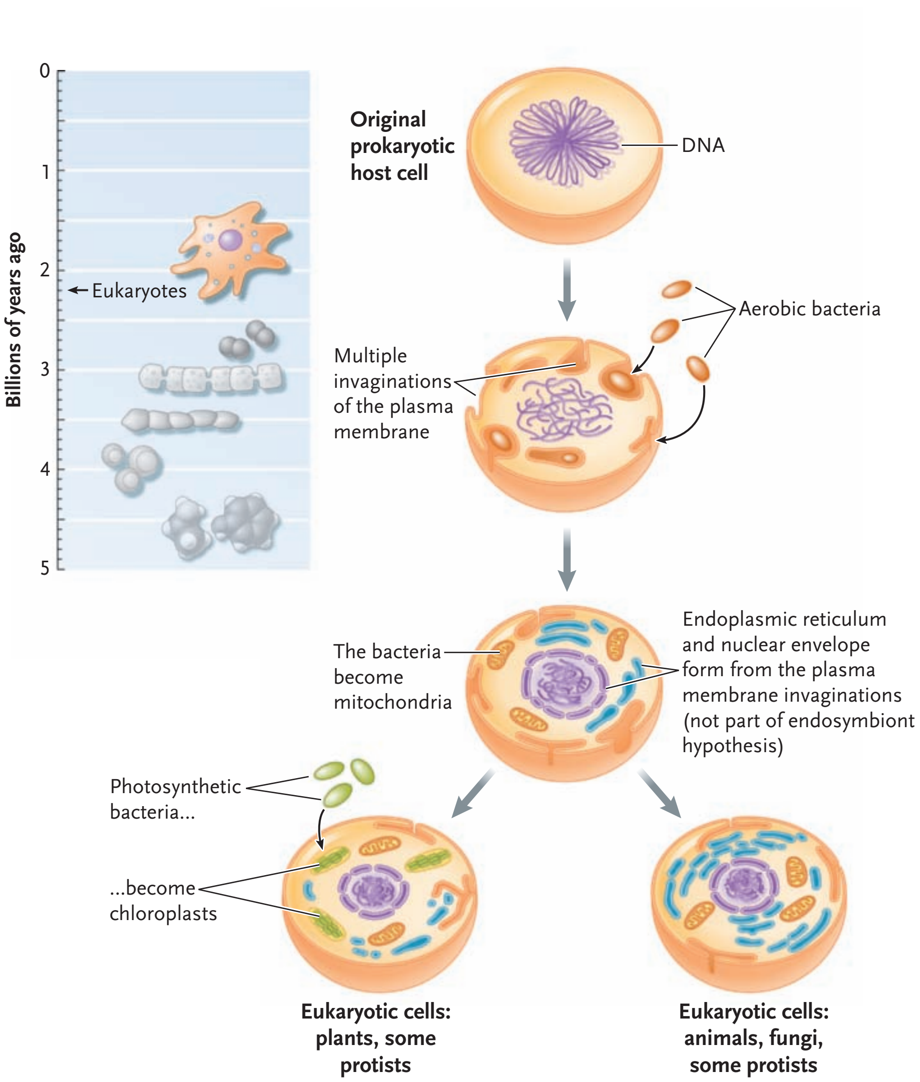


Figure 24.7
The endosymbiont hypothesis. Mitochondria and chloroplasts of eukaryotic cells are thought to have originated from various bacteria that lived as endosymbionts within other cells.

capable of using oxygen. Only the aerobes could fully exploit the energy stored in organic molecules, but predatory anaerobes could capture that energy by eating aerobic cells. These anaerobic prokaryotes had become efficient predators, and lived by ingesting other cells. Among the ingested cells were some aerobic prokaryotes; instead of being digested, some of them persisted in the cytoplasm of the predators and continued to respire aerobically in their new location. They had become *endosymbionts,* organisms that live symbiotically within a host cell. The cytoplasm of the host anaerobe, formerly limited to the use of organic molecules as final electron acceptors, was now home to an aerobe capable of carrying out the much more efficient transfer of electrons to oxygen.

As a part of the transition to a true eukaryotic cell, the cell also evolved to acquire other membranous structures, the major ones being the nuclear envelope, the ER, and the Golgi complex. Endocytosis, the process of infolding of the plasma membrane (see Figure 5.14), is believed to be responsible for the evolution of these structures. (These events are not part of the endosymbiont hypothesis.) Researchers believe that, in cell lines leading from prokaryotes to eukaryotes, pockets of the plasma membrane formed during endocytosis may have extended inward and surrounded the nuclear region. Some of these membranes fused around the DNA, forming the nuclear envelope and, hence, the nucleus. The remaining membranes formed vesicles in the cytoplasm that gave rise to the ER and the Golgi complex **(Figure 24.8).**

Next, according to the endosymbiont hypothesis, many functions duplicated in the aerobic endosymbiont were taken over by the host cell. As part of this transfer of function, most of the genes of the aerobe moved to the cell nucleus and became integrated into the host cell's DNA. At the same time, the host anaerobe became dependent for its survival on the respiratory capacity of the symbiotic aerobe. The ingested aerobe presumably benefited as well, because the host cell brought in large quantities of food molecules to be oxidized. This gradual process of mutual adaptation culminated in transformation of the cytoplasmic aerobes into mitochondria. The first eukaryotic cells had appeared, the ancestors of all modern-day eukaryotes.

The endosymbiont hypothesis proposes that a similar mechanism led to the appearance of the membrane-bound plastids (the general term for chloroplasts and related organelles, both photosynthetic and nonphotosynthetic) some time after mitochondria evolved. Plastids originated when aerobic cells that had mitochondria, but were unable to carry out photosynthesis, ingested photosynthetic prokaryotes resembling present-day cyanobacteria (see Figure 24.7). These photosynthetic prokaryotes gradually changed into plastids by evolutionary processes similar to those that produced mitochondria. The cells with both plastids and mitochondria founded the cell lines that gave rise to the modern eukaryotic algae and plants.

Several Lines of Evidence Support the Endosymbiont Hypothesis

Researchers reasoned that if the endosymbiont hypothesis is correct, then both mitochondria and plastids would have structures and biochemical reactions more like those of prokaryotes than those of eukaryotes. This has been shown to be the case. For example, both organelles typically contain circular DNA molecules that closely resemble prokaryotic DNA, and code for rRNAs and ribosomes that resemble prokaryotic forms.

Another line of evidence supports a key assumption of the endosymbiont hypothesis by showing that engulfed cells or organelles can survive in the cytoplasm of the ingesting cell. Among animals, no less than 150 living genera, distributed among 11 phyla, include species that contain eukaryotic algae or cyanobacteria as residents in the cytoplasm of their cells. For example, larvae of the marine snail *Elysia* initially contain no chloroplasts, but after they begin feeding on algae, chloroplasts from the algal cells are taken up into the cells lining the gut. When the larvae develop into adult snails, the chloroplasts continue to carry out photosynthesis in their new location and produce carbohydrates that are used by the snails. The uptake of functional chloroplasts has also been observed among the Protoctista (the protists; see Chapter 26); **Figure 24.9** shows a protist with chloroplasts that closely resemble cyanobacteria.

How long did it take for evolutionary mechanisms to produce fully eukaryotic cells? The oldest known fossil eukaryotes are 2.2 billion years old. If prokaryotic cells first evolved some 3.5 billion years ago, it took up to 1.3 billion years for eukaryotic cells to evolve from prokaryotes (see Figure 24.2). If so, this long interval probably reflects the complexity of the adaptations leading from prokaryotic to eukaryotic cells. Of course, it is possible that eukaryotic cells evolved more quickly, and we have yet to find the evidence.

Eukaryotic Cells May Have Evolved from a Common Ancestral Line Shared with Archaeans

The system of classification that has gained acceptance among biologists, and the one used in this book, groups all living organisms into three domains. One domain, the Eukarya, contains the eukaryotes. The second domain, the Bacteria, includes one of two groups of prokaryotes, the bacteria, which consists of both photosynthesizing and nonphotosynthesizing species. The third domain, the Archaea, contains the other group of prokaryotes, many of which inhabit extreme environments, including highly saline environments and hot springs.

There is little question that the three domains originated from a common ancestral cell line, because all share common fundamental characteristics—they all use the same genetic code, for example, and DNA and RNA molecules carry out the same basic functions in transcription and translation. However, the events leading from this common ancestry to the three domains of life remain unclear. The most difficult questions surround the role of the archaeans in both bacterial and eukaryotic evolution.

Archaeans have some features that are typical of bacteria, including a genome organized into a single, circular DNA molecule that is suspended in a nuclear region of the cytoplasm with no surrounding nuclear envelope. There are no membrane-bound organelles in the cytoplasm equivalent to mitochondria, chloroplasts, the ER, or the Golgi complex. However, the archaeans also have some features that are typically eukaryotic. One is the presence of interrupting, noncoding sequences called introns (see Section 15.3) in their genes;

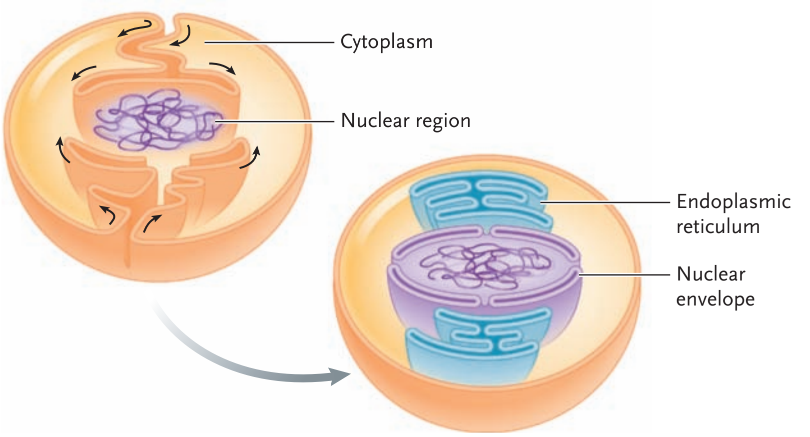
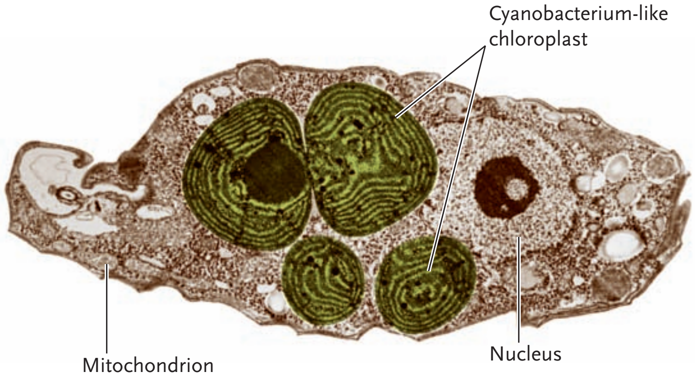


Figure 24.8
A hypothetical route for formation of the nuclear envelope and endoplasmic reticulum, through segments of the plasma membrane that were brought into the cytoplasm by endocytosis.



Robert Trench, Professor Emeritus, University of British Columbia

Figure 24.9
Cyanophora paradoxa, a protist with chloroplasts that closely resemble cyanobacteria without cell walls.

in some archaean genes that have counterparts in eukaryotes, the introns occur in exactly the same positions. By contrast, introns are rare or nonexistent in bacteria. The archaeans also have some characteristics that are unique to their domain, including features of gene and rRNA sequences, and features of cell wall and plasma membrane structure that are found nowhere else among living organisms. The characteristics shared by archaeans and eukaryotes suggest that their roots may lie in a common ancestral line that split off from the line leading to bacteria. At some point, this ancestral line split into the lines leading to archaeans and eukaryotes.

Multicellular Eukaryotes Probably Evolved in Colonies of Cells

The first eukaryotes were unicellular. They are the ancestors of the present-day diversity of unicellular eukaryotes. Multicellular eukaryotes evolved from unicellular eukaryotes and then diverged to produce the present-day multicellular eukaryotes. Molecular clock analysis indicates the first multicellular eukaryote likely arose between 800 and 1000 million years ago, while the first fossil records (of small algae) are from 600 to 800 million years ago.

According to the prevalent theory, multicellular eukaryotes arose by the congregation of cells of the same species into a colony. The ability to act in a coordinated way, probably increased the capacity of colonies to adapt to changes in the environment. Subsequently, differentiation of cells into various specialized cell types with distinct functions produced organisms with a wider range of capabilities and adaptability. Cell differentiation in a colony would have required cell signals that affected gene expression. That is, because each cell in the colony has the same genome, the development of specific func-

UNANSWERED QUESTIONS

What was the first polymer of life?

As discussed in this chapter, many researchers hypothesize that RNA was the first polymer of life because it both self-replicates and can catalyze chemical reactions. In addition, it is neatly connected with contemporary life, which is based on nucleic acids and proteins. There are several problems with this hypothesis, however. One of them is that the synthesis of RNA building blocks, nucleotides, and in particular their ribose fragment, is quite difficult under primordial conditions. To circumvent this difficulty, several researchers have proposed that other genetic polymers, whose monomers are simpler to synthesize, might have preceded RNA. For example, Albert Eschenmoser of the Swiss Federal Institute of Technology in Zurich, Switzerland, replaced ribose with the sugar pyranose, and Peter Nielsen from the University of Copenhagen, Denmark, synthesized a polymer with a peptide-like backbone. These polymers are stable and capable of self-replication. Another popular proposal is that the initial complement of nucleic acid bases was different from A, U, G, and C. One reason for this proposal is poor stability of cytosine in water. Although we have no evidence that transitional polymers were present on early Earth, it is important to realize that alternatives to nucleic acids exist and might be used by life elsewhere.

The protein-first hypothesis is currently not in favor with scientists, even though these polymers are excellent catalysts of chemical reactions and their building blocks, amino acids, existed on prebiotic Earth. This is because there is no known mechanism for proteins to self-replicate. Some researchers speculate that a limited replication of proteins is possible. An alternative hypothesis, supported by computer simulations, is that replication of individual polymers was not necessary at the origin of life and, instead, the reproduction of protein functions in a population was initially sufficient. Currently, neither view has much experimental support, but as we learn more about the structure and functions of small proteins major surprises might be in store.

Can we recreate protocells in a laboratory?

As you read this chapter, you must have noticed that our knowledge about the origin of life is still incomplete. But do we know enough to test our understanding by building in a laboratory a simple life capable of self-reproduction and Darwinian evolution? Several groups of scientists are attempting to do just that. Conceptually, the simplest design is "the minimal RNA cell" proposed by Jack Szostak from Harvard Medical School. It consists of only two ribozymes encapsulated in a membrane-bound structure. One of them is capable of copying both ribozymes; the other catalyzes the synthesis of the membrane-forming molecules from their precursors. In principle, such a system could self-reproduce and undergo evolution through mutations of the ribozymes. However, the apparent simplicity of this construct is somewhat deceiving—no actual ribozymes that function together in this way are currently known. An international team of scientists is attempting to build a simple cell using a set of already existing components, as originally proposed by Steen Rasmussen from Los Alamos National Laboratory and Liaohai Chen from Argonne National Laboratory. This cell would differ from everything we know, however, and would therefore represent an example of "alien life." Craig Venter and several other researchers have taken yet another approach. Starting with a simple, contemporary microorganism as a template, they are trying to delete nonessential genes or substitute natural or synthetic genes that are smaller in size. So far, each of these strategies has encountered a surprising number of conceptual and technical difficulties, and none has been successful. This shows that synthesizing life is more complex that one would expect. If any of these efforts eventually succeeds, it will open the doors not only to many new investigations on the origin of life on Earth but also to the exploration of alternative forms of life and to applications of artificial cells in biotechnology and medicine.

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tions (phenotypes) would require intracellular signals that would change the program of gene regulation. Over time, as genomes evolved, the division of function among cells led to the evolution of the tissues and organ systems of complex eukaryotes.

Multicellularity evolved several times in early eukaryotes, producing a number of lineages of algae as well as the ancestors of present day fungi, plants, and animals.

Life May Have Been the Inevitable Consequence of the Physical Conditions of the Primitive Earth

The events outlined in this chapter, leading from Earth's origin to the appearance of eukaryotic cells, may seem improbable. But, as scientist and author George Wald of Harvard University put it, given the total time span of these events, more than 3.5 billion years, "the impossible becomes possible, the possible probable, and the probable virtually certain. One has only to wait; time itself performs the miracles."

Some researchers go a step further and maintain that the evolution of life on our planet was an inevitable outcome of the initial physical and chemical conditions established by Earth's origin, among them a reducing atmosphere (at least in some locations), a size that generates moderate gravitational forces, and a distance from the Sun that results in average surface temperatures between the freezing and boiling points of water. Given the same conditions and sufficient time, according to these scientists, it is inevitable that life has evolved or is evolving now on other planets in the universe.

The chapters to follow in this unit trace the course of evolution and its products after eukaryotic cells were added to the prokaryotes already on Earth. Among prokaryotes, evolution established two major groups, the Bacteria and Archaea; among eukaryotes, further evolution established the protists, fungi, plants, and animals. The survey begins in the next chapter with a description of present-day Bacteria and Archaea, and of the viruses that infect prokaryotes and eukaryotes.

STUDY BREAK

Summarize the key points of the theory of endosymbiont origins for mitochondria and chloroplasts.

Review

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24.1 The Formation of Molecules Necessary for Life

- Living cells are characterized by a boundary membrane, one or more nucleic acid coding molecules in a nuclear region, a system for using the coded information to make proteins, and a metabolic system providing energy for those activities.
- Oparin and Haldane independently hypothesized that life arose de novo under the conditions they thought prevailed on the primitive Earth, including a reducing atmosphere that lacked oxygen. Reduction reactions, fueled by natural energy acting on the primitive atmosphere, produced organic molecules. Random aggregations of these molecules were able to carry out primitive reactions characteristic of life that gradually became more complex until life appeared. Chemistry simulation experiments support the hypothesis that organic molecules would form under these conditions (Figure 24.4).
- Present thinking is that early Earth's atmosphere was not reducing, but in fact contained significant amounts of oxidants. This has caused skepticism about Oparin and Haldane's hypothesis. One new theory proposes that life developed near hydrothermal vents in the sea floor.

Animation: Miller's reaction chamber experiment

Animation: Milestones in the history of life

24.2 The Origin of Cells

- Organic molecules produced in early Earth's environment by chance formed aggregates that became membrane-bound in protocells, primitive cell-like structures with some of the properties of life. Protocells may have been the precursors of cells (Figure 24.5).
- Next, living cells may have developed from protocells by the development of several critical components, notably energy-harnessing pathways, and a system based on nucleic acids that could store and pass on the information required to make proteins.
- Subsequently, fully cellular life evolved, with a nuclear region containing DNA and the mechanisms for copying its information into RNA messages; a cytoplasmic region containing systems for utilizing energy and systems for translating RNA messages into proteins; a membrane separating the cell from its surroundings; and a reproductive system duplicating the informational molecules and dividing them among daughter cells.
- The first living cells were prokaryotes. Eventually, some early cells developed the capacity to carry out photosynthesis using water as an electron donor; the oxygen produced as a byproduct accumulated and the oxidizing character of Earth's atmosphere increased. From this time on organic molecules produced in the environment were quickly broken down by oxidation, and life could arise only from preexisting life, as in today's world.

24.3 The Origins of Eukaryotic Cells

- According to the endosymbiont hypothesis, mitochondria developed from ingested prokaryotes that were capable of using oxygen as final electron acceptor; chloroplasts developed from ingested cyanobacteria (Figure 24.7).
- Eukaryotic structures such as the ER, Golgi complex, and nuclear envelope appeared through infoldings of the plasma membrane as a part of endocytosis (Figure 24.8).
- Multicellular eukaryotes probably evolved by differentiation of cells of the same species that had congregated into colonies. Multicellularity evolved several times, producing lineages of several algae and ancestors of fungi, plants, and animals.

Animation: Eukaryotic evolution

Questions

Self-Test Questions

1. Earth was formed ____ years ago, whereas the oldest known living cell formed about ____ years ago.
   a. 400×10^3; 3.6×10^6
   b. 4.6×10^9; 1.0×10^9
   c. 3.8×10^9; 4.6×10^7
   d. 4.6×10^9; 3.5×10^9
   e. 2.0×10^9; 600×10^6
2. Which of the following is *not* a characteristic of all living organisms?
   a. They replicate genetic information and convert the information into proteins.
   b. They pass genetic information between generations.
   c. They get energy from molecules in a controlled fashion.
   d. They use external energy to drive internal reactions requiring energy.
   e. They use mitochondria to transform energy for their cells' needs.
3. The greatest leap in evolution is from:
   a. nonlife to prokaryotes.
   b. prokaryotes to one-celled eukaryotes.
   c. ancient archaeans to modern archaeans.
   d. one-celled eukaryotes to fungi.
   e. one-celled eukaryotes to insects.
4. According to the Oparin-Haldane hypothesis, the atmosphere when life began was believed to be composed primarily of:
   a. H_2O, N_2, and CO_2.
   b. H_2, H_2O, NH_3, and CH_4.
   c. H_2O, N_2, O_2, and CO_2.
   d. O_2 and no H_2.
   e. H_2 only.
5. The Miller-Urey experiment:
   a. was based on the belief the atmosphere was oxidizing.
   b. was able to synthesize amino acids and macromolecules from reduced gases.
   c. did not require much energy or a continuous energy source to keep synthesizing.
   d. did not require water to produce organic molecules.
   e. used free oxygen as a reactant.
6. An unknown organism was found in a park. It was one-celled, had no nuclear membrane around its DNA, and contained no mitochondria and no chloroplasts. It belongs to the group:
   a. eukaryotes.
   b. vertebrates or plants.
   c. bacteria or archaea.
   d. plants or fungi.
   e. fungi.
7. Hydrothermal vents are theorized as sources for the origin of life because:
   a. the temperature of the water around them supports most life.
   b. most organic molecules undergo dehydration synthesis at high temperatures.
   c. the amino acids degrade in the colder water soon after synthesis.
   d. water is needed by living things.
   e. reducing conditions with needed molecules surround them.
8. The proposed first macromolecule for the beginning of life is:
   a. DNA to code the cell's activities.
   b. protein to be used in cell functions.
   c. ribozymes to act as information and catalytic molecules.
   d. H_2O as needed by all living things.
   e. chlorophyll for photosynthesis.
9. As part of the evolution of eukaryotic cell, endocytosis, the process of infolding of the plasma membrane, led to the formation of:
   a. chromosomes.
   b. the cell wall.
   c. ribosomes.
   d. the nuclear envelope.
   e. microtubules.
10. Which of the following is *not* part of the evidence supporting the theory of endosymbiosis: Both mitochondria and plastids:
    a. are each the size of many bacterial cells.
    b. have structures and biochemical reactions more like prokaryotes than eukaryotes.
    c. code mRNA, rRNA, and tRNA similar to prokaryotes.
    d. contain circular DNA.
    e. have DNA similar to nuclear DNA.

Questions for Discussion

1. What evidence supports the idea that life originated through inanimate chemical processes?
2. Explain, in terms of hydrophilic and hydrophobic interactions, how protocells might have formed in water from aggregations of lipids, proteins, and nucleic acids.
3. What conditions would likely be necessary for a planet located elsewhere in the universe to evolve life similar to that on Earth?
4. Most scientists agree that life on Earth can arise only from preexisting life, but also that life could have originated spontaneously on the primordial Earth. Can you reconcile these seemingly contradictory statements?

Experimental Analysis

Suppose you discover a hot springs-fed pool on a remote mountain never before explored by humans. In the pool you find a cellular life form that appears to be prokaryotic. What experiments would you do to distinguish between the alternative hypotheses that this organism evolved on Earth from ancestral prokaryotes or is descended from a life form that arrived at that location in a meteorite?

Evolution Link

In the evolution unit, you learned how changes in the environment can foster evolutionary changes in biological systems. How have changing biological systems influenced the evolution of changes in Earth's physical environment?

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? Go to www.thomsonedu.com/login to investigate both sides of the issue and then vote.