UNIT 5

The Evolutionary History of Biological Diversity

Chapter 26

The Tree of Life: An Introduction to Biological Diversity

Key Concepts

26.1 **Conditions on early Earth made the origin of life possible**

26.2 **The fossil record chronicles life on Earth**

26.3 **As prokaryotes evolved, they exploited and changed young Earth**

26.4 **Eukaryotic cells arose from symbioses and genetic exchanges between prokaryotes**

26.5 **Multicellularity evolved several times in eukaryotes**

26.6 **New information has revised our understanding of the tree of life**

Framework

The evolutionary history of life is chronicled in the fossil record. Division between eras in the geologic record are marked by major biological transitions, often linked with continental drift and mass extinctions. This chapter presents hypotheses on how life began on Earth between 4.0 and 3.5 billion years ago, how prokaryotes evolved and changed Earth, how eukaryotic cells arose from endosymbioses and genetic exchange between prokaryotes, and how multicellularity may have evolved.

From these proposed beginnings, an incredible biological diversity has evolved. These diverse organisms are grouped into multiple kingdoms within a three-domain system—Archaea, Bacteria, and Eukarya.

Chapter Review

26.1 Conditions on early Earth made the origin of life possible

Synthesis of Organic Compounds on Early Earth Earth formed about 4.6 billion years ago and was bombarded by huge rocks until about 3.9 billion years ago. As Earth cooled, water vapor condensed into oceans, and the atmosphere probably contained nitrogen and its oxides, carbon dioxide, methane, ammonia, and hydrogen sulfide.

In the 1920s, A. Oparin and J. Haldane independently hypothesized that conditions on the primitive Earth, in particular the reducing atmosphere, lightning, and intense ultraviolet radiation, favored the synthesis of organic compounds from inorganic precursors available in the atmosphere and seas.

In 1953, S. Miller and H. Urey tested the Oparin-Haldane hypothesis with an apparatus that simulated the hypothetical conditions of early Earth. After a week of applying sparks (lightning) to a warmed flask of water (the primeval sea) in an atmosphere of

H_2O, H_2, CH_4, and NH_3, Miller and Urey found a variety of amino acids and other organic molecules in the flask. Numerous laboratory replications using various combinations of atmospheric gases have been able to produce organic compounds. It is not clear, however, that the atmosphere was reducing enough or that it played a significant role in producing organic molecules.

Another hypothesis focuses on volcanoes and deep-sea vents as the possible locations of these early reactions and sources of chemical precursors.

It is also possible that organic compounds could reach Earth on meteorites. Carbonaceous chondrites are rocks from meteorites that contain carbon compounds, including amino acids similar to those produced in the Miller-Urey experiment. Scientists continue to look for signs of liquid water, oxygen in the atmosphere, and the possibility of life on other planets.

Abiotic Synthesis of Polymers Macromolecules are also needed for life. Researchers have created polypeptides by dripping dilute solutions of organic monomers onto hot sand or rock in the laboratory. Such polymers may have acted as catalysts on early Earth.

Protobionts Life requires accurate replication and metabolism, and the two are interdependent. **Protobionts** are aggregates of abiotically produced organic molecules surrounded by a membrane. Laboratory experiments indicate that protobionts could have formed spontaneously. When a mixture of organic ingredients includes lipids, droplets, called liposomes, become surrounded by a lipid bilayer. This bilayer acts as a selectively permeable membrane. If enzymes are added, liposomes can carry out simple metabolic reactions. An energy-storing membrane potential may develop across this membrane.

The "RNA World" and the Dawn of Natural Selection Once protobionts containing self-replicating molecules that carried genetic information had formed, natural selection could begin to shape the properties of protobionts.

RNA probably functioned as the first hereditary material. The discovery of RNA catalysts, called **ribozymes,** indicates that RNA molecules may have been capable of ribozyme-catalyzed replication. Ribozymes have been produced that can make complementary copies of parts of their sequence. Natural selection has been observed with RNA in the laboratory, in which sequences that are most stable and autocatalytic prevail in the population.

RNA-directed protein synthesis may have begun with the weak binding of specific amino acids to bases along RNA molecules and their linkage to form a short polypeptide. This polypeptide may then have behaved as an enzyme to help the RNA molecule replicate.

Protobionts with self-replicating, catalytic RNA could grow, split, pass some of their RNA to daughters, and be acted on by natural selection. Differential reproductive success of these offspring would have accumulated metabolic and hereditary improvements. DNA, a more stable genetic molecule, eventually replaced RNA as the carrier of genetic information.

■ INTERACTIVE QUESTION 26.1

Why do we say that for life to have begun required both accurate replication and metabolism?

26.2 The fossil record chronicles life on Earth

How Rocks and Fossils Are Dated The order in which fossils appear in the strata of sedimentary rocks indicates their relative age. Index fossils, such as shells of widespread animals, are used to correlate strata from different locations. Gaps may appear in the sequence, indicating that an area was above sea level or underwent erosion during some period of geologic time.

Radiometric dating is used to determine the ages of rocks and fossils. Each radioactive isotope has a fixed rate of decay—its **half-life,** which is the number of years it takes for 50% of an original sample to decay. During an organism's lifetime, it accumulates radioactive isotopes in proportions equal to the relative abundance of the isotopes in the environment. After the organism dies, the isotopes decay at their fixed rate. Carbon-14, with a half-life of 5,730 years, is used for determining the age of fossils up to 75,000 years old; potassium-40, which decays to the gas argon-40, can be used to date volcanic rock and thus infer the age of fossils associated with those rocks.

Patterns of **magnetic reversals,** when the orientation of Earth's magnetic field has reversed, can also be used to date rocks.

■ INTERACTIVE QUESTION 26.2

A fossil has one-eighth of the atmospheric ratio of C-14 to C-12. Estimate the age of this fossil.

The Geologic Record Geologists have developed a geologic record of Earth's history. The Archaean and the Proterozoic eons lasted approximately 4 billion years and are collectively referred to as the Precambrian. The Phanerozoic eon covers the last half billion years and is divided into three eras: the Paleozoic, Mesozoic, and Cenozoic. These eras are delineated by major transitions, such as mass extinctions and extensive radiations. The eras are subdivided into periods and epochs, which are often associated with lesser extinctions shown in the fossil record.

Mass Extinctions A species may become extinct due to a change in its physical or biological environment. Mass extinctions have occurred during periods of major environmental change.

The Permian mass extinction, occurring at the boundary between the Paleozoic and Mesozoic eras about 250 mya, claimed about 96% of marine animal species and many terrestrial ones. These extinctions may be related to massive volcanic eruptions in Siberia, which probably warmed the global climate and slowed the mixing of oceans, reducing the oxygen supply to marine organisms.

The Cretaceous mass extinction, which marks the boundary between the Mesozoic and Cenozoic eras about 65 mya, claimed more than one-half of the marine species, many families of terrestrial plants and animals, and most of the dinosaurs. Possibly an asteroid or comet collided with Earth and caused the Cretaceous extinction. The thin layer of clay rich in iridium (an element common in meterorites) that separates Mesozoic from Cenozoic sediments may have been the fallout from a huge cloud of dust created by the collision. This cloud would have blocked sunlight and severely affected weather. The huge Chicxulub crater on the Yucatán coast of Mexico may have been the site of the impact.

■ INTERACTIVE QUESTION 26.3

Why do extensive adaptive radiations often follow mass extinctions?

26.3 As prokaryotes evolved, they exploited and changed young Earth

The oldest known fossils are 3.5-billion-year-old **stromatolites,** which are rock like layers of bacteria and sediment. They resemble the banded mats of sediment that form around certain modern-day bacterial colonies. It is possible that the earliest life forms may have emerged as early as 3.9 billion years ago.

The First Prokaryotes Early protobionts must have used molecules available in the primitive soup for their growth and replication. They were eventually replaced with autotrophs that could produce their needed compounds from molecules in the environment. Some of these may have diversified and become able to use light energy. Heterotrophs then emerged that could live on products of the autotrophs or on the autotrophs themselves. These autotrophs and heterotrophs—the prokaryotes that diverged into the bacteria and the archaea—were the sole inhabitants of Earth from 3.5 to about 2 billion years ago.

Electron Transport Systems The chemiosmotic synthesis of ATP is common to all three domains. Transmembrane proton pumps probably used ATP to expel H^+ to regulate pH. Electron transport chains that coupled the oxidation of organic acids to transport of H^+ out of the cell would have saved the cell ATP. When electron transport systems extruded extra H^+, the diffusion of H^+ back into the cell could reverse the proton pumps and generate ATP.

Photosynthesis and the Oxygen Revolution Prokaryotes capable of non-oxygen-producing photosynthesis probably appeared early in prokaryotic history. Cyanobacteria may have evolved as early as 3.5 billion years ago and are the only living photosynthetic prokaryotes that generate O_2. Banded iron formations in marine sediments and the rusting of iron in terrestrial rocks that began about 2.7 billion years ago provide evidence of oxygen accumulation from the photosynthesis of cyanobacteria. The relatively rapid accumulation of atmospheric oxygen around 2.2 billion years ago caused the extinction of many prokaryotic groups and relegated others to anaerobic habitats.

■ INTERACTIVE QUESTION 26.4

What adaptation evolved in some prokaryotes that enabled them to thrive in this new oxygen-rich atmosphere?

26.4 Eukaryotic cells arose from symbioses and genetic exchanges between prokaryotes

The First Eukaryotes Chemical traces of eukaryotes may date back to 2.7 billion years ago. Fossils that are generally accepted as eukaryotic date from 2.1 billion years ago.

Endosymbiotic Origin of Mitochondria and Plastids The cytoskeleton of eukaryotic cells allows them to change shape and engulf other cells. The first eukaryotes may have been predators of other cells. The cytoskeleton is also necessary for the movement of chromosomes in mitosis and meiosis.

The first eukaryotic cells may have engulfed an aerobic heterotrophic prokaryote and packaged it inside a vacuole. The prokaryote became an *endosymbiont,* living within the host cell. Eventually the relationship became mutualistic, and finally the endosymbiont evolved into a mitochondrion. Plastids, including chloroplasts, may have evolved through a similar endosymbiotic process. In this **serial endosymbiosis,** mitochondria probably arose first because they or their genetic remnants are present in all eukaryotes.

A great deal of evidence supports the endosymbiotic origin of plastids and mitochondria. Comparisons of small-subunit ribosomal RNA (SSU-rRNA) indicate that the alpha proteobacteria are the closest relatives of mitochondria, and that cyanobacteria are the closest relatives of plastids. Transposable elements probably transferred some of the genes present in mitochondria and plastids to the nucleus of the host cell.

■ INTERACTIVE QUESTION 26.5

List some of the evidence supporting an endosymbiotic origin of mitochondria and plastids?

Eukaryotic Cells as Genetic Chimeras Some researchers propose that the nucleus evolved from an archaeal endosymbiont. Genes with close relatives in both bacteria and archaea have been found in nuclei, perhaps as a result of **genetic annealing,** involving horizontal gene transfers between many bacterial and archaeal lineages. According to the "you are what you eat" hypothesis, evolving eukaryotes occasionally incorporated some of the genes of their various bacterial and archaeal prey into their nucleus.

The Golgi apparatus and endoplasmic reticulum perhaps originated from infoldings of the plasma membrane. Homologs of cytoskeletal proteins have been found in bacteria. Despite the lack of the 9 + 2 microtubule apparatus in any prokaryote, some researchers speculate that flagella and cilia may have evolved from symbiotic bacteria.

26.5 Multicellularity evolved several times in eukaryotes

The Earliest Multicellular Eukaryotes Although molecular clocks estimate that the common multicellular ancestor arose 1.5 billion years ago, the oldest known fossils are small algae from 1.2 billion years ago. Larger animals appear in the fossil record in the late Proterozoic. A diversity of algae and animals, including embryolike structures, has been found in a Chinese site dating from 570 million years ago.

According to the **snowball Earth hypothesis,** a severe ice age that occurred from 750 to 570 million years ago accounted for the limited diversity and distribution of multicellular eukaryotes, with the first major diversification occurring after the Earth thawed.

The Colonial Connection The first multicellular organisms were **colonies** of autonomously replicating cells in which some cells became specialized. Some prokaryotes show cellular specialization, such as the nitrogen-fixing cells called heterocysts found in the filamentous cyanobacterium *Nostoc.*

A multicellular organism generally develops from a single cell, which divides to form an organism with many specialized cells. Multicellularity evolved several times among early eukaryotes.

The "Cambrian Explosion" Fossils of Porifera (sponges) and Cnidaria date from the late Proterozoic. The appearance of most of the major phyla of animals in the first 20 million years of the Cambrian period, beginning 542 mya, is referred to as the "Cambrian explosion." But molecular evidence indicates that many animal phyla began to diverge between 1 billion and 700 million years ago.

Colonization of Land by Plants, Fungi, and Animals Cyanobacteria coated damp terrestrial surfaces more than a billion years ago, but plants, fungi, and animals colonized land only about 500 million years ago, during the early Paleozoic era. The move onto land was associated with adaptations that helped prevent dehydration and permitted reproduction on land. Plants and fungi appear to have colonized the land together in symbiotic associations. Arthropods and tetrapod vertebrates are the most widespread and diverse land animals.

Continental Drift The continents rest on great plates of crust that float on the molten mantle. Earthquakes, islands, and mountains are formed in regions where these shifting plates abut. Large-scale continental drift brought all the landmasses together into a supercontinent named **Pangaea** about 250 million years ago (mya), near the end of the Paleozoic era. This tremendous change had a great environmental impact as shorelines were eliminated, shallow coastal areas were drained, and the majority of the land became part of the continental interior. Many species became extinct, and new opportunities for remaining species became available. About 180 mya, during the Mesozoic era, Pangaea broke up and the continents drifted apart, creating a huge geographic isolation event.

■ INTERACTIVE QUESTION 26.6

Marsupials evolved in what is now North America, yet their greatest diversity is found in Australia. How can you account for this biogeographic distribution?

■ INTERACTIVE QUESTION 26.7

Explain the snowball Earth hypothesis.

26.6 New information has revised our understanding of the tree of life

Previous Taxonomic Systems Intuitively and historically, we have divided the diversity of life into two kingdoms—plants and animals. R. Whittaker proposed a five-kingdom system in 1969. The prokaryotes were set apart from the eukaryotes and placed in the kingdom Monera. The kingdoms Plantae, Fungi, and Animalia consist of multicellular eukaryotes, defined partly by characteristics of nutrition. The kingdom Protista included unicellular eukaryotes or simple multicellular organisms that are believed to have descended from them.

Reconstructing the Tree of Life: A Work in Progress As systematists increase their understanding of phylogenetic relationships, alternative classification systems are proposed. The current **three-domain system** places the three major evolutionary lineages into a superkingdom taxon. The domains Bacteria and Archaea represent the early evolutionary divergence within the prokaryotes, and the domain Eukarya includes all the kingdoms of eukaryotes. Using molecular systematics and cladistics, systematists propose splitting the Protista into five or more kingdoms. New data will continue to be used in the challenge of constructing a classification system that reflects the evolutionary history of life.

Word Roots

proto- = first (*protobionts:* aggregates of abiotically produced molecules)

stromato- = something spread out; **-lite** = a stone (*stromatolite:* rocks made of banded domes of sediment in which are found the most ancient forms of life)

Structure Your Knowledge

1. What do scientists think the primitive Earth was like? How could life possibly arise in such an inhospitable environment?
2. Develop a simple concept map of Whittaker's five-kingdom system, indicating the key characteristics that are used to differentiate the kingdoms.
3. Now draw a map that shows the current three-domain system. Why do systematists keep changing the classification system?

Test Your Knowledge

MULTIPLE CHOICE: *Choose the one best answer.*

1. Index fossils are fossils of
   - **a.** unique organisms that are used to determine the relative rates of evolution in different areas.
   - **b.** widespread organisms that allow geologists to correlate strata of rocks from different locations.
   - **c.** transitional forms that link major evolutionary groups.
   - **d.** extinct organisms that indicate the separation of different eras.
   - **e.** fossils that have been dated using magnetic reversal data.
2. The half-life of carbon-14 is 5,730 years. A fossil that is 22,920 years old would have what amount of the normal proportion of C-14 to C-12?

   a. $\frac{1}{2}$ **c.** $\frac{1}{6}$ **e.** $\frac{1}{16}$

   b. $\frac{1}{4}$ **d.** $\frac{1}{8}$

3. The Permian mass extinction between the Paleozoic and Mesozoic eras
   a. affected a large percentage of marine and terrestrial species.
   b. coincided with the breaking apart of Pangaea.
   c. made way for the adaptive radiation of mammals, birds, and pollinating insects.
   d. appears to have been caused by a large asteroid striking Earth.
   e. did all of the above.

4. The primitive atmosphere of Earth may have favored the synthesis of organic molecules because it
   a. was highly oxidative.
   b. was reducing and had energy sources in the form of lightning and UV radiation.
   c. had a great deal of methane and organic fuels.
   d. had plenty of water vapor, carbon, oxygen, and nitrogen, providing the C, H, O, and N needed for organic molecules.
   e. consisted almost entirely of hydrogen gas.

5. Life on Earth is thought to have begun
   a. 540 million years ago, at the beginning of the Paleozoic era.
   b. 700 million years ago, during the Precambrian.
   c. 2.7 billion years ago, when oxygen began to accumulate in the atmosphere.
   d. between 3.5 and 4.0 billion years ago.
   e. 4.5 billion years ago, when the Earth formed.

6. Stromatolites are
   a. early prokaryotic fossils found in sediments around hydrothermal vents.
   b. a protobiont that forms when lipids assemble into a bilayer surrounding organic molecules.
   c. members of the kingdom Protista that are both motile and photosynthetic.
   d. fossils appearing to be eukaryotes that are about twice the size of bacteria.
   e. layered communities of bacteria, fossils of which represent the oldest known prokaryotes.

7. Liposomes are
   a. spontaneously forming droplets surrounded by a lipid membrane.
   b. prokaryotes that lived as endosymbionts in larger prokaryotic cells.
   c. polypeptides formed in the laboratory by dripping organic monomers onto hot rocks.
   d. abiotically produced lipids.
   e. RNA self-replicating molecules.

8. Which of the following is a proposed hypothesis for the origin of genetic information?
   a. Early DNA molecules coded for RNA, which then catalyzed the production of proteins.
   b. Early polypeptides became associated with RNA bases and catalyzed their linkage into RNA molecules.
   c. Short RNA strands were capable of self-replication and evolved by natural selection.
   d. As protobionts grew and split, they distributed copies of their molecules to their offspring.
   e. Early RNA molecules coded for DNA, which then dictated the order of amino acids in a polypeptide.

9. Which of the following provides the poorest evidence that life may have formed spontaneously?
   a. the discovery of ribozymes, showing that prebiotic RNA molecules may have been autocatalytic.
   b. the laboratory synthesis of liposomes.
   c. the fossil record.
   d. the abiotic synthesis of polymers from monomers dripped onto hot rocks.
   e. the production of organic compounds in the Miller-Urey experimental apparatus.

10. Banded iron formations in marine sediments provide evidence of
   a. the first prokaryotes around 3.5 billion years ago.
   b. oxidized iron layers in terrestrial rocks.
   c. the accumulation of oxygen in the seas from the photosynthesis of cyanobacteria.
   d. the evolution of photosynthetic archaea near deep-sea vents.
   e. the crashing of meteorites onto Earth, possibly transporting abiotically produced organic molecules from space.

11. Simple animals such as jellies and worms first appear in the fossil record around 600 million years ago. This time period may correspond to
   a. the thawing of snowball Earth.
   b. the first appearance of multicellular eukaryotes in the fossil record.
   c. the Cambrian explosion of animal forms.
   d. the colonization of land by plants and fungi, providing the food source for animals to follow.
   e. the rapid increase in atmospheric oxygen that allowed for the active lifestyle of animals.

12. The first generally accepted fossil evidence of eukaryotic cells

a. dates from 1.2 billion years ago.

b. appears in sediments around deep-sea vents.

c. is found in stromatolites.

d. dates from 2.7 billion years ago when oxygen accumulated in the atmosphere.

e. appears after prokaryotes had been evolving on Earth for 1.5 billion years.

13. According to the theory of serial endosymbiosis,

a. multicellularity evolved when colonies of cells became specialized and began to reproduce from eggs.

b. plants were able to colonize land with fungi as symbionts in their roots.

c. the mitochondria and plastids of eukaryotic cells were originally prokaryotic endosymbionts that became permanent parts of the host cell.

d. the infoldings and specializations of the plasma membrane led to the evolution of the endomembrane system.

e. the nuclear membrane evolved first, then mitochondria, and then plastids.

14. Evidence that the evolution of eukaryotic cells may have involved genetic annealing from multiple lineages comes from

a. the universal presence of ribosomes in all cells.

b. evidence of the transfer of genes from endosymbiotic prokaryotes to the host cell's nucleus.

c. the presence of genes related to both bacteria and to archaea in eukaryotic nuclei.

d. evidence of "chemical signatures" of eukaryotes that date from 2.7 billion years ago.

e. Both b and c provide such evidence.

15. Mitochondria and plastids contain DNA and ribosomes and make some, but not all, of their proteins. Some of their proteins are coded for by nuclear DNA and produced in the cytoplasm. What may explain this division of labor?

a. Over the course of evolution, some of the original endosymbiont's genes were transferred to the host cell's nucleus.

b. The host cell's genome always included genes for making mitochondrial and plastid proteins.

c. These organelles do not have sufficient resources to make all their proteins and rely on the help of the cell.

d. Some mitochondria and plastid genes were contributed by early bacterial prokaryotes that shared genes with other primitive cells.

e. The smaller prokaryotic ribosomes in these organelles cannot produce the eukaryotic proteins required for their functions.

16. Why is the diversity of life now organized into three domains?

a. Molecular evidence indicates that the protists really include three separate lineages.

b. The domains Bacteria and Archaea reflect the early evolutionary divergence of these two lineages, and they differ from eukaryotes.

c. The eukaryotes are more alike than are the prokaryotes and thus belong in one big group.

d. The division into plants, animals, and bacteria is more intuitive and accessible to most people.

e. The origin of life involved three distinct stages—protobiont, prokaryote, and eukaryote—and each domain represents one of those stages.