Chapter 25

The History of Life on Earth

Lecture Outline

Overview: Lost Worlds

- The largest fully terrestrial animal in Antarctica is a 5-mm-long fly.
- Five hundred million years ago, Antarctica was surrounded by warm ocean waters filled with tropical invertebrates.
- Later, the continent was covered with forests. Dinosaurs and, later, predatory “terror birds” hunted in these forests.
- All over the world, past organisms differed from those alive today.
- **Macroevolution** is the pattern of evolution over large time scales.
    - Macroevolutionary changes include the origin of photosynthesis, the evolution of terrestrial vertebrates, and the impact of mass extinctions on the diversity of life.

Concept 25.1 Conditions on early Earth made the origin of life possible.

- Most biologists now think it is credible that chemical and physical processes on early Earth, aided by the emerging force of natural selection, produced very simple cells.
- According to one hypothetical scenario, there were four main stages in this process:
    1. The abiotic synthesis of small organic molecules (monomers)
    2. The joining of monomers into macromolecules
    3. The packaging of these molecules into “protobionts,” droplets with membranes that maintained a distinct internal chemistry
    4. The origin of self-replicating molecules that eventually made inheritance possible
- The scenario is speculative but does lead to predictions that can be tested in laboratory experiments.
- Earth and the other planets in the solar system formed about 4.6 billion years ago, condensing from a vast cloud of dust and rocks surrounding the young sun.
- It is unlikely that life could have originated or survived in the first few hundred million years after Earth’s formation.
    - The planet was bombarded by huge bodies of rock and ice left over from the formation of the solar system.

  - These collisions generated enough heat to vaporize all available water and prevent the formation of the seas.
  - This phase ended about 3.9 billion years ago.

Abiotic synthesis of organic monomers is a testable hypothesis.

- As the bombardment of early Earth slowed, conditions on the planet were very different from those of today.
- The first atmosphere may have been a reducing atmosphere thick with water vapor along with nitrogen and its oxides, carbon dioxide, methane, ammonia, hydrogen, and hydrogen sulfide.
  - Similar compounds are released from volcanic eruptions today.
- As Earth cooled, the water vapor condensed into the oceans and much of the hydrogen was lost into space.
- In the 1920s, Russian chemist A. I. Oparin and British scientist J. B. S. Haldane independently postulated that conditions on early Earth favored the synthesis of organic compounds from inorganic precursors.
  - They reasoned that this could not happen today because high levels of oxygen in the atmosphere attack chemical bonds.
  - A reducing environment in the early atmosphere would have promoted the joining of simple molecules to form more complex ones.
- The considerable energy required to make organic molecules could have been provided by lightning and the intense ultraviolet radiation that penetrated the primitive atmosphere.
  - Young suns emit more ultraviolet radiation. The lack of an ozone layer in the early atmosphere would have allowed this radiation to reach Earth.
- Haldane suggested that the early oceans were a solution of organic molecules, a “primitive soup” from which life arose.
- In 1953, Stanley Miller and Harold Urey tested the Oparin-Haldane hypothesis by creating, in the laboratory, the conditions that had been postulated for early Earth.
  - They discharged sparks in an “atmosphere” of gases and water vapor.
  - The Miller-Urey experiment produced a variety of amino acids and other organic molecules.
- Attempts to reproduce the Miller-Urey experiment with other gas mixtures also produced organic molecules, although in smaller quantities.
- It is unclear whether the atmosphere contained enough methane and ammonia to be reducing.
  - There is growing evidence that the early atmosphere was made up of primarily nitrogen and carbon dioxide and was neither reducing nor oxidizing.
  - Miller-Urey–type experiments with such atmospheres have not produced organic molecules.
- It is likely that small “pockets” of the early atmosphere near volcanic openings were reducing.

- Alternative sites proposed for the synthesis of organic molecules include submerged volcanoes and deep-sea vents where hot water and minerals gush into the deep ocean.
    - These regions are rich in inorganic sulfur and iron compounds, which are important in ATP synthesis by present-day organisms.
- Miller-Urey–type experiments show that the abiotic synthesis of organic molecules is possible.
- Some of the organic compounds from which the first life on Earth arose may have come from space.
- Support for this idea comes from analyses of the chemical composition of meteorites.
    - A 4.5-billion-year-old carbonaceous chondrite meteorite collected in southern Australia was found to contain more than 80 amino acids, in similar proportions to those produced in the Miller-Urey experiment.
    - These amino acids contained an equal mix of D and L isomers and could not have been contaminants from living organisms on Earth. Living things make and use only L isomers.

Laboratory simulations of early-Earth conditions have produced organic polymers.

- All living cells contain an array of macromolecules, including enzymes, other proteins, and nucleic acids. Could such macromolecules have formed on early Earth?
- The abiotic origin hypothesis predicts that monomers should link to form polymers without enzymes and other cellular equipment.
- Researchers have produced amino acid polymers after dripping solutions of amino acids onto hot sand, clay, or rock.
    - Unlike proteins, these polymers are a complex mix of linked and cross-linked amino acids.
- Such polymers may have acted as weak catalysts for reactions on early Earth.

Protobionts can form by self-assembly.

- Life is defined by two properties: accurate replication and metabolism.
- Neither property can exist without the other.
- DNA molecules carry genetic information, including the information needed for accurate replication.
    - The replication of DNA requires elaborate enzymatic machinery, along with a copious supply of nucleotide building blocks provided by cell metabolism.
- Although Miller-Urey experiments have yielded some of the nitrogenous bases of DNA and RNA, they have not produced anything like nucleotides.
- Thus, nucleotides were likely not part of the early organic soup.
- Self-replicating molecules and a metabolism-like source of the building blocks must have appeared together.
- The necessary conditions may have been provided by **protobionts**, aggregates of abiotically produced molecules surrounded by a membrane or membrane-like structure.

- Protobionts exhibit some of the properties associated with life, including reproduction and metabolism, and can maintain an internal chemical environment different from their surroundings.
- Laboratory experiments show the spontaneous formation of protobionts from abiotically produced organic compounds.
    - For example, droplets of abiotically produced organic compounds called liposomes form when lipids and other organic molecules are added to water.
    - The hydrophobic molecules in the mixture form a bilayer at the droplet surface, much like the lipid bilayer of a membrane.
    - Because the liposome bilayer is selectively permeable, liposomes undergo osmotic swelling or shrinking in different salt concentrations.
    - Some liposomes can perform simple metabolic reactions.

RNA may have been the first genetic material.

- The first genetic material was probably RNA, not DNA.
- Thomas Cech and Sidney Altman found that RNA molecules not only play a central role in protein synthesis but also are important catalysts in modern cells.
- RNA catalysts, called **ribozymes,** can make complementary copies of short pieces of RNA when supplied with nucleotide building blocks.
- Laboratory experiments have demonstrated that RNA sequences can evolve under abiotic conditions.
    - Unlike double-stranded DNA, single-stranded RNA molecules can assume a variety of three-dimensional shapes specified by their nucleotide sequences.
    - RNA molecules have both a genotype (nucleotide sequence) and a phenotype (three-dimensional shape) that interact with surrounding molecules.
    - Under particular conditions, some RNA sequences are more stable and replicate faster and with fewer errors than other sequences.
- Occasional copying errors create mutations; selection screens these mutations for the most stable or the best at self-replication.
    - Beginning with a diversity of RNA molecules that must compete for monomers to replicate, the sequence best suited to the temperature, salt concentration, and other features of the surrounding environment and having the greatest autocatalytic activity will increase in frequency.
    - Its descendents will be a family of closely related RNA sequences, differing due to copying errors.
    - Some copying errors will result in molecules that are more stable or more capable of self-replication.
- Similar selection events may have occurred on early Earth.
- Modern molecular biology may have been preceded by an “RNA world,” in which small RNA molecules that carried genetic information replicated and stored information about the protobionts that carried them.

- A protobiont with self-replicating, catalytic RNA would differ from others without RNA or with RNA that had fewer capabilities.
- If that protobiont could grow, split, and pass on its RNA molecules to its daughters, the daughters would have some of the properties of their parent.
- The first protobionts must have had limited amounts of genetic information, specifying only a few properties.
- Because their properties were heritable, they could be acted on by natural selection.
- The most successful of these protobionts would have increased in numbers because they could exploit available resources and produce similar daughter protobionts.
- Once RNA sequences that carried genetic information appeared in protobionts, many further changes were possible.
- One refinement was the replacement of RNA as the repository of genetic information by DNA.
    - Double-stranded DNA is a more stable molecule, and it can be replicated more accurately.
- Once DNA appeared, RNA molecules began to take on their modern roles as intermediates in the translation of genetic programs.
- The "RNA world" gave way to a "DNA world."

Concept 25.2 The fossil record documents the history of life.

- The fossil record shows that there have been great changes in the organisms that have lived on Earth.
    - Many past organisms were unlike living organisms.
    - Many organisms that were once common are now extinct.
    - New groups of organisms arose from previously existing ones.
- The fossil record is an incomplete chronicle of evolutionary change.
    - Few organisms are preserved as fossils. Many fossils that do form are later destroyed by geologic processes, and only a fraction of them are discovered.
- The fossil record is biased in favor of species that persisted for a long time, that were abundant and widespread, that lived in certain environments, and that had hard parts that fossilized readily.
- Despite its limitations, the fossil record provides a detailed account of biological change over geologic time.
- Sedimentary rocks are the richest source of fossils.
- The relative sequence of fossils in sedimentary rock *strata* tells us the order in which the fossils were formed, although it does not tell us their ages.
- Geologists have developed methods for obtaining absolute dates for fossils.

- One of the most common techniques is **radiometric dating,** which is based on the decay of radioactive isotopes.
    - An isotope's characteristic **half-life,** the number of years it takes for 50% of the original sample to decay, is unaffected by temperature, pressure, or other environmental variables.
    - Carbon-14 decays rapidly, with a half-life of 5,730 years. Uranium-238 decays slowly, with a half-life of 4.5 billion years.
- Fossils contain isotopes of elements that accumulated while the organisms were alive.
    - For example, the carbon in a living organism contains the most common carbon isotope, carbon-12, as well as a radioactive isotope, carbon-14.
    - When an organism dies, it stops accumulating carbon, and the carbon-14 that it contained at the time of death slowly decays to nitrogen-14.
    - By measuring the ratio of carbon-14 to total carbon or to nitrogen-14 in a fossil, scientists can determine the fossil's age.
- Carbon-14 is useful for dating fossils up to about 75,000 years old.
    - Fossils older than that contain too little carbon-14 to be detected by current techniques.
- It is more difficult to date old fossils in sedimentary rocks.
    - Organisms do not incorporate radioisotopes with long half-lives, such as uranium-238.
- The sedimentary rocks in which fossils are found tend to be composed of sediments of differing ages.
- Paleontologists can determine the absolute age of fossils sandwiched between layers of volcanic rock.
    - For example, paleontologists might measure the amount of potassium-40 in those layers.
    - Potassium-40 has a half-life of 1.3 billion years old. If the two surrounding rock layers were determined to be 525 and 535 million years old, the fossils likely represent organisms that lived about 530 million years ago.
- The magnetism of rocks also provides dating information.
    - When volcanic or sedimentary rock forms, iron particles in the rock align themselves with Earth's magnetic field.
    - When the rock hardens, the orientation of the iron particles is frozen in time.
- Geologists have determined that Earth's north and south magnetic poles have reversed repeatedly in the past.
    - These magnetic reversals have left their record on rocks throughout the world.
- Patterns of magnetic reversal can be matched with corresponding patterns elsewhere, allowing rocks to be dated when other methods are not available.
- Fossils provide evidence of the origin of new groups of organisms.
- Along with amphibians and reptiles, mammals are considered *tetrapods*, with four limbs.
- Mammals with unique anatomical features that fossilize readily have a good fossil record.

  - The lower jaw of most tetrapods is composed of several bones. In mammals, each side is composed of a single dentary bone.
  - The hinge between the upper and lower jaws is composed of a different set of bones in mammals and other tetrapods.
  - Mammals also have a unique set of three bones to transmit sound in the middle ear, compared with one such bone in other tetrapods.
  - Finally, mammalian teeth are differentiated into incisors, canines, and cusped molars.
- The fossil record shows that the unique features of mammals evolved in a series of gradual modifications in a group of tetrapods called *synapsids*.
- The features of mammals arose gradually in a previously existing group, the cynodonts.

Concept 25.3 Key events in life's history include the origins of single-celled and multicelled organisms and the colonization of land.

- By studying rocks and fossils at many different sites, geologists have established a **geologic record** of the history of life on Earth, which is divided into three eons.
- The first two eons—the Archaean and the Proterozoic—together lasted approximately 4 billion years.
  - These two eons are referred to as the Precambrian.
- The Phanerozoic eon covers the last half billion years and encompasses much of the time that multicellular eukaryotic life has existed on Earth.
  - It is divided into three eras: Paleozoic, Mesozoic, and Cenozoic.
  - Each era represents a distinct age in the history of Earth and life on Earth.
  - The boundaries between eras correspond to times of mass extinction, when many forms of life disappeared.
- The oldest known fossils are 3.5-billion-year-old **stromatolites,** rocklike structures composed of layers of cyanobacteria and sediment.
  - If complex bacterial communities existed 3.5 billion years ago, it seems reasonable that life originated much earlier, perhaps 3.9 billion years ago, when Earth first cooled to a temperature at which liquid water could exist.
- Prokaryotes dominated evolutionary history from 3.5 to 2.0 billion years ago.

The evolution of modern photosynthesis led to an oxygen revolution.

- Most atmospheric O_2 is of biological origin, from the water-splitting step of photosynthesis.
- When oxygenic photosynthesis first evolved, the free O_2 it produced likely dissolved in the surrounding water.
- When O_2 reached a high enough concentration to react with dissolved iron, the iron precipitated as iron oxide, which accumulated as red layers of rock in banded iron formations.
- Additional O_2 dissolved in the seas and lakes until they were saturated with O_2.

- After this, the O_2 finally began to “gas out” of water and enter the atmosphere.
- About 2.7 billion years ago, oxygen began accumulating in the atmosphere and terrestrial rocks with oxidized iron formed.
- Although oxygen accumulation was gradual between 2.7 and 2.2 billion years ago, it shot up to 10% of current values shortly afterward.
- This oxygen revolution had an enormous impact on life.
    - In certain chemical forms, oxygen attacks chemical bonds, inhibits enzymes, and damages cells.
    - The increase in atmospheric oxygen likely doomed many prokaryote groups.
    - Some species survived in habitats that remained anaerobic, where their descendents survive as obligate anaerobes.
    - Other species evolved mechanisms to use O_2 in cellular respiration, which uses oxygen to help harvest the energy stored in organic molecules.
- What caused the acceleration in atmospheric O_2 levels, following its early, gradual rise?
    - One hypothesis suggests that this rise followed the evolution of eukaryotic cells with chloroplasts.

Eukaryotic cells are more complex than prokaryotic cells.

- Eukaryotic cells differ in many respects from the smaller cells of bacteria and archaea.
- Even the simplest single-celled eukaryote is far more complex in structure than any prokaryote, with a nuclear envelope, mitochondria, and endomembrane system.
- Without a cytoskeleton, prokaryotes are unable to change cell shape.
- How did the complex organization of the eukaryotic cell evolve from the simpler prokaryotic condition?
    - A process called **endosymbiosis** probably led to mitochondria and *plastids* (the general term for chloroplasts and related organelles).
    - The endosymbiotic hypothesis suggests that mitochondria and plastids were formerly small prokaryotes that began living within larger cells.
    - The term *endosymbiont* is used for a cell that lives within a *host cell*.
- The prokaryotic ancestors of mitochondria and plastids probably gained entry to the host cell as undigested prey or internal parasites.
- The symbiosis became mutually beneficial.
    - A heterotrophic host could use nutrients released from photosynthetic endosymbionts.
    - An anaerobic host benefited from an aerobic endosymbiont.
- As they became increasingly interdependent, the host and endosymbionts became a single organism.
- All eukaryotes have mitochondria or their genetic remnants.
- The hypothesis of **serial endosymbiosis** supposes that mitochondria evolved before plastids.

- A great deal of evidence supports an endosymbiotic origin of plastids and mitochondria.
    - The inner membranes of both organelles have enzymes and transport systems that are homologous to those in the plasma membranes of modern prokaryotes.
    - Both mitochondria and plastids replicate by a splitting process similar to prokaryotic binary fission.
    - Like prokaryotes, each organelle has a single, circular DNA molecule that is not associated with histone.
    - These organelles contain tRNAs, ribosomes, and other molecules needed to transcribe and translate their DNA into protein.
    - Ribosomes of mitochondria and plastids are similar to prokaryotic ribosomes in size, nucleotide sequence, and sensitivity to antibiotics.

Some single-celled eukaryotes gave rise to multicellular forms whose descendants include a variety of algae, plants, fungi, and animals.

- A great range of eukaryotic unicellular forms evolved to create the diversity of present-day unicellular forms.
- Comparisons of DNA sequences suggest that the common ancestor of multicellular eukaryotes lived 1.5 billion years ago.
    - The oldest known fossils of multicellular eukaryotes are relatively small algae that lived 1.2 billion years ago.
- Large and diverse multicellular eukaryotes first appear in the fossil record 600 million years ago.
    - The Ediacaran biota were soft-bodied organisms that lived from 575 to 545 million years ago.
- Why were multicellular eukaryotes so limited in size, diversity, and distribution until the late Proterozoic?
- Geologic evidence suggests that a series of severe ice ages gripped Earth from 750 to 580 million years ago.
    - At times during this period, glaciers covered all of Earth's landmasses, and the seas were largely iced over.
    - According to the "snowball Earth" hypothesis, life would have been confined to deep-sea vents and hot springs or to equatorial regions of the ocean that lacked ice cover.
- The first major diversification of multicellular eukaryotic organisms corresponds to the time of the thawing of snowball Earth, about 575 million years ago.
- Many phyla of animals appear suddenly in the fossil record in a phenomenon known as the **Cambrian explosion**.
    - Cnidaria (the phylum that includes sea anemones), Porifera (sponges), and Mollusca (molluscs) appear in older rocks from the late Proterozoic.
- Prior to the Cambrian explosion, animals were small, soft-bodied, or both, and there was little evidence of predation.

- Within 10 million years, predators longer than 1 meter emerged, with claws and other predatory structures.
- Prey showed defensive adaptations, such as sharp spines and heavy body armor.
- Molecular evidence suggests that animal phyla originated and began to diverge between 1 billion and 700 million years ago.
  - Recent fossil finds from China have produced a diversity of algae and animals from 570 million years ago, including beautifully preserved embryos.

Plants, fungi, and animals colonized the land about 500 million years ago.

- The colonization of land was one of the pivotal milestones in the history of life.
- There is fossil evidence that cyanobacteria and other photosynthetic prokaryotes coated damp terrestrial surfaces well more than a billion years ago.
- However, macroscopic life in the form of plants, fungi, and animals did not colonize land until about 500 million years ago, during the early Paleozoic era.
- The gradual evolution from aquatic to terrestrial habitats was associated with adaptations that allowed organisms to prevent dehydration and to reproduce on land.
  - For example, plants evolved a vascular system for internal transport and a waterproof coating of wax on their photosynthetic surfaces to slow the loss of water.
- About 420 million years ago, small plants (about 10 cm high) had vascular tissue but lacked true roots and leaves.
- Fifty million years later, plants had diversified greatly to include large reeds and treelike plants with true roots and leaves.
- Plants colonized land in association with fungi.
  - In the modern world, the roots of most plants are associated with fungi that aid in the absorption of water and minerals from the soil.
  - The fungi obtain organic nutrients from the plant.
  - This ancient symbiotic association is evident in some of the oldest fossilized roots.
- The most widespread and diverse terrestrial animals are arthropods (including insects and spiders) and tetrapods.
- The earliest tetrapods lived about 365 million years ago and appear to have evolved from a group of lobe-finned fishes.
- Tetrapods include humans.
- Our lineage diverged from other hominoids (apes) around 6 to 7 million years ago.
- Our species originated about 160,000 years ago.

Concept 25.4 The rise and fall of dominant groups reflect continental drift, mass extinctions, and adaptive radiations.

Earth's continents drift across the planet's surface on great plates of crust.

- Earth's continents move over time.

- Since the origin of eukaryotes 1.5 billion years ago, there have been three occasions (1.1 billion, 600 million, and 250 million years ago) in which all of Earth's landmasses came together for a time to form a supercontinent.
    - Geologists estimate that a new supercontinent will form roughly 250 million years from now.
- Earth's continents drift across the planet's surface on great plates of crust that float on the hot, underlying mantle, in a process called **continental drift**.
    - Geologists can measure the rate at which plates are moving—usually a few centimeters per year.
    - Geologists can infer the past locations of the continents using the magnetic signal recorded in rocks when they formed.
    - As a continent shifts its position over time, the direction of magnetic north recorded in its newly formed rocks also changes.
- Many important geologic processes occur at plate boundaries.
    - Plates may slide along the boundary of other plates, forming regions where earthquakes are common.
    - When an oceanic plate collides with a terrestrial plate, the denser oceanic plate slides under the terrestrial plate.
    - When two oceanic or two terrestrial plates collide, violent upheavals occur and mountains form along the plate boundaries.
- Plate movements are slow, but their cumulative effects are dramatic.
- Continental drift has had a major influence on life on Earth.
- About 250 million years ago, all the continental landmasses came together into a supercontinent called **Pangaea**.
- The formation of Pangaea had a tremendous impact on the physical environment and climate, driving many species to extinction and providing new opportunities for those that survived.
    - Ocean basins deepened, sea level lowered, and shallow coastal seas drained.
    - Many marine species living in shallow waters were driven extinct by the loss of habitat.
    - The interior of the supercontinent was severe, cold, and dry, leading to much terrestrial extinction.
- Another effect of continental drift is the climate change that results when a continent shifts northward or southward.
    - The southern tip of Labrador, Canada, was once located near the equator.
- When faced with such changes in climate, organisms adapt, move to a new location, or become extinct.
    - Most organisms stranded on Antarctica went extinct when it moved to its present position.

- The shifting positions of the continents have rerouted the world's ocean currents, causing the global climate to become colder and contributing to the formation of polar ice caps over the past 15 million years.
- Continental drift promotes allopatric speciation.
    - As supercontinents break apart, regions that were connected become geographically isolated.
    - Lineages of plants and animals diverge from those on other continents.
- Continental drift explains much about the former and current distribution of organisms.
- Fossils of the same species of Permian freshwater reptiles have been discovered in both Brazil and Ghana, which were joined together when these reptiles were alive.
- Australian flora and fauna contrast sharply from those of the rest of the world.
    - Marsupial mammals fill ecological roles in Australia analogous to those filled by placental mammals on other continents.
    - Marsupials probably evolved first in what is now Asia and North America and then reached Australia via South America and Antarctica while the continents were still joined.
    - The breakup of the southern continents set Australia adrift.
    - In Australia, marsupials diversified and the few early eutherians became extinct.
    - On other continents, marsupials became extinct and eutherians diversified.

Mass extinctions have destroyed the majority of species on Earth.

- A species may become extinct for many reasons.
- A species' habitat may be destroyed, or its environment may change in a direction unfavorable to the species.
- Biological factors may change, as evolutionary changes in one species influence others.
- On a number of occasions, global environmental changes were so rapid and major that the rate of extinction increased dramatically.
- The result of these environmental changes is a **mass extinction**, in which large numbers of species become extinct.
- Five mass extinctions are documented in the fossil record over the last 500 million years.
- In each mass extinction, 50% or more of the Earth's species became extinct.
- The five mass extinctions are particularly well documented for shallow-water, marine, hard-bodied animals, the organisms for which the fossil record is most complete.
- The Permian mass extinction defines the boundary between the Paleozoic and Mesozoic eras.
    - Ninety-six percent of marine animal species went extinct in less than 5 million years.
    - Terrestrial life was also affected. For example, 8 out of 27 orders of insects went extinct.
- The Permian mass extinction happened at a time of enormous volcanic eruptions in what is now Siberia.

  - An area of 1.6 million km^2 (roughly half the size of western Europe) was covered with a layer of lava hundreds to thousands of meters thick.
  - These eruptions may have produced enough carbon dioxide to warm the global climate by about 6°C.
  - Reduced temperature differences between the equator and the poles would have slowed the mixing of ocean water.
  - The resulting oxygen deficit in the oceans may have played a large role in the Permian extinction.
- The Cretaceous extinction of 65 million years marks the boundary between the Mesozoic and Cenozoic eras.
  - More than half of all marine species and many families of terrestrial plants and animals, including the dinosaurs, went extinct.
- A clue to the Cretaceous mass extinction is a thin layer of clay enriched in iridium that separates sediments from the Mesozoic and Cenozoic eras.
  - Iridium is a very rare element on Earth but is common in meteorites and other objects that fall to Earth.
  - Walter and Luis Alvarez and their colleagues at the University of California, Berkeley, proposed that this clay is fallout from a huge cloud of debris that was thrown into the atmosphere when an asteroid or a large comet collided with Earth.
  - The cloud would have blocked sunlight and disrupted the global climate for several months.
  - A 65-million-year-old Chicxulub crater scar has been found beneath sediments on the Yucatán coast of Mexico.
  - At 180 km in diameter, it is the right size to have been caused by an object with a diameter of 10 km.
- Is a sixth mass extinction under way? Human actions such as habitat destruction are modifying the global environment to such an extent that many species are threatened with extinction.
- More than a thousand species have become extinct in the last 400 years. This rate is 100 to 1,000 times the typical background rate seen in the fossil record.
- It is hard to document the current extinction rate.
  - Tropical rain forests harbor many undiscovered species. Clear-cutting such an area may drive a species to extinction before we know of its existence.
  - Nevertheless, it is clear that many species are declining at an alarming rate.
- A mass extinction can remove a thriving and complex community.
- Once an evolutionary lineage disappears, it cannot reappear.
- It typically takes 5 to 10 million years for diversity of life to recover to previous levels after a mass extinction.
- It took 100 million years for the number of marine families to recover after the Permian mass extinction.

- Mass extinctions can also alter ecological communities by changing the types of organisms that make them up.
    - After the Permian and Cretaceous mass extinctions, the percentage of predatory marine organisms increased substantially, increasing predation pressure on prey and competition among predators.
    - Mass extinctions can remove lineages that have advantageous features.

Adaptive radiation is the evolution of many diversely adapted species from a common ancestor when new environmental opportunities arise.

- **Adaptive radiations** occur when a few organisms make their way into new areas, when novel adaptations arise, or when extinction opens up ecological niches for surviving species.
    - Large-scale adaptive radiations followed each of the five mass extinctions.
    - Adaptive radiations occurred in groups of organisms that possessed major evolutionary innovations, such as seeds or armored body coverings.
    - Organisms colonizing regions with little competition from other species have undergone major adaptive radiations.
- Mammals underwent a dramatic adaptive radiation following the extinction of the dinosaurs 65 million years ago.
    - Although mammals originated 180 million years ago, they remained small, nocturnal, and morphologically similar before the Cretaceous extinction.
    - A few mammals were intermediate in size—up to a meter in length—but none approached the size of the dinosaurs.
    - Early mammals may have been restricted in size and diversity because of competition from the larger and more diverse dinosaurs.
    - With the disappearance of the dinosaurs (except for birds), mammals diversified to fill the ecological roles once occupied by terrestrial dinosaurs.
- In some adaptive radiations, groups of organisms increased in diversity as they came to play entirely new ecological roles in their communities.
- Examples include the rise of photosynthetic prokaryotes; the evolution of predatory animals during the Cambrian explosion; and the plants, insects, and tetrapod radiations that followed the colonization of land.
- Each of these radiations was associated with major evolutionary innovations that facilitated life on land.
    - The radiation of land plants followed the evolution of key adaptations such as stems that supported the plant against gravity and a waxy coat that protected leaves from water loss.
- Organisms that arise in an adaptive radiation may serve as a new source of food for still other organisms.
    - For example, the diversification of land plants stimulated a series of adaptive radiations in insects that ate or pollinated plants, making insects the most diverse group of animals on Earth today.
- Adaptive radiations may occur in regional areas, too.

  - The Hawaiian archipelago is a showcase of adaptive radiation.
  - Located 3,500 km from the nearest continent, the volcanic islands were formed "naked" and were gradually populated by stray organisms that arrived by wind or ocean currents.
  - The islands are physically diverse, with a range of altitudes and rainfall amounts.
  - Multiple invasions, followed by speciation events, have ignited an explosion of adaptive radiations of novel species.

Concept 25.5 Major changes in body form can result from changes in the sequence and regulation of developmental genes.

- The fossil record tells us *what* the great changes in the history of life have been and *when* they occurred.
- An understanding of continental drift, mass extinction, and adaptive radiation explains *how* these changes came about.
- Genetic mechanisms—especially changes in genes that influence development—underlie changes in the fossil record.
- "Evo-devo" is a field of interdisciplinary research that examines how slight genetic divergences can become magnified into major morphological differences between species.
  - Genes that program development influence the rate, timing, and spatial pattern of changes in form as an organism develops from a zygote to an adult.
- **Heterochrony,** an evolutionary change in the rate or timing of developmental events, has led to many striking evolutionary transformations.
  - Slight changes in relative rates of growth can change the adult form substantially.
  - This can be seen in the contrasting adult skull shapes of humans and chimpanzees, which both developed from fairly similar fetal skulls.
- Heterochrony can alter the relative timing of reproductive and nonreproductive development.
  - If the rate of reproductive development accelerates compared to the development of other organs, then a sexually mature stage can retain juvenile structures—a process called **paedomorphosis.**
  - Some species of salamander have the typical external gills and flattened tail of an aquatic juvenile but are sexually mature with functioning gonads.
- Macroevolution can also result from changes in genes that control the placement and spatial organization of body parts.
  - For example, master regulatory genes called **homeotic genes** determine such basic features as where a pair of wings and a pair of legs develop on a bird or how a plant's flower parts are arranged.
- The products of one class of homeotic genes, the *Hox* genes, provide positional information in an animal embryo.
- This information prompts cells to develop into structures appropriate for a particular location.

    - For example, a change in the location where *Scr* and *Ubx Hox* genes in crustaceans are expressed converts a swimming appendage to a feeding appendage.
- The evolution of vertebrates may have been influenced by two duplications of *Hox* genes found in all vertebrate genomes.
    - These duplications may have contributed to novel vertebrate characteristics.
- The recent discovery of 570-million-year-old fossils of animal embryos suggests that a set of genes sufficient to produce complex animals existed at least 35 million years *before* the Cambrian explosion.
    - The Cambrian explosion may have been due in part to new genes (created by gene duplication events) taking on a wide range of new functions in a variety of animal lineages.
- A recent study examined developmental changes associated with the divergence of six-legged insects from crustacean-like multi-legged ancestors.
    - In insects, the *Ubx* gene is expressed in the abdomen. In crustaceans, it is expressed in the body trunk.
    - The *Ubx* gene suppresses leg formation in insects but not in crustaceans.
    - Researchers cloned the *Ubx* gene from an insect and a crustacean and genetically engineered fruit fly embryos to express either gene throughout their bodies.
    - The insect *Ubx* gene suppressed 100% of the limbs in the *Drosophila* embryos, while the crustacean gene suppressed only 15%.
    - The researchers then constructed a series of "hybrid" *Ubx* genes, each of which contained known segments of the insect *Ubx* gene and known segments of the crustacean gene.
    - By this method, the researchers were able to pinpoint the exact amino acid changes responsible for the suppression of additional limbs in insects.
    - This study provided experimental evidence linking a particular change in the sequence of a developmental gene to the origin of the six-legged insect body plan.
- Changes in the nucleotide sequence of a gene may affect its function wherever it is expressed. In contrast, the regulation of gene expression can be limited to a single cell type.
    - Thus, a change in the regulation of a developmental gene may be less harmful than a change in the gene's sequence.
- David Kingsley and his colleagues identified a key developmental gene, *Pitx1*, that influences whether three-spine stickleback fish have a set of large ventral spines.
    - These spines, which deter predatory fish, are present in marine sticklebacks but absent in lake-dwelling sticklebacks.
    - In lakes, large invertebrate predators such as dragonfly larvae capture juvenile sticklebacks by grasping their spines.
    - Kingsley's group found that expression of *Pitx1* has changed in lake-dwelling sticklebacks. The protein-coding sequence of the gene is unchanged.
    - Lake sticklebacks still express *Pitx1* in regions not related to the production of spines, such as the mouth.

Concept 25.6 Evolution is not goal oriented.

- To paraphrase François Jacob, evolution is like tinkering—it is a process in which new forms arise by the slight modification of existing forms.
- Large changes can result from the gradual modification of existing structures or the slight modification of existing developmental genes.
- According to Charles Darwin's concept of *descent with modification*, novel and complex structures can arise as gradual modifications of ancestral structures.
- In many cases, complex structures have evolved incrementally from simpler versions that performed the same basic function.
- For example, the human eye is a complex organ with many parts that work together to form an image and transmit it to the brain.
- Many animals depend on much simpler eyes. The simplest ones are patches of light-sensitive photoreceptor cells.
- These simple eyes, found in a variety of animals such as limpets, appear to have had a single evolutionary origin.
    - The eyes of a limpet lack a lens and cannot form an image, but they do allow the limpet to tell light from dark.
    - Limpets cling more tightly to their rock when a shadow falls on them. This behavior reduces a limpet's risk of predation.
    - The "simple" eyes of limpets improve their survival and reproduction.
- A variety of complex animal eyes have evolved independently many times.
    - Squids and octopuses have eyes as complex as those of humans.
    - Although complex mollusc eyes evolved independently of complex vertebrate eyes, both evolved from an ancestral simple cluster of photoreceptor cells.
- The evolution of complex eyes took place step by step through a series of incremental modifications that benefited the eyes' owners at every stage.
- The genes that act as "master regulators" of eye development are shared by all animals that have eyes.
- Throughout their evolutionary history, eyes retained their basic function of vision.
- Other structures gradually took on new roles, leading to evolutionary novelties.
    - As cynodonts gave rise to early mammals, the articular and quadrate bones that formerly made up the jaw hinge were gradually incorporated into the middle ear region of mammals, where they came to play a role in the transmission of sound.
- Structures that evolve in one context but become co-opted for another function are called *exaptations*.
    - Such structures do not evolve in anticipation of future use.
- Natural selection cannot predict the future; it can only improve a structure in the context of its *current* utility.
- Novel features can arise gradually via a series of intermediate stages, but they must be functional in the organism's current context.
- Some evolutionary lineages show a trend toward larger or smaller body size.
- For example, the evolution of the modern horse can be interpreted to have been a steady series of changes from a small, browsing ancestor (*Hyracotherium*) with four toes on its

front feet to modern horses (*Equus*) with only one toe per foot and teeth modified for grazing on grasses.

- It is possible to select a succession of animals intermediate between *Hyracotherium* and modern horses to show trends toward increased size, reduced number of toes, and modifications of teeth for grazing.
- If we look at *all* fossil horses, however, the illusion of coherent, progressive evolution leading directly to modern horses vanishes.
    - *Equus* is the only surviving twig of an evolutionary bush that included several adaptive radiations among both grazers and browsers.
- Differences among species in survival can also produce a macroevolutionary trend.
- The species selection model developed by Steven Stanley considers species as analogous to individual organisms.
    - Speciation is their birth, extinction is their death, and new species are their offspring.
- Stanley suggests that just as individual organisms undergo natural selection, species undergo *species selection*.
    - The species that endure the longest and generate the greatest number of new species determine the direction of major evolutionary trends.
    - The species selection model suggests that "differential speciation success" plays a role in macroevolution similar to the role of differential reproductive success in microevolution.
- Evolutionary trends can also result directly from natural selection.
    - For example, when the ancestors of modern horses invaded the grasslands that spread during the middle Cenozoic, there was strong selection for fast-running grazers that could escape predation.
- The appearance of an evolutionary trend does not imply some intrinsic drive toward a preordained state of being.
- Evolution is the result of interactions between organisms and their current environments, leading to changes in evolutionary trends as conditions change.