

Chapter 22

Descent with Modification: A Darwinian View of Life

Lecture Outline

Overview: Endless Forms Most Beautiful

- Keen observers of living things have long noted that organisms are well suited to their environments, that there is a rich diversity of life on Earth, and that life shows a striking unity.
- Charles Darwin's fascination with "endless forms most beautiful" led him to propose a scientific explanation for these broad observations.
- On November 24, 1859, Darwin published his hypothesis in *On the Origin of Species by Means of Natural Selection*, ushering in the era of evolutionary biology.
- Darwin defined **evolution** as *descent with modification*, proposing that Earth's many species are descendants of ancestral species that were very different from those alive today.
 - Evolution can also be defined more narrowly as a change in the genetic composition of a population over time.
- Evolution is both a *pattern* and a *process*.
 - The *pattern* of evolutionary change is revealed in observations about the natural world.
 - The *process* of evolution consists of the mechanisms that have produced the diversity and unity of living things.

Concept 22.1 The Darwinian revolution challenged traditional views of a young Earth inhabited by unchanging species.

- At age 22, Charles Darwin set out on a sea voyage that began his intellectual voyage toward the fundamental concept of modern biology
- His hypothesis had its roots in the work of many other individuals.
- The Greek philosopher Aristotle (384–322 A.D.) opposed any concept of evolution and viewed species as fixed and unchanging.
 - Aristotle believed that all living forms could be arranged on a ladder of increasing complexity (*scala naturae*) with perfect, permanent species on every rung.
- The Old Testament account of creation held that species were individually designed by God and, therefore, perfect.
- In the 1700s, natural theology viewed the adaptations of organisms as evidence that the Creator had designed each species for a purpose.

- Carolus Linnaeus (1707–1778), a Swedish physician and botanist, developed a binomial system for naming species according to genus and species and classifying species into a hierarchy of increasingly complex categories.
 - In contrast to the linear hierarchy of the *scala naturae*, Linnaeus adopted a nested classification system, grouping similar species into increasingly general categories.
 - For Linnaeus, similarity between species did not imply evolutionary kinship but rather the pattern of their creation.
- Darwin's views were influenced by **fossils**, remains or traces of organisms from the past mineralized in sedimentary rocks.
 - Sedimentary rocks form when mud and sand settle to the bottom of seas, lakes, and marshes.
 - New layers of sediment cover older ones, creating layers of rock called **strata**.
 - Erosion may later carve through sedimentary rock to expose older strata at the surface.
 - Fossils within layers of sedimentary rock show that a succession of organisms have populated Earth throughout time.
- **Paleontology**, the study of fossils, was largely developed by the French anatomist Georges Cuvier (1769–1832).
- In examining rock strata in the Paris Basin, Cuvier noted that the older the strata, the more dissimilar the fossils from modern life.
 - Cuvier recognized that extinction had been a common occurrence in the history of life.
 - Instead of evolution, Cuvier advocated **catastrophism**, speculating that boundaries between strata were due to local floods or droughts that destroyed the species then present.
 - He suggested that the denuded areas were later repopulated by species immigrating from unaffected areas.
- In contrast to Cuvier's catastrophism, Scottish geologist James Hutton (1726–1797) proposed a theory of **gradualism**, which held that profound geologic changes took place through the cumulative effect of slow but continuous processes identical to those currently operating.
 - Thus, valleys were formed by rivers flowing through rocks, and sedimentary rocks were formed from soil particles that eroded from land and were carried by rivers to the sea.
- Later, geologist Charles Lyell (1797–1875) proposed a theory of **uniformitarianism**, which held that geologic processes had not changed throughout Earth's history.
- Hutton's and Lyell's observations and theories had a strong influence on Darwin.
 - First, if geologic changes result from slow, continuous processes rather than sudden events, then the Earth must be far older than the 6,000 years estimated by theologians from biblical inference.
 - Second, slow and subtle processes persisting for long periods of time can also act on living organisms, producing substantial change over a long period of time.
- In 1809, French biologist Jean-Baptiste de Lamarck (1744–1829) published a theory of evolution based on his observations of fossil invertebrates in the collections of the Natural History Museum of Paris.
- By comparing fossils and current species, Lamarck found what appeared to be several lines of descent.
- Each line of descent was a chronological series of older to younger fossils, leading to a modern species.

- Lamarck explained his observations with two principles: *use and disuse* of parts and the *inheritance of acquired characteristics*.
 - Use and disuse was the concept that body parts that are used extensively become larger and stronger, while those that are not used deteriorate.
 - The inheritance of acquired characteristics stated that modifications acquired during the life of an organism can be passed on to offspring.
 - A classic example is the long neck of the giraffe. Lamarck reasoned that the long, muscular neck of the modern giraffe evolved over many generations as the ancestors of giraffes reached for leaves on higher branches and passed this characteristic on to their offspring.
- Lamarck thought that evolutionary change was driven by the innate drive of organisms to increasing complexity.
- Lamarck's theory was a visionary attempt to explain the fossil record and the current diversity of life with recognition of gradual evolutionary change.
 - However, modern genetics has provided no evidence that acquired characteristics can be inherited.
 - Acquired traits such as a bodybuilder's bigger biceps do not change the genes transmitted through gametes to offspring.

Concept 22.2 Descent with modification by natural selection explains the adaptations of organisms and the unity and diversity of life.

- Charles Darwin (1809–1882) was born in western England.
- As a boy, he had a consuming interest in nature.
- When Darwin was 16, his father sent him to the University of Edinburgh to study medicine.
- Darwin left Edinburgh without a degree and enrolled at Cambridge University with the intent of becoming a clergyman.
 - At that time, most naturalists and scientists belonged to the clergy.
- After graduation, Darwin joined the crew of the survey ship HMS *Beagle* as ship naturalist and conversation companion to Captain Robert FitzRoy.
 - FitzRoy chose Darwin because of his education and because his age and social class were similar to those of the captain.

The voyage of the Beagle

- The primary mission of the five-year voyage of the *Beagle* was to chart poorly known stretches of the South American coastline.
- Darwin had the freedom to explore extensively on shore while the crew surveyed the coast.
- Darwin collected thousands of specimens of the exotic and diverse flora and fauna of South America.
 - He explored the Brazilian jungles, the grasslands of the Argentine pampas, the desolation of Tierra del Fuego near Antarctica, and the heights of the Andes.
- Darwin noted that the plants and animals of South America were very different from those of Europe.
 - Organisms from temperate regions of South America more closely resembled organisms from the tropics of South America than those from temperate regions of Europe.

- South American fossils, though different from modern species, more closely resembled modern species from South America than those from Europe.
- While on the *Beagle*, Darwin read Lyell's *Principles of Geology*.
 - Darwin experienced geologic change firsthand when a violent earthquake rocked the coast of Chile, causing the coastline to rise by several feet.
 - He found fossils of ocean organisms high in the Andes and inferred that the rocks containing the fossils had been raised there by a series of similar earthquakes.
 - These observations reinforced Darwin's acceptance of Lyell's ideas and led him to doubt the traditional view of a young and static Earth.
- Darwin's interest in the geographic distribution of species was further stimulated by the *Beagle's* visit to the Galápagos Islands, a group of young volcanic islands 900 km west of the South American coast.
 - Darwin was fascinated by the unusual organisms found there.
 - Darwin noted that while most of the animal species on the Galápagos lived nowhere else, they resembled species living on the South American mainland.
 - He hypothesized that the islands had been colonized by plants and animals from the mainland that had subsequently diversified on the different islands.

Darwin's focus on adaptation

- During his travels, Darwin observed many examples of **adaptations**, characteristics of organisms that enhance their survival and reproduction in specific environments.
- After his return to Great Britain in 1836, Darwin began to perceive that the origin of new species and the adaptation of species to their environment were closely related processes.
- Could a new species arise from an ancestral form by the gradual accumulation of adaptations to a different environment?
 - For example, clear differences in the beaks among the 13 species of finches that Darwin collected in the Galápagos are adaptations to the specific foods available on their home islands.
 - Darwin explained that adaptations arise by **natural selection**, a process in which individuals with certain inherited characteristics leave more offspring than individuals with other characteristics.
- By the early 1840s, Darwin had developed the major features of his theory of natural selection as the mechanism for evolution.
- In 1844, Darwin wrote a long essay on the origin of species and natural selection, but he was reluctant to publish and continued to compile evidence to support his theory.
- In June 1858, Alfred Russel Wallace (1823–1913), a young naturalist working in the East Indies, sent Darwin a manuscript containing a theory of natural selection essentially identical to Darwin's.
- Later that year, both Wallace's paper and extracts of Darwin's essay were presented to the Linnaean Society of London.
- Darwin quickly finished *The Origin of Species* and published it the next year.
- Although both Darwin and Wallace developed similar ideas independently, the theory of evolution by natural selection is attributed to Darwin because he developed his ideas earlier and supported the theory much more extensively.
 - The theory of evolution by natural selection was presented in *The Origin of Species* with immaculate logic and an avalanche of supporting evidence.

- Within a decade, *The Origin of Species* had convinced most biologists that biological diversity was the product of evolution.

The Origin of Species

- Darwin never used the word *evolution* in the first edition of *The Origin of Species*, although the final word of the book is *evolved*.
- Instead Darwin used the phrase *descent with modification*.
 - All organisms are related through descent from a common ancestor that lived in the remote past.
 - Over evolutionary time, the descendants of that common ancestor have accumulated diverse modifications, or adaptations, that allow them to survive and reproduce in specific habitats.
 - Over long periods of time, descent with modification has led to the rich diversity of life we see today.
- Viewed from the perspective of descent with modification, the history of life is like a tree, with multiple branches from a common trunk.
 - Closely related species, the twigs on a common branch of the tree, shared the same line of descent until their recent divergence from a common ancestor.
- Linnaeus recognized that some organisms resemble each other more closely than others, but he did not explain these similarities by evolution.
 - Linnaeus's taxonomic scheme fit well with Darwin's theory.
 - To Darwin, the Linnaean hierarchy reflected the branching history of the tree of life.
 - Organisms at various taxonomic levels are united through descent from common ancestors.

Artificial selection, natural selection, and adaptation

- Darwin proposed a mechanism—natural selection—to explain the observable patterns of evolution.
- Darwin's views on the role of environmental factors in the screening of heritable variation were heavily influenced by **artificial selection**.
 - Humans have modified a variety of domesticated plants and animals over many generations by selecting individuals with the desired traits as breeding stock.
- Darwin described four observations of nature, from which he drew two inferences.
 - Observation #1: Members of a population vary greatly in their traits.
 - Observation #2: Offspring inherit traits from their parents.
 - Observation #3: All species are capable of producing more offspring than the environment can support.
 - Observation #4: Due to lack of food or other resources, many of these offspring do not survive.
 - Inference #1: Individuals whose inherited traits give them a higher probability of surviving and reproducing in a given environment than other individuals tend to leave more offspring than other individuals.
 - Inference #2: This unequal ability of individuals to survive and reproduce will cause favorable traits to accumulate over generations.

- A 1798 essay on human population by Thomas Malthus heavily influenced Darwin's views on "overreproduction."
 - Malthus contended that much human suffering—disease, famine, war—was the inescapable consequence of the potential for human populations to increase faster than food supplies and other resources.
- The capacity to overproduce seems to be a characteristic of all species.
- Only a tiny fraction of offspring produced complete their development and reproduce successfully to leave offspring of their own.
 - The rest are eaten, starved, diseased, unmated, or unable to tolerate physical conditions of the environment, such as salinity or temperature.
- An organism's traits can influence not only its own survival and reproductive success, but also how well its offspring cope with environmental challenges.
 - For example, an organism might have a heritable trait that gives its offspring an advantage in escaping predators, obtaining food, or tolerating physical conditions.
 - When such advantages increase the number of offspring that survive and reproduce, the traits that are favored will likely appear at a greater frequency in the next generation.
- Thus, over time, natural selection imposed by factors such as predators, lack of food, or physical conditions can increase the proportion of favorable traits in a population.
- If artificial selection can achieve so much change in a relatively short period of time, Darwin reasoned, then natural selection should be capable of considerable modification of species over thousands of generations.
- Even if the advantages of some heritable traits over others are slight, the advantageous variations will gradually accumulate in the population, and less favorable variations will diminish.
- Over time, this process increases the frequency of individuals with adaptations and hence refines the match between organisms and their environment.
- To summarize:
 - Natural selection is a process in which individuals that have certain heritable characteristics survive and reproduce at a higher rate than other individuals.
 - Over time, natural selection can increase the match between organisms and their environment.
 - If an environment changes, or if individuals move to a new environment, natural selection may result in adaptation to these new conditions, sometimes giving rise to new species in the process.
- Three important points need to be emphasized about evolution through natural selection.
 1. Although natural selection occurs through interactions between individual organisms and their environment, individuals do not evolve. A population is the smallest group that can evolve over time.
 2. Natural selection can act only on *heritable traits*, traits that are passed from organisms to their offspring. Characteristics acquired by an organism during its lifetime may enhance its survival and reproductive success, but there is no evidence that such characteristics can be inherited by offspring.
 3. Environmental factors vary from place to place and from time to time. A trait that is favorable in one environment may be useless or even detrimental in another environment.

Concept 22.3 Evolution is supported by an overwhelming amount of scientific evidence.

- *The Origin of Species* presented a broad range of evidence to support the concept of descent with modification.
- Four types of data document the pattern of evolution and tell us about the processes by which it occurs: direct observations of evolution, the fossil record, homology, and biogeography.

Direct observations of evolutionary change

- The power of evolution by natural selection as a unifying theory is its versatility as a natural explanation for diverse data from many fields of biology.
- We will consider two examples of natural selection as a mechanism of evolution in populations.
- The first example concerns differential predation and guppy populations.
- Predation is a potent force shaping the adaptations of prey.
 - Predators are most likely to feed on prey that do not avoid detection, flee, or defend themselves.
 - Those prey are less likely to reproduce and pass their traits on to their offspring than those individuals whose traits help them evade predation.
- Guppies (*Poecilia reticulata*) live in the wild in pools in the Aripo River system in Trinidad.
- John Endler observed that the color patterns of male guppies are extremely variable: No two males look alike.
- Female guppies are attracted to brightly colored males and are more likely to choose them as mates than to choose males with drab coloring.
- Brightly colored males are more conspicuous to predators, however.
 - If a guppy population contained both brightly colored and drab males, predators might be expected to eat more of the brightly colored ones.
- Endler investigated the trade-off between attracting mates and attracting predators.
 - In the field, Endler observed that the color patterns of male guppies corresponded to the intensity of predation.
 - In pools with few predators, male guppies tended to be very bright.
 - In pools with many predator species, males were brightly drab.
 - Based on these observations, Endler hypothesized that more intense predation caused natural selection to favor the trait of drab coloration in male guppies.
 - He tested this hypothesis by transferring brightly colored guppies to a pool with many predators.
 - As he predicted, over time the transplanted guppy population became less brightly colored.
 - Endler also transferred guppies with drab colors (from a pool with many predators) to a pool with few predators.
 - In their new environment, brightly colored males rapidly came to dominate the guppy population.

- Endler's experiments demonstrate that natural selection can cause rapid evolution in wild populations.
- A second example of ongoing natural selection is the evolution of drug-resistant pathogens (disease-causing organisms).
 - The evolution of drug resistance is a particular problem in bacteria and viruses, which exhibit rapid rates of reproduction.
- HIV (human immunodeficiency virus) is the virus that causes AIDS.
- Researchers have developed numerous drugs to combat HIV, but using these medications selects for viruses resistant to the drugs.
 - A few drug-resistant viruses may be present by chance at the beginning of treatment.
 - The drug-resistant pathogens are more likely to survive treatment and pass on the genes that enable them to resist the drug to their progeny.
 - As a result, the frequency of drug resistance in the viral population rapidly increases.
- Scientists designed the drug 3TC to interfere with reverse transcriptase, the enzyme that HIV uses to copy its RNA genome into the DNA of the host cell.
 - Because 3TC is similar in shape to the cytosine nucleotide of DNA, HIV's reverse transcriptase incorporates 3TC into its growing DNA chain instead of cytosine. This error terminates elongation of DNA and thus prevents HIV reproduction.
 - 3TC-resistant varieties of HIV have a form of reverse transcriptase that can discriminate between cytosine and 3TC.
 - These viruses have no advantage in the absence of 3TC. In fact, they replicate more slowly than viruses with normal reverse transcriptase.
 - Once 3TC is added to their environment, it becomes a powerful selective agent, favoring reproduction of resistant individuals.
- The examples of the guppies and drug-resistant viruses highlight two important points about natural selection.
 1. Natural selection is an editing mechanism, not a creative force. It can act only on existing variation in the population; it cannot *create* favorable traits, it *selects for* favorable traits that are already present in the population.
 2. Natural selection favors traits that increase fitness in the current, local environment. What is adaptive in one situation is not adaptive in another.
 - For example, male guppies with drab colors are at an advantage in a pool with many predators, but at a disadvantage in a pool with few predators.
 - In the absence of 3TC, HIV with the modified form of reverse transcriptase grows more slowly than HIV with normal reverse transcriptase.

The fossil record

- The fossil record shows that evolutionary changes have occurred over time in various groups of organisms.
- Over longer time scales, fossils document the origin of major groups of organisms.
 - For example, an increasingly good fossil record shows the early evolution of cetaceans, a mammalian order that includes whales, dolphins, and porpoises.
 - The earliest cetaceans lived 50 to 60 million years ago. Prior to that time, most mammals were terrestrial.

- Over the last several decades, a series of fossils have been found in Pakistan, Egypt, and North America that document the transition from terrestrial to aquatic life, leading to the loss of hind limbs and the development of flippers.
- The fossil record provides evidence about the pattern of evolution.
- The fossil record can also be used to test our current understanding of evolutionary patterns.
 - Fossil fishes predate all other vertebrates, with amphibians next, followed by reptiles, then mammals and birds.
 - This is consistent with the history of vertebrate descent supported by many other types of evidence.

Homology

- Further evidence for evolution comes from similarities in the characteristics of different organisms.
 - Descent with modification can explain why certain traits in related species have an underlying similarity even if they have very different functions.
 - Characteristics present in an ancestral organism are altered (by natural selection) in its descendants over time as they face different environmental conditions.
- Similarity in characteristic traits from common ancestry is known as **homology**.
 - For example, the forelimbs of human, cats, whales, and bats share the same skeletal elements, even though the appendages have very different functions.
 - These forelimbs are **homologous structures** that represent variations on the ancestral tetrapod forelimb.
- Homologies that are not obvious in adult organisms may become evident when we look at embryonic development.
 - For example, all vertebrate embryos have a tail posterior to their anus, as well as structures called pharyngeal pouches in their throat at some stage in their development.
 - The homologous throat pouches develop into very different adult structures, such as the gills of fish or parts of the ears and throat in humans and other mammals.
- Some of the most interesting homologous structures are **vestigial organs**, structures that have marginal, if any, importance to a living organism but that had important functions in the organism's ancestors.
 - For example, the skeletons of some snakes and of fossil whales retain vestiges of the pelvis and leg bones of walking ancestors.
- Similarities among organisms can also be seen at the molecular level.
 - For example, all species of life have the same basic genetic machinery of RNA and DNA, and the genetic code is essentially universal.
 - The ubiquity of the genetic code provides evidence of a single origin of life.
 - It is likely that the language of the genetic code has been passed along through all the branches of the tree of life ever since its inception in an early life form.
 - Organisms as dissimilar as humans and bacteria share genes that have been inherited from a very distant common ancestor.
 - Like the forelimbs of humans and whales, these genes have often acquired different functions.
- Homologies mirror the taxonomic hierarchy of the tree of life.
 - Some homologies, such as the genetic code, are shared by all living things because they arose in the deep ancestral past.

- Other homologies that evolved more recently are shared by only smaller branches of the tree of life.
 - For example, all tetrapods (amphibians, reptiles, birds, and mammals) share the same five-digit limb structure. The ancestor of tetrapods did not have this feature.
- Thus homologies are found in a nested pattern, with all life sharing the deepest layer and each smaller group adding new homologies to those it shares with the larger group.
- This hierarchical pattern of homology is exactly what we would expect if life evolved and diversified from a common ancestor.
- The pattern of descent from common ancestors and the resulting homologies can be shown in an **evolutionary tree**, which reflects evolutionary relationships among groups of organisms.
- Evolutionary trees are hypotheses that summarize our current understanding of patterns of common descent.
- Some trees are supported by a variety of data, including anatomical and DNA sequence data.
- Scientists can use well-supported evolutionary trees to make predictions about the biology of organisms.
- Distantly related organisms may resemble each other because of **convergent evolution**, the independent evolution of similar features.
 - For example, many marsupial mammals from Australia resemble specific eutherian mammals from other continents.
 - The two types of mammals are similar because of convergent evolution. Their resemblance is **analogous**, not homologous.

Biogeography

- Evidence for evolution also comes from the geographic distribution of species—**biogeography**.
- The geographic distribution of organisms is influenced by many factors, including **continental drift**.
 - Two hundred fifty million years ago, all of Earth's landmasses joined to form a single large continent called **Pangaea**.
 - **Pangaea** broke apart 200 million years ago. By 20 million years ago, the continents were within a few hundred kilometers of their present locations.
- From our understanding of evolution and continental drift, we can predict where fossils of various types of organisms might be found.
- We can use our understanding of evolution to explain biogeographic data.
 - For example, islands generally have **endemic** species that are found nowhere else on Earth.
 - Most island species are closely related to species from the nearest mainland or a neighboring island, reflecting the pattern of colonization of the island.
 - The colonists eventually give rise to new species as they adapt to their environments.
 - Two islands with similar environments are populated, not by closely related species, but rather by species that resemble those of the nearest mainland.

What is theoretical about the Darwinian view of life?

- Some people dismiss the Darwinian view as “just a theory.”
- As we have seen, however, the pattern of evolution has been documented directly and is supported by the great deal of evidence.

- Darwin's explanation of natural selection as the primary cause of evolutionary change makes sense of large amounts of data.
 - The effects of natural selection can be observed in nature.
- What is theoretical about evolution?
 - The term *theory* has a very different meaning in science than in everyday use.
 - The word *theory* in colloquial use is closer to the concept of a hypothesis in science.
- In science, a theory is more comprehensive than a hypothesis, accounting for many observations and much data and attempting to explain and integrate a great variety of phenomena.
- A unifying theory does not become widely accepted unless its predictions stand up to thorough and continual testing by experiments and additional observation.
 - That has certainly been the case with the theory of evolution by natural selection.
- Scientists continue to test Darwin's theory.
 - For example, although Darwin thought that evolution was a very slow process, we now know that new species can form in a few thousand years or less.
 - Evolutionary biologists now recognize that natural selection is not the only mechanism responsible for evolutionary history.
 - Other factors may have played an important role, particularly in the evolution of genes and proteins.
- By attributing the diversity of life to natural causes, Darwin gave biology a sound scientific basis.
- As Darwin said, "There is grandeur in this view of life."