**Chapter 22 Descent with Modification: Darwinian View of Life**

**Lecture Outline**

Overview: Darwin Introduces a Revolutionary Theory

•On November 24, 1859, Charles Darwin published On the Origin of Species by Means of Natural Selection.

•Darwin’s book drew a cohesive picture of life by connecting what had once seemed a bewildering array of unrelated facts.

•Darwin made two major points in The Origin of Species: 1.Today’s organisms descended from ancestral species that were different from modern species.

2.Natural selection provided a mechanism for this evolutionary change.

•The basic idea of natural selection is that a population can change over time if individuals that possess certain heritable traits leave more offspring than other individuals.

•Natural selection results in evolutionary adaptation, an accumulation of inherited characteristics that increase the ability of an organism to survive and reproduce in its environment.

•Eventually, a population may accumulate enough change that it constitutes a new species.

•In modern terms, we can define evolution as a change over time in the genetic composition of a population. •Evolution also refers to the gradual appearance of all biological diversity.

•Evolution is such a fundamental concept that its study is relevant to biology at every level, from molecules to ecosystems. •Evolutionary perspectives continue to transform medicine, agriculture, biotechnology, and conservation biology.

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

Western culture resisted evolutionary views of life.

•Darwin’s view of life contrasted with the traditional view of an Earth that was a few thousand years old, populated by life forms that were created at the beginning and had remained fundamentally unchanged. •The Origin of Species challenged a worldview that had been long accepted.

•The Greek philosopher Aristotle (384–322 B.C.E.) 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, founded taxonomy, a system for naming species and classifying species into a hierarchy of increasingly complex categories. •Linnaeus developed the binomial system of naming organisms according to genus and species.

•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.

Theories of geologic gradualism prepared the path for evolutionary biologists.

•In contrast to Cuvier’s catastrophism, Scottish geologist James Hutton (1726–1797) proposed a theory of gradualism that held that profound geological 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 geological 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.

Lamarck placed fossils in an evolutionary context.

•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 was a chronological series of older to younger fossils, leading to a modern species.

•He 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 could be passed 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 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 body builder’s bigger biceps do not change the genes transmitted through gametes to offspring.

**Concept 22.2** In The Origin of Species, Darwin proposed that species change through natural selection

•Charles Darwin (1809–1882) was born in western England. •As a boy, he developed 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 and viewed the world in the context of natural theology.

•Darwin received his B.A. in 1831.

•After graduation Darwin joined 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 that of the captain.

Field research helped Darwin frame his view of life.

•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.

•He collected thousands of specimens of the exotic and diverse flora and fauna of South America. •Darwin 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 distinct from those of Europe. •Organisms from temperate regions of South America more closely resembled those from the tropics of South America than those from temperate regions of Europe.

•Further, 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. •He experienced geological 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 Galapagos, a group of young volcanic islands 900 km west of the South American coast. •Darwin was fascinated by the unusual organisms found there.

•After his return to England, Darwin noted that while most of the animal species on the Galapagos 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.

•After his return to Great Britain in 1836, Darwin began to perceive that the origin of new species and adaptation of species to their environment were closely related processes. •For example, clear differences in the beaks among the 13 species of finches that Darwin collected in the Galapagos are adaptations to the specific foods available on their home islands.

•By the early 1840s, Darwin had developed the major features of his theory of natural selection as the mechanism for evolution.

•In 1844, he 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.

•While 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 developed two main ideas: that evolution explains life’s unity and diversity and that natural selection is the mechanism of adaptive evolution.

•Darwin scarcely used the word evolution in The Origin of Species. •Instead he 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 descendents of that common ancestor have accumulated diverse modifications, or adaptations, that allow them to survive and reproduce in specific habitats.

•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. •However, his 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.

•How does natural selection work, and how does it explain adaptation?

•Evolutionary biologist Ernst Mayr has dissected the logic of Darwin’s theory into three inferences based on five observations. •Observation #1: All species have such great potential fertility that their population size would increase exponentially if all individuals that are born reproduced successfully.

•Observation #2: Populations tend to remain stable in size, except for seasonal fluctuations.

•Observation #3: Environmental resources are limited. •Inference #1: Production of more individuals than the environment can support leads to a struggle for existence among the individuals of a population, with only a fraction of the offspring surviving each generation.

•Observation #4: Individuals of a population vary extensively in their characteristics; no two individuals are exactly alike.

•Observation #5: Much of this variation is heritable. •Inference #2: Survival in the struggle for existence is not random, but depends in part on inherited traits. Those individuals whose inherited traits are best suited for survival and reproduction in their environment are likely to leave more offspring than less fit individuals.

•Inference #3: This unequal ability of individuals to survive and reproduce will lead to a gradual change in a population, with favorable characteristics accumulating 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, homelessness, 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.

•In each generation, environmental factors filter heritable variations, favoring some over others. •Differential reproductive success—whereby organisms with traits favored by the environment produce more offspring than do organisms without those traits—results in the favored traits being disproportionately represented in the next generation.

•This increasing frequency of the favored traits in a population is evolutionary change.

•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.

•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.

•Darwin’s main ideas can be summarized in three points. •Natural selection is differential success in reproduction (unequal ability of individuals to survive and reproduce) that results from individuals that vary in heritable traits and their environment.

•The product of natural selection is the increasing adaptation of organisms to their environment.

•If an environment changes over time, or if individuals of a species move to a new environment, natural selection may result in adaptation to the new conditions, sometimes giving rise to a 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 (a group of interbreeding individuals of a single species that share a common geographic area) is the smallest group that can evolve. Evolutionary change is measured as changes in relative proportions of heritable traits in a population over successive generations.

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.

•Darwin envisioned the diversity of life as evolving by a gradual accumulation of minute changes through the actions of natural selection operating over vast spans of time.

**Concept 22.3** Darwin’s theory explains a wide range of observations

•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.

•Our first example concerns differential predation and guppy populations.

•Guppies (Poecilia reticulata) live in the wild in pools in the Aripo River system in Trinidad.

•John Endler and David Reznick have been studying these small fish for more than a decade.

•The researchers observed significant differences between populations of guppies that live in different pools in the river system. •Populations varied in the average age and size of sexual maturity.

•These variations were correlated to the type of predator present in each pool.

•In some pools, the main predator is the small killifish, which eats juvenile guppies.

•In other pools, the major predator is the large pike-cichlid, which eats adult guppies.

•Guppies in populations preyed on by pike-cichlids begin reproducing at a younger age and are smaller at maturity than guppies in populations preyed on by killifish.

•To test whether these differences are due to natural selection, Reznick and Endler introduced guppies from pike-cichlid locations to new pools that contained killifish but no guppies. •After eleven years, the transplanted guppies were, on average, 14% heavier at maturity than the nontransplanted populations.

•Their average age at maturity had also increased.

•These results support the hypothesis that natural selection caused the changes in the transplanted population. •Because pike-cichlids prey mainly on reproductively mature adults, the chance that a guppy will survive to reproduce several times is low.

•The guppies with the greatest reproductive success in ponds with pike-cichlid predators are those that mature at a young age and small size, enabling them to produce at least one brood before growing to a size preferred by pike-cichlids.

•In ponds with killifish predators, guppies that survive early predation can grow slowly and produce many broods of young.

•A second example of ongoing natural selection is the evolution of drug-resistant HIV (human immunodeficiency virus).

•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 offspring.

•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 HIV highlight two important points about natural selection. •First, natural selection is an editing mechanism, not a creative force. It can only act on existing variation in the population; it cannot create favorable traits.

•Second, 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, guppies that mature at an early age and small size are at an advantage in a pool with pike-cichlids, but at a disadvantage in a pool with killifish.

•In the absence of 3TC, HIV with the modified form of reverse transcriptase grows more slowly than HIV with normal reverse transcriptase.

Evidence of evolution pervades biology.

•In the cases described, natural selection brought about change rapidly enough that it could be observed directly.

•Darwin’s theory also provides a cohesive explanation for observations in the fields of anatomy, embryology, molecular biology, biogeography, and paleontology.

•Descent with modification can explain why certain traits in related species have an underlying similarity even if they have very different functions.

•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 structures called pharyngeal pouches in their throat at some stage in their development.

•These embryonic structures develop into very different, but still homologous, adult structures, such as the gills of fish or the Eustacian tubes that connect the middle ear with the throat in mammals.

•Some of the most interesting homologous structures are vestigial organs, structures that have marginal, if any, importance to a living organism, but which 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.

•Comparative anatomy confirms that evolution is a remodeling process, an alteration of existing structures. •Because evolution can only modify existing structures and functions, it may produce structures that are less than perfect.

•For example, the back and knee problems of bipedal humans are an unsurprising outcome of adapting structures originally evolved to support four-legged mammals.

•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.

•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 only by smaller branches of the tree of life. •For example, all tetrapods (amphibians, reptiles, birds, and mammals) share the same five-digit limb structure.

•Thus homologies are found in a nested pattern, with all life sharing the deepest layer and each smaller group adding new homologies to those they share with the larger group.

•This hierarchical pattern of homology is exactly what we would expect if life evolved and diversified from a common ancestor.

•Anatomical resemblances among species are generally reflected in their genes (DNA) and gene products (proteins). •If hierarchies of homology reflect evolutionary history, then we should expect to find similar patterns whether we are comparing molecules or bones.

•Different kinds of homologies will coincide because they have followed the same branching pattern through evolutionary history.

•The geographical distribution of species—biogeography—first suggested evolution to Darwin. •Species tend to be more closely related to other species from the same area than to other species with the same way of life that live in different areas. •Consider Australia, home to a unique group of marsupial mammals, which complete their development in an external pouch.

•Some marsupial mammals superficially resemble eutherian mammals (which complete their development in the uterus) from other continents. •For example, the Australian sugar glider and North American flying squirrel are adapted to the same mode of life and look somewhat similar.

•However, the sugar glider shares more characteristics with other Australian marsupials than with the flying squirrel.

•The resemblance between the two gliders is an example of convergent evolution.

•Islands and island archipelagos have provided strong evidence of evolution. •Islands generally have many species of plants and animals that are endemic, found nowhere else in the world.

•As Darwin observed when he reassessed his collections from the Beagle’s voyage, these endemic species are typically more closely related to species living on the nearest mainland (despite different environments) than to species from other island groups.

•In island chains, or archipelagos, individual islands may have different, but related, species. The first mainland invaders reached one island and then evolved into several new species as they colonized other islands in the archipelago. •Several well-investigated examples of this phenomenon include the diversification of finches on the Galapagos Islands and fruit flies (Drosophila) on the Hawaiian Archipelago.

•The succession of fossil forms is consistent with what is known from other types of evidence about the major branches of descent in the tree of life. •For example, considerable evidence suggests that prokaryotes are the ancestors of all life and should precede all eukaryotes in the fossil record. In fact, the oldest known fossils are prokaryotes.

•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.

•The Darwinian view of life also predicts that evolutionary transitions should leave signs in the fossil record.

•Paleontologists have discovered fossils of many such transitional forms that link ancient organisms to modern species. •For example, fossil evidence documents the origin of birds from one branch of dinosaurs.

•Recent discoveries include fossilized whales that link these aquatic mammals to their terrestrial ancestors.

What is theoretical about the Darwinian view of life?

•Some people dismiss the Darwinian view as “just a theory.” •As we have seen, Darwin’s explanation 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 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 this theory. •For example, many evolutionary biologists now question whether natural selection is 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.”