

AP Biology  
Summer Packet  
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Summer Packet

1. The AP Curriculum covers a lot of information so check out what you are getting into by registering at <http://apcentral.collegeboard.com>. You will recognize the acorn logo. Copy and read the course overview and lab summaries. The AP test consists of 100 multiple choice questions with 80 minutes allotted as well as 4 free response questions with a 10 minute reading period and a 90 minute writing period. They do not release recent multiple choice questions to view but they do release the free response questions. There are practice tests and scoring guidelines provided on this site with many other tips. Bring a sample test, course overview, or lab summary the first day of class so I know you registered and at least found the site.

2. Evolution is the underlining theme in AP Biology so we will start with this the beginning of school. I provided you with three sets of lecture notes for chapters 22, 23, and 24 as well as questions for these three chapters. The questions are not due the first day but we will be covering all of this information the first two weeks. If you want to get a jump start read the chapters and answer the questions. I also provided you with an evolution summary review sheet for the three chapters.

3. There are other extra learning opportunities you may wish to consider for this subject. A. You may watch one of the three versions of the movie "Inherit the Wind". B. You may copy and read one chapter from Charles Darwin's book "On the Origin of Species". C. You may research information on the Scopes Monkey Trial. D. You may watch any educational program on animals/plants etc. and make a note of the evolutionary references that are made during the program. Discovery, PBS, and TLC have many interesting shows on living organisms. Provide the title, date, time and channel the programmed aired.

4. You are expected to make an evolutionary timeline which is due the first day of class. Instructions and guidelines are provided as another attachment.

The only two things that are required the first day of class are the timeline and a copy of something from the AP Biology website. This class is intended to be fast paced so working in advanced will give you an academic advantage. Have a nice summer and I will look forward to seeing you this August. If you have any questions feel free to call me.

Cheryl Varner

### AP Biology Time-line

Due date: First day of class- DO NOT LEAVE IT AT HOME

Your assignment is to create a time-line of the geologic record of the earth and the living creatures on it. Your timeline should be at least 1 meter in length but not limited to that. It MUST CORRECTLY REPRESENT the time intervals of the events. Do not evenly space out the events but show them in their time context. Use table 26.1 on page 519 to get this information. You must include eras, periods, epochs, age and some important events in the history of life. You must show the 5 greatest extinctions. The extinctions are in Figure 26.8 on page 518. Hold a piece of paper over the table so at least 5 peaks show up. These would be the greatest extinctions. Your time line must also have a scale.

This assignment is the only one due the first day of class. If you have problems call me at home. You will be graded using the following rubric.

Rubric 75 points This is due the first day of class for full points.

1. \_\_\_\_ Neatness/Color/Overall Appearance 10 points
2. \_\_\_\_ Proper intervals with scale (not just evenly spaced) 25 points
3. \_\_\_\_ Title/your name 5 points
4. \_\_\_\_ Era's 5 points
5. \_\_\_\_ Periods 5 points
6. \_\_\_\_ Epochs 5 points
7. \_\_\_\_ Important events in the history of life 10 points
8. \_\_\_\_ Extinctions 10 points

## Chapter 22

### Descent with Modification: A Darwinian View of Life

#### Lecture Outline

Overview 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.

#### A. The Historical Context for Evolutionary Theory

1. 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.

2. 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.

3. 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.

B. The Darwinian Revolution 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.

1. 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.

2. *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 descendants 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.
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.

4. 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.

5. 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.||

## Chapter 23

### The Evolution of Populations

#### Lecture Outline

Overview One common misconception about evolution is that organisms evolve, in a Darwinian sense, during their lifetimes. Natural selection does act on individuals. Each individual's combination of inherited traits affects its survival and its reproductive success relative to other individuals in the population. However, the evolutionary impact of natural selection is only apparent in the changes in a population of organisms over time. It is the population, not the individual, that evolves. Consider the example of bent grass (*Agrostis tenuis*) growing on the tailings of an abandoned mine. These tailings are rich in toxic heavy metals. While many bent grass seeds land on the mine tailings each year, the only plants that germinate, grow, and reproduce are those that possess genes enabling them to tolerate metallic soils.

These ♣ plants tend to produce metal-tolerant offspring. Individual plants do not evolve to become more metal-tolerant during their lifetimes.

A. Population Genetics Considers How Populations Change Genetically over Time Darwin proposed a mechanism for change in species over time. What was missing from Darwin's explanation was an understanding of inheritance that could explain how chance variations arise in a population while also accounting for the precise transmission of these variations from parents to offspring. The widely accepted hypothesis of the time—that the traits of parents are blended in their offspring—would eliminate the differences in individuals over time. Just a few years after Darwin published *On the Origin of Species*, Gregor Mendel proposed a model of inheritance that supported Darwin's theory. Mendel's particulate hypothesis of inheritance stated that parents pass on discrete heritable units (genes) that retain their identities in offspring. Although Gregor Mendel and Charles Darwin were contemporaries, Darwin never saw Mendel's paper, and its implications were not understood by the few scientists who did read it at the time. Mendel's contribution to evolutionary theory was not appreciated until half a century later.

1. The modern evolutionary synthesis integrated Darwinian selection and Mendelian inheritance. When Mendel's research was rediscovered in the early 20th century, many geneticists believed that his laws of inheritance conflicted with Darwin's theory of natural selection. Darwin emphasized quantitative characters, those that vary along a continuum.

♣ These characters are influenced by multiple loci. Mendel and later geneticists investigated discrete —either-or|| traits. It was not obvious that there was a genetic basis to quantitative characters. Within a few decades, geneticists determined that quantitative characters are influenced by multiple genetic loci and that the alleles at each locus follow Mendelian laws of inheritance. These discoveries helped reconcile Darwin's and Mendel's ideas and led to the birth of population genetics, the study of how populations change genetically over time. A comprehensive theory of evolution, the modern synthesis, took form in the early 1940s. It integrated discoveries and ideas from paleontology, taxonomy, biogeography, and population genetics. The first architects of the modern synthesis included statistician R. A. Fisher, who demonstrated the rules by which Mendelian characters are inherited, and biologist J. B. S. Haldane, who explored the rules of natural selection. Later contributors included geneticists Theodosius Dobzhansky and Sewall Wright, biogeographer and taxonomist Ernst Mayr, paleontologist George Gaylord Simpson, and botanist G. Ledyard Stebbins. The modern synthesis emphasizes: The importance of populations as the units of evolution. The central role of natural selection as the most important mechanism of adaptive evolution. The idea of gradualism to explain how large changes can evolve as an accumulation of small changes over long periods of time. While many evolutionary biologists are now challenging some of the assumptions of the modern synthesis, it has shaped our ideas about how populations evolve.

2. A population's gene pool is defined by its allele frequencies. A population is a localized group of individuals that belong to the same species. One definition of a species is a group of natural populations whose individuals have the potential to interbreed and produce fertile offspring. Populations of a species may be isolated from each other and rarely exchange genetic material. Members of a population are far more likely to breed with members of the same population than

with members of other populations. Individuals near the population's center are, on average, more closely related to one another than to members of other populations. The total aggregate of genes in a population at any one time is called the population's gene pool. It consists of all alleles at all gene loci in all individuals of a population. If only one allele exists at a particular locus in a population, that allele is said to be fixed in the gene pool, and all individuals will be homozygous for that gene. If there are two or more alleles for a particular locus, then individuals can be either homozygous or heterozygous for that gene. Each allele has a frequency in the population's gene pool.

For example, imagine a population of 500 wildflower plants with two alleles (CR and CW) at a locus that codes for flower pigment. Suppose that in the imaginary population of 500 plants, 20 (4%) are homozygous for the CW allele (CWCW) and have white flowers. Of the remaining plants, 320 (64%) are homozygous for the CR allele (CRCR) and have red flowers. These alleles show incomplete dominance. 160 (32%) of the plants are heterozygous (CRCW) and produce pink flowers. Because these plants are diploid, the population of 500 plants has 1,000 copies of the gene for flower color. The dominant allele (CR) accounts for 800 copies ( $320 \times 2$  for CRCR +  $160 \times 1$  for CRCW). The frequency of the CR allele in the gene pool of this population is  $800/1,000 = 0.8$ , or 80%. The CW allele must have a frequency of  $1.0 - 0.8 = 0.2$ , or 20%. When there are two alleles at a locus, the convention is to use  $p$  to represent the frequency of one allele and  $q$  to represent the frequency of the other. Thus  $p$ , the frequency of the CR allele in this population, is 0.8. The frequency of the CW allele, represented by  $q$ , is 0.2.

3. The Hardy-Weinberg Theorem describes a nonevolving population. The Hardy-Weinberg theorem describes the gene pool of a nonevolving population. This theorem states that the frequencies of alleles and genotypes in a population's gene pool will remain constant over generations unless acted upon by agents other than Mendelian segregation and recombination of alleles. The shuffling of alleles by meiosis and random fertilization has no effect on the overall gene pool of a population. In our imaginary wildflower population of 500 plants, 80% (0.8) of the flower color alleles are CR, and 20% (0.2) are CW. How will meiosis and sexual reproduction affect the frequencies of the two alleles in the next generation? We assume that fertilization is completely random and all male-female mating combinations are equally likely. Because each gamete has only one allele for flower color, we expect that a gamete drawn from the gene pool at random has a 0.8 chance of bearing an CR allele and a 0.2 chance of bearing an CW allele. Suppose that the individuals in a population not only donate gametes to the next generation at random, but also mate at random. In other words, all male-female matings are equally likely. The allele frequencies in this population will not change from one generation to the next. Its genotype frequencies, which can be predicted from the allele frequencies, will also remain unchanged. For the flower-color locus, the population's genetic structure is in a state of Hardy-Weinberg equilibrium. Using the rule of multiplication, we can determine the frequencies of the three possible genotypes in the next generation. The probability of picking two CR alleles (to obtain a CRCR genotype) is  $0.8 \times 0.8 = 0.64$ , or 64%.

The probability of picking two CW alleles (to obtain a CWCW genotype) is  $0.2 \times 0.2 = 0.04$ , or 4%. Heterozygous individuals are either CRCW or CWCR, depending on whether the CR allele arrived via sperm or egg. The probability of being heterozygous (with a CRCW genotype) is  $0.8 \times 0.2 = 0.16$  for CRCW,  $0.2 \times 0.8 = 0.16$  for CWCR, and  $0.16 + 0.16 = 0.32$ , or 32%, for CRCW + CWCR. As you can see, the processes of meiosis and random fertilization have maintained the same allele and genotype frequencies that existed in the previous generation. The Hardy-Weinberg theorem states that the repeated shuffling of a population's gene pool over generations does not increase the frequency of one allele over another. Theoretically, the allele frequencies in our flower population should remain at 0.8 for CR and 0.2 for CW forever. To generalize the example, in a population with two alleles with frequencies of  $p$  and  $q$ , the combined frequencies must add to 100%. Therefore  $p + q = 1$ . If  $p + q = 1$ , then  $p = 1 - q$  and  $q = 1 - p$ . In the wildflower example,  $p$  is the frequency of red alleles (CR) and  $q$  is the frequency of white alleles (CW). The probability of generating an CRCR offspring is  $p^2$  (an application of the rule of multiplication).

In our example,  $p = 0.8$  and  $p^2 = 0.64$ . The probability of generating a CWCW offspring is  $q^2$ . In our example,  $q = 0.2$  and  $q^2 = 0.04$ . The probability of generating a CRCW offspring is  $2pq$ . In our example,  $2 \times 0.8 \times 0.2 = 0.32$ . The genotype frequencies must add up to 1.0:  $p^2 + 2pq + q^2 = 1.0$ . For the wildflowers,  $0.64 + 0.32 + 0.04 = 1.0$ . This general formula is the Hardy-Weinberg equation. Using this formula, we can calculate frequencies of alleles in a gene pool if we know the frequency of genotypes, or the frequency of genotypes if we know the frequencies of alleles.

4. Five conditions must be met for a population to remain in Hardy-Weinberg equilibrium. The Hardy-Weinberg theorem describes a hypothetical population that is not evolving. However, real populations do evolve, and their allele and genotype frequencies do change over time. That is because the five conditions for nonevolving populations are rarely met for long in nature. A population must satisfy five conditions if it is to remain in Hardy-Weinberg equilibrium:

1. Extremely large population size. In small populations, chance fluctuations in the gene pool can cause genotype frequencies to change over time. These random changes are called genetic drift.
2. No gene flow. Gene flow, the transfer of alleles due to the migration of individuals or gametes between populations, can change the proportions of alleles.
3. No mutations. Introduction, loss, or modification of genes will alter the gene pool.
4. Random mating. If individuals pick mates with certain genotypes, or if inbreeding is common, the mixing of gametes will not be random.
5. No natural selection. Differential survival or reproductive success among genotypes will alter their frequencies. Evolution usually results when any of these five conditions are not met.

Although natural populations are rarely, if ever, in true Hardy-Weinberg equilibrium, the rate of evolutionary change in many populations is so slow that they appear to be close to equilibrium. In such cases, we can use the Hardy-Weinberg equation to estimate genotype and allele frequencies. We can use the theorem to estimate the percentage of the human population that carries the allele for the inherited disease phenylketonuria (PKU). About 1 in 10,000 babies born in the United States is born with PKU, a metabolic condition that results in mental retardation and other problems if left untreated. The disease is caused by a recessive allele. Is the U.S. population in Hardy-Weinberg equilibrium with respect to the PKU gene?

1. The U.S. population is very large.
2. Populations outside the United States have PKU allele frequencies similar to those seen in the United States, so gene flow will not alter allele frequencies significantly.
3. The mutation rate for the PKU gene is very low.
4. People do not choose their partners based on whether or not they carry the PKU allele, and inbreeding (marriage to close relatives) is rare in the United States.
5. Selection against PKU only acts against the rare heterozygous recessive individuals. From the epidemiological data, we know that frequency of homozygous recessive individuals ( $q^2$  in the Hardy-Weinberg theorem) = 1 in 10,000, or 0.0001. The frequency of the recessive allele ( $q$ ) is the square root of 0.0001 = 0.01. The frequency of the dominant allele ( $p$ ) is  $p = 1 - q$ , or  $1 - 0.01 = 0.99$ . The frequency of carriers (heterozygous individuals) is  $2pq = 2 \times 0.99 \times 0.01 = 0.0198$ , or about 2%. Thus, about 2% of the U.S. population carries the PKU allele.

#### B. Mutation and Sexual Recombination Produce Genetic Variation

1. New genes and new alleles originate only by mutation. A mutation is a change in the nucleotide sequence of an organism's DNA. Most mutations occur in somatic cells and are lost when the individual dies. Only mutations in cell lines that form gametes can be passed on to offspring, and only a small fraction of these spread through populations and become fixed. A new mutation that is transmitted in a gamete to an offspring can immediately change the gene pool of a population by introducing a new allele. A point mutation is a change of a single base in a gene. Point mutations can have a significant impact on phenotype, as in the case of sickle-cell disease. However, most point mutations are harmless.

Much of the DNA in eukaryotic genomes does not code for protein products.

However, some noncoding regions of DNA do regulate gene expression.

Changes in these regulatory regions of DNA can have profound effects. Because the genetic

code is redundant, some point mutations in genes that code for proteins may not alter the protein's amino acid composition. On rare occasions, a mutant allele may actually make its bearer better suited to the environment, increasing reproductive success. This is more likely when the environment is changing. Some mutations alter gene number or sequence. Chromosomal mutations that delete or rearrange many gene loci at once are almost always harmful. In rare cases, chromosomal rearrangements may be beneficial.

For example, the translocation of part of one chromosome to a different chromosome could link genes that act together to positive effect. Gene duplication is an important source of new genetic variation. Small pieces of DNA can be introduced into the genome through the activity of transposons. Such duplicated segments can persist over generations and provide new loci that may eventually take on new functions by mutation and subsequent selection. New genes may also arise when the coding subsections of genes known as exons are shuffled within the genome, within a single locus or between loci. Such beneficial increases in gene number appear to have played a major role in evolution. For example, mammalian ancestors carried a single gene for detecting odors that has been duplicated through various mutational mechanisms. Modern humans have close to 1,000 olfactory receptor genes. 60% of these genes have been inactivated in humans, due to mutations. Mice, who rely more on their sense of smell, have lost only 20% of their olfactory receptor genes. Mutation rates vary from organism to organism. Mutation rates are low in animals and plants, averaging about 1 mutation in every 100,000 genes per generation. In microorganisms and viruses with short generation spans, mutation rates are much higher and can rapidly generate genetic variation.

2. Sexual recombination also produces genetic variation. On a generation-to-generation timescale, sexual recombination is far more important than mutation in producing the genetic differences that make adaptation possible. Sexual reproduction rearranges alleles into novel combinations every generation. Bacteria and viruses can also undergo recombination, but they do so less regularly than animals and plants. Bacterial and viral recombination may cross species barriers.

C. Natural Selection, Genetic Drift, and Gene Flow Can Alter a Population's Genetic Composition  
Although new mutations can modify allele frequencies, the change from generation to generation is very small. Recombination reshuffles alleles but does not change their frequency. Three major factors alter allele frequencies to bring about evolutionary change: natural selection, genetic drift, and gene flow.

1. Natural selection is based on differential reproductive success. Individuals in a population vary in their heritable traits. Those with variations better suited to the environment tend to produce more offspring than those with variations that are less well suited. As a result of selection, alleles are passed on to the next generation in frequencies different from their relative frequencies in the present population. Imagine that in our imaginary wildflower population, white flowers are more visible to herbivorous insects and thus have lower survival. Imagine that red flowers are more visible to pollinators. Such differences in survival and reproductive success would disturb the Hardy-Weinberg equilibrium. The frequency of the CW allele would decline and the frequency of the CR allele would increase.

2. Genetic drift results from chance fluctuations in allele frequencies in small populations. Genetic drift occurs when changes in gene frequencies from one generation to another occur because of chance events (sampling errors) that occur in small populations. For example, you would not be too surprised if a thrown coin produced seven heads and three tails in ten tosses, but you would be surprised if you saw 700 heads and 300 tails in 1,000 tosses—you would expect close to 500 of each. The smaller the sample, the greater the chance of deviation from the expected result. In a large population, allele frequencies will not change from generation to generation by chance alone. However, in a small wildflower population with a stable size of only ten plants, genetic drift can completely eliminate some alleles. Genetic drift at small population sizes may occur as a result of two situations: the bottleneck effect or the founder effect. The bottleneck effect occurs when the numbers of individuals in a large population are drastically reduced by a disaster. By chance, some alleles may be overrepresented and others underrepresented among the survivors.

Some alleles may be eliminated altogether. Genetic drift will continue to change the gene pool until the population is large enough to eliminate the effect of chance fluctuations. The bottleneck effect is an important concept in conservation biology of endangered species. Populations that have suffered bottleneck incidents have lost genetic variation from the gene pool.

This reduces ♣ individual variation and may reduce adaptation.

For example, in the 1890s, ♣ hunters reduced the population of northern elephant seals in California to 20 individuals.

Now that it is a protected species, the population has ♣ increased to more than 30,000.

However, a study of 24 gene loci in a ♣ representative sample of seals showed no variation. One allele had been fixed for each gene.

Populations of the closely related southern elephant seal, ♣ which did not go through a bottleneck, show abundant genetic variation. The founder effect occurs when a new population is started by only a few individuals who do not represent the gene pool of the larger source population. At an extreme, a population could be started by a single pregnant female or single seed with only a tiny fraction of the genetic variation of the source population. Genetic drift would continue from generation to generation until the population grew large enough for sampling errors to be minimal. Founder effects have been demonstrated in human populations that started from a small group of colonists.

3. A population may lose or gain alleles by gene flow. Gene flow is genetic exchange due to migration of fertile individuals or gametes between populations. For example, if a nearby wildflower population consisted entirely of white flowers, its pollen (CW alleles only) could be carried into our target population. This would increase the frequency of CW alleles in the target population in the next generation. Gene flow tends to reduce differences between populations. If extensive enough, gene flow can amalgamate neighboring populations into a single population with a common gene pool. Humans today migrate much more freely than in the past, and gene flow has become an important agent of evolutionary change in human populations that were previously isolated.

4. Natural selection is the primary mechanism of adaptive evolution. Of all the factors that can change a gene pool, only natural selection leads to adaptation of an organism to its environment. Natural selection accumulates and maintains favorable genotypes in a population. Most populations have extensive genetic variation. Not all variation is heritable. For example, body builders alter their genotypes but do not pass on their huge muscles to their children. Only the genetic component of variation can have evolutionary consequences as a result of natural selection. This is because only heritable traits pass from generation to generation.

#### D. Genetic Variation Is the Substrate for Natural Selection

1. Genetic variation occurs within and between populations. Both quantitative and discrete characters contribute to variation within a population. Quantitative characters are those that vary along a continuum within a population. For example, plant height in a wildflower population ranges from short to tall. Quantitative variation is usually due to polygenic inheritance in which the additive effects of two or more genes influence a single phenotypic character.

Discrete characters, such as flower color, are usually determined by a single locus with different alleles that produce distinct phenotypes. Phenotypic polymorphism occurs when two or more discrete phenotypes are represented in high enough frequencies to be noticeable in a population. The contrasting forms are called morphs, as in the red-flowered and white-flowered morphs in our wildflower population. Human populations are polymorphic for a variety of physical (e.g., freckles) and biochemical (e.g., blood types) characters. Polymorphism applies only to discrete characters, not quantitative characters. Human height, which varies in a continuum, is not a phenotypic polymorphism. Population geneticists measure genetic variation by determining the amount of heterozygosity at the level of whole genes (gene variability) and at the molecular level of DNA (nucleotide variability). Average heterozygosity measures gene variability, the average percent of gene loci that are heterozygous. In the fruit fly (*Drosophila*), about 86% of their 13,000 gene loci are homozygous (fixed). About 14% (1,800 genes) are heterozygous.

Nucleotide variability measures the mean level of difference in nucleotide sequences (base pair

differences) among individuals in a population. In fruit flies, about 1% of the bases differ between two individuals. Two individuals differ, on average, at 1.8 million of the 180 million nucleotides in the fruit fly genome. Why does average heterozygosity tend to be greater than nucleotide diversity? This is because a gene can consist of thousands of bases of DNA. A difference at only one of these bases is sufficient to make two alleles of that gene different and count toward average heterozygosity. Humans have relatively little genetic variation. Nucleotide diversity is only 0.1%. You and your neighbor probably have the same nucleotide at 999 out of every 1,000 nucleotide sites in your DNA. Geographic variation results from differences in phenotypes or genotypes between populations or between subgroups of a single population that inhabit different areas. Natural selection contributes to geographic variation by modifying gene frequencies in response to differences in local environmental factors. Genetic drift can also lead to variation among populations through the cumulative effect of random fluctuations in allele frequencies. Geographic variation can occur on a local scale, within a population, if the environment is patchy or if dispersal of individuals is limited, producing subpopulations. This is termed spatial variation. Geographic variation in the form of graded change in a trait along a geographic axis is called a cline. Clines may represent intergrade zones where individuals from neighboring, genetically different, populations interbreed. Alternatively, clines may reflect the influence of natural selection based on gradation in some environmental variable.

For example, the average body size of many North American species of birds and mammals increases gradually with increasing latitude, allowing Northern populations to conserve heat in cold environments by decreasing the ratio of surface area to volume.

2. Let's take a closer look at natural selection. The terms —struggle for existence|| and —survival of the fittest|| are misleading because they suggest that individuals compete directly in contests. In some animal species, males do compete directly for mates. Reproductive success is generally subtler and depends on factors other than battle for mates. For example, a barnacle may produce more eggs than its neighbors because it is more efficient at filtering food from the water. Wildflowers may be successful because they attract more pollinators. These examples of adaptive advantage are all components of evolutionary fitness. Fitness is defined as the contribution an individual makes to the gene pool of the next generation, relative to the contributions of other individuals. Population geneticists define relative fitness as the contribution of a genotype to the next generation compared to the contribution of alternative genotypes for the same locus. Consider our wildflower population. Let's assume that individuals with red flowers produce fewer offspring than those with white or pink flowers, which produce equal numbers of offspring. The relative fitness of the most successful variants is set at 1.0 as a basis for comparison, so the relative fitness of white (CWCW) and pink (CRCW) plants is 1.0. If plants with red flowers (CRCR) produce only 80% as many offspring, their relative fitness is 0.8. Although population geneticists measure the relative fitness of a genotype, it is important to remember that natural selection acts on phenotypes, not genotypes. The whole organism is subjected to natural selection. The relative fitness of an allele depends on the entire genetic and environmental context in which it is expressed. Survival alone does not guarantee reproductive success. Relative fitness is zero for a sterile organism, even if it is robust and long-lived. On the other hand, longevity may increase fitness if long-lived individuals leave more offspring than short-lived individuals. In many species, individuals that mature quickly, become fertile at an early age, and live for a short time have greater relative fitness than individuals that live longer but mature later.

3. There are three modes of selection: directional, disruptive, and stabilizing. Natural selection can alter the frequency distribution of heritable traits in three ways, depending on which phenotypes in a population are favored. The three modes of selection are called directional, disruptive, and stabilizing selection. Directional selection is most common during periods of environmental change or when members of a population migrate to a new habitat with different environmental conditions.

Directional selection shifts the frequency curve for a phenotypic character in one direction by

favoring individuals who deviate from the average. For example, fossil evidence indicates that the average size of black bears in Europe increased during each glacial period, only to decrease again during the warmer interglacial periods. Large bears have a smaller surface-to-volume ratio and are better at conserving body heat during periods of extreme cold. Disruptive selection occurs when environmental conditions favor individuals at both extremes of the phenotypic range over those with intermediate phenotypes. For example, two distinct bill types are present in Cameroon's black-bellied seedcrackers. Larger-billed birds are more efficient in feeding on hard seeds and smaller-billed birds are more efficient in feeding on soft seeds. Birds with intermediate bills are relatively inefficient at cracking both types of seeds and thus have lower relative fitness. Disruptive selection can be important in the early stages of speciation. Stabilizing selection favors intermediate variants and acts against extreme phenotypes. Stabilizing selection reduces variation and maintains the status quo for a trait. Human birth weight is subject to stabilizing selection. Babies much larger or smaller than 3–4 kg have higher infant mortality than average-sized babies.

4. Diploidy and balancing selection preserve genetic variation. The tendency for natural selection to reduce variation is countered by mechanisms that preserve or restore variation, including diploidy and balanced polymorphisms. Diploidy in eukaryotes prevents the elimination of recessive alleles via selection because recessive alleles do not affect the phenotype in heterozygotes. Even recessive alleles that are unfavorable can persist in a population through their propagation by heterozygous individuals. Recessive alleles are only exposed to selection when both parents carry the same recessive allele and combine two recessive alleles in one zygote. This happens only rarely when the frequency of the recessive allele is very low. The rarer the recessive allele, the greater the degree of protection it has from natural selection. Heterozygote protection maintains a huge pool of alleles that may not be suitable under the present conditions but may become beneficial when the environment changes. Natural selection itself preserves variation at some gene loci. Balancing selection occurs when natural selection maintains stable frequencies of two or more phenotypes in a population, a state called balanced polymorphism. One mechanism producing balanced polymorphism is heterozygote advantage. In some situations, individuals who are heterozygous at a particular locus have greater fitness than homozygotes. In these cases, natural selection will maintain multiple alleles at that locus. Heterozygous advantage maintains genetic diversity at the human gene for one chain of hemoglobin. Homozygous recessive individuals suffer from sickle-cell disease. Homozygous dominant individuals are vulnerable to malaria. Heterozygous individuals are resistant to malaria. The frequency of the sickle-cell allele is highest in areas where the malarial parasite is common. In some African tribes, it accounts for 20% of the gene pool, a very high frequency for such a harmful allele. Even at this high frequency, only 4% of the population suffers from sickle-cell disease ( $q^2 = 0.2 \times 0.2 = 0.04$ ), while 32% of the population is resistant to malaria ( $2pq = 2 \times 0.8 \times 0.2 = 0.32$ ). The aggregate benefit of the sickle-cell allele in the population balances its aggregate harm. A second mechanism promoting balanced polymorphism is frequency-dependent selection. Frequency-dependent selection occurs when the fitness of any one morph declines if it becomes too common in the population. Predators may develop —search images|| of the most common forms of prey. A prey morph that becomes too common may become disproportionately vulnerable to predation. Frequency-dependent selection has been observed in a number of predator-prey interactions in the wild. Some genetic variations, neutral variations, have negligible impact on fitness, and thus natural selection does not affect these alleles. For example, the diversity of human fingerprints seems to confer no selective advantage to some individuals over others. Most of the base differences between humans that are found in untranslated parts of the genome appear to confer no selective advantage. Pseudogenes, genes that have become inactivated by mutations, accumulate genetic variations. Over time, some neutral alleles will increase and others will decrease by the chance effects of genetic drift. There is no consensus among biologists on how much genetic variation can be classified as neutral or even if any variation can be considered truly neutral. It is almost impossible to demonstrate that an allele brings no benefit at all to an organism. Also, variant alleles may be neutral in one

environment but not in another. Even if only a fraction of the extensive variation in a gene pool significantly affects an organism, there is still an enormous reservoir of raw material for natural selection and adaptive evolution.

5. Sexual selection may lead to pronounced secondary differences between the sexes. Charles Darwin was the first scientist to investigate sexual selection, which is natural selection for mating success. Sexual selection results in sexual dimorphism, marked differences between the sexes in secondary sexual characteristics not directly associated with reproduction. Males and females may differ in size, coloration, and ornamentation. In vertebrates, males are usually the larger and showier sex. It is important to distinguish between intrasexual and intersexual selection. Intrasexual selection is direct competition among individuals of one sex (usually males) for mates of the opposite sex. Competition may take the form of direct physical battles between individuals. The stronger ♣ individuals gain status.

More commonly, ritualized displays discourage ♣ lesser competitors and determine dominance. Evidence is growing that intrasexual selection can take place between females as well. Intersexual selection or mate choice occurs when members of one sex (usually females) are choosy in selecting their mates from individuals of the other sex. Because females invest more in eggs and parental care, they are choosier about their mates than males. A female tries to select a mate that will confer a fitness advantage on their mutual offspring. In many cases, the female chooses a male based on his showy appearance or behavior. Some male showiness does not seem to be adaptive except in attracting mates and may put the male at considerable risk.

For example, ♣ bright plumage may make male birds more visible to predators.

Even if these ♣ extravagant features have some costs, individuals that possess them will have enhanced fitness if they help an individual gain a mate.

Every time a ♣ female chooses a mate based on appearance or behavior, she perpetuates the alleles that caused her to make that choice.

She also allows a male with ♣ that particular phenotype to perpetuate his alleles. How do female preferences for certain male characteristics evolve? Are there fitness benefits to showy traits? Several researchers are testing the hypothesis that females use male sexual advertisements to measure the male's overall health. Males with serious parasitic infections may have dull, disheveled plumage.

These individuals ♣ are unlikely to win many females. If a female chooses a showy mate, she may be choosing a healthy one, and her benefit is a greater probability of having healthy offspring.

6. Sex is an evolutionary enigma. As a mechanism of rapid population growth, sex is far inferior to asexual reproduction. Consider a population in which half the females reproduce only asexually and half the females reproduce only sexually.

Assume that both types of females produce ♣ equal numbers of offspring each generation.

The asexual condition will ♣ increase in frequency, because:

All offspring of asexual females will be ◊ reproductive daughters.

Only half of the offspring of sexual females will ◊ be daughters; the other half will necessarily be males. Sex is maintained in the vast majority of eukaryotic species, even those that also reproduce asexually. Sex must confer some selective advantage to compensate for the costs of diminished reproductive output.

Otherwise, migration of asexual individuals or mutation permitting asexual reproduction would outcompete sexual individuals and the alleles favoring sex. The traditional explanation for the maintenance of sex was that the process of meiosis and fertilization generate genetic variation on which natural selection can act. However, the assumption that sex is maintained in spite of its disadvantages because it produces future adaptation in a variable world is difficult to defend. Natural selection acts in the present, favoring individuals here and now that best fit the current, local environment. Let us instead consider how the genetic variation promoted by sex might be advantageous in the short term, on a generation-to-generation timescale. Genetic variability may be important in resistance to disease. Parasites and pathogens recognize and infect their hosts by attaching to receptor molecules on the host's cells. There should be an advantage to producing

offspring that vary in their resistance to different diseases. One offspring may have cellular markers that make it resistant to virus A, while another is resistant to virus B. This hypothesis predicts that gene loci that code for receptors to which pathogens attack should have many alleles.

In ♣ humans, there are hundreds of alleles for each of two gene loci that give cell surfaces their molecular fingerprints. At the same time, parasites evolve very rapidly in their ability to use specific host receptors. However, sex provides a mechanism for changing the distribution of alleles and varying them among offspring. This coevolution in which host and parasite must evolve quickly to keep up with each other has been called a —Red Queen race.||

7. Natural selection cannot fashion perfect organisms. There are at least four reasons natural selection cannot produce perfection.

1. Evolution is limited by historical constraints. Evolution does not scrap ancestral features and build new complex structures or behavior from scratch. Evolution co-opts existing features and adapts them to new situations. For example, birds might benefit from having wings plus four legs. However, birds descended from reptiles that had only two pairs of limbs. Co-opting the forelimbs for flight left only two hind limbs for movement on the ground.

2. Adaptations are often compromises. Each organism must do many different things. Because the flippers of a seal must allow it to walk on land and also swim efficiently, their design is a compromise between these environments. Similarly, human limbs are flexible and allow versatile movements, but are prone to injuries, such as sprains, torn ligaments, and dislocations. Better structural reinforcement would compromise agility.

3. Chance and natural selection interact. Chance events affect the subsequent evolutionary history of populations.

For example, founders of new populations may not necessarily be the individuals best suited to the new environment, but rather those individuals that were carried there by chance.

4. Selection can only edit existing variations. Natural selection favors only the fittest variations from those phenotypes that are available. New alleles do not arise on demand. Natural selection works by favoring the best variants available. The many imperfections of living organisms are evidence for evolution.

## Chapter 24

### The Origin of Species

#### Lecture Outline

Overview Darwin visited the Galápagos Islands and found them filled with plants and animals that lived nowhere else in the world. He realized that he was observing newly emerged species on these young islands. Speciation—the origin of new species—is at the focal point of evolutionary theory because the appearance of new species is the source of biological diversity. Microevolution is the study of adaptive change in a population. Macroevolution addresses evolutionary changes above the species level. It deals with questions such as the appearance of evolutionary novelties (e.g., feathers and flight in birds) that can be used to define higher taxa. Speciation addresses the question of how new species originate and develop through the subdivision and subsequent divergence of gene pools. The fossil record chronicles two patterns of speciation: anagenesis and cladogenesis. Anagenesis, phyletic evolution, is the accumulation of changes associated with the gradual transformation of one species into another. Cladogenesis, branching evolution, is the budding of one or more new species from a parent species.

Only cladogenesis promotes biological diversity by increasing the number of species.

A. What Is a Species? Species is a Latin word meaning “kind” or “appearance.” Traditionally, morphological differences have been used to distinguish species. Today, differences in body function, biochemistry, behavior, and genetic makeup are also used to differentiate species. Are organisms truly divided into the discrete units we called species, or is this classification an arbitrary attempt to impose order on the natural world?

1. The biological species concept emphasizes reproductive isolation. In 1942, Ernst Mayr proposed the biological species concept. A species is defined as a population or group of populations whose members have the potential to breed with each other in nature to produce viable, fertile offspring, but who cannot produce viable, fertile offspring with members of other species. A biological species is the largest set of populations in which genetic exchange is possible and that is genetically isolated from other populations. Species are based on interfertility, not physical similarity.

For example, eastern and western meadowlarks have similar shapes and coloration, but differences in song help prevent interbreeding between the two species. In contrast, humans have considerable diversity, but we all belong to the same species because of our capacity to interbreed.

2. Prezygotic and postzygotic barriers isolate the gene pools of biological species. Because the distinction between biological species depends on reproductive incompatibility, the concept hinges on reproductive isolation, the existence of biological barriers that prevent members of two species from producing viable, fertile hybrids. A single barrier may not block all genetic exchange between species, but a combination of several barriers can effectively isolate a species' gene pool. Typically, these barriers are intrinsic to the organisms, not due to simple geographic separation. Reproductive isolation prevents populations belonging to different species from interbreeding, even if their ranges overlap. Reproductive barriers can be categorized as prezygotic or postzygotic, depending on whether they function before or after the formation of zygotes. Prezygotic barriers impede mating between species or hinder fertilization of ova if members of different species attempt to mate.

These barriers include habitat isolation, behavioral isolation, temporal isolation, mechanical isolation, and gametic isolation. Habitat isolation. Two organisms that use different habitats (even in the same geographic area) are unlikely to encounter each other to even attempt mating. Two species of garter snakes in the genus *Thamnophis* occur in the same areas. Because one lives mainly in water and the other is primarily terrestrial, they rarely encounter each other. Behavioral isolation. Many species use elaborate courtship behaviors unique to the species to attract mates. In many species, elaborate courtship displays identify potential mates of the correct species and synchronize gonadal maturation. In the blue-footed booby, males perform a high-step dance that calls the female's attention to the male's bright blue feet. Temporal isolation. Two species that breed during different times of day, different seasons, or different

years cannot mix gametes. The geographic ranges of the western spotted skunk and the eastern spotted skunk overlap. However, they do not interbreed because the former mates in late summer and the latter in late winter. Mechanical isolation. Closely related species may attempt to mate but fail because they are anatomically incompatible and transfer of sperm is not possible. For example, mechanical barriers contribute to the reproductive isolation of flowering plants that are pollinated by insects or other animals. With many insects, the male and female copulatory organs of closely related species do not fit together, preventing sperm transfer. Gametic isolation. The gametes of two species do not form a zygote because of incompatibilities preventing fertilization. In species with internal fertilization, the environment of the female reproductive tract may not be conducive to the survival of sperm from other species. For species with external fertilization, gamete recognition may rely on the presence of specific molecules on the egg's coat, which adhere only to specific molecules on sperm cells of the same species. A similar molecular recognition mechanism enables a flower to discriminate between pollen of the same species and pollen of a different species. If a sperm from one species does fertilize the ovum of another, postzygotic barriers may prevent the hybrid zygote from developing into a viable, fertile adult. These barriers include reduced hybrid viability, reduced hybrid fertility, and hybrid breakdown. Reduced hybrid viability. Genetic incompatibility between the two species may abort the development of the hybrid at some embryonic stage or produce frail offspring. This is true for the occasional hybrids between frogs in the genus *Rana*. Most do not complete development, and those that do are frail. Reduced hybrid fertility. Even if the hybrid offspring are vigorous, the hybrids may be infertile, and the hybrid cannot backbreed with either parental species. This infertility may be due to problems in meiosis because of differences in chromosome number or structure. For example, while a mule, the hybrid product of mating between a horse and donkey, is a robust organism, it cannot mate (except very rarely) with either horses or donkeys. Hybrid breakdown. In some cases, first generation hybrids are viable and fertile. However, when they mate with either parent species or with each other, the next generation is feeble or sterile. Strains of cultivated rice have accumulated different mutant recessive alleles at two loci in the course of their divergence from a common ancestor. Hybrids between them are vigorous and fertile, but plants in the next generation that carry too many of these recessive alleles are small and sterile. These strains are in the process of speciating. Reproductive barriers can occur before mating, between mating and fertilization, or after fertilization.

3. The biological species concept has some major limitations.

While the biological species concept has had an important impact on evolutionary theory, it is limited when applied to species in nature. For example, one cannot test the reproductive isolation of morphologically similar fossils, which are separated into species based on morphology. Even for living species, we often lack information on interbreeding needed to apply the biological species concept. In addition, many species (e.g., bacteria) reproduce entirely asexually and are assigned to species based mainly on structural and biochemical characteristics. Many bacteria transfer genes by conjugation and other processes, but this transfer is different from sexual recombination.

4. Evolutionary biologists have proposed several alternative concepts of species. Several alternative species concepts emphasize the processes that unite the members of a species. The ecological species concept defines a species in terms of its ecological niche, the set of environmental resources that a species uses and its role in a biological community. As an example, a species that is a parasite may be defined in part by its adaptations to a specific organism. This concept accommodates asexual and sexual species.

The paleontological species concept focuses on morphologically discrete species known only from the fossil record. There is little or no information about the mating capability of fossil species, and the biological species concept is not useful for them. The phylogenetic species concept defines a species as a set of organisms with a unique genetic history. Biologists compare the physical characteristics or molecular sequences of species to those of other organisms to distinguish groups of individuals that are sufficiently different to be considered separate species. Sibling species are species that appear so similar that they cannot be distinguished on morphological

grounds. Scientists apply the biological species concept to determine if the phylogenetic distinction is confirmed by reproductive incompatibility. The morphological species concept, the oldest and still most practical, defines a species by a unique set of structural features. The morphological species concept has certain advantages. It can be applied to asexual and sexual species, and it can be useful even without information about the extent of gene flow. However, this definition relies on subjective criteria, and researchers sometimes disagree about which structural features identify a species.

In practice, scientists use the morphological species concept to distinguish most species. Each species concept may be useful, depending on the situation and the types of questions we are asking.

**B. Modes of Speciation** Two general modes of speciation are distinguished by the way gene flow among populations is initially interrupted. In allopatric speciation, geographic separation of populations restricts gene flow. In sympatric speciation, speciation occurs in geographically overlapping populations when biological factors, such as chromosomal changes and nonrandom mating, reduce gene flow.

1. **Allopatric speciation:** geographic barriers can lead to the origin of species. Several geological processes can fragment a population into two or more isolated populations. Mountain ranges, glaciers, land bridges, or splintering of lakes may divide one population into isolated groups. Alternatively, some individuals may colonize a new, geographically remote area and become isolated from the parent population.

For example, mainland organisms that colonized the Galápagos Islands were isolated from mainland populations. How significant a barrier must be to limit gene exchange depends on the ability of organisms to move about. A geological feature that is only a minor hindrance to one species may be an impassible barrier to another. The valley of the Grand Canyon is a significant barrier for the ground squirrels that have speciated on opposite sides. For birds that can fly across the canyon, it is no barrier. Once geographic separation is established, the separated gene pools may begin to diverge through a number of mechanisms. Mutations arise. Sexual selection favors different traits in the two populations. Different selective pressures in differing environments act on the two populations. Genetic drift alters allele frequencies. A small, isolated population is more likely to have its gene pool changed substantially over a short period of time by genetic drift and natural selection. For example, less than 2 million years ago, small populations of stray plants and animals from the South American mainland colonized the Galápagos Islands and gave rise to the species that now inhabit the islands.

However, very few small, isolated populations develop into new species; most simply persist or perish in their new environment. To confirm that allopatric speciation has occurred, it is necessary to determine whether the separated populations have become different enough that they can no longer interbreed and produce fertile offspring when they come back in contact. In some cases, researchers bring together members of separated populations in a laboratory setting. Biologists can also assess allopatric speciation in the wild. For example, females of the Galápagos ground finch *Geospiza difficilis* respond to the songs of males from the same island but ignore the songs of males of the same species from other islands.

2. **Sympatric speciation:** a new species can originate in the geographic midst of the parent species. In sympatric speciation, new species arise within the range of the parent populations. Here reproductive barriers must evolve between sympatric populations. In plants, sympatric speciation can result from accidents during cell division that result in extra sets of chromosomes, a mutant condition known as polyploidy. In animals, it may result from gene-based shifts in habitat or mate preference. An individual can have more than two sets of chromosomes. An autopolyploid mutant is an individual that has more than two chromosome sets, all derived from a single species. For example, a failure of mitosis or meiosis can double a cell's chromosome number from diploid ( $2n$ ) to tetraploid ( $4n$ ). The tetraploid can reproduce with itself (self-pollination) or with other tetraploids. It cannot mate with diploids from the original population, because of abnormal meiosis by the triploid hybrid offspring. A more common mechanism of producing polyploid individuals occurs when allopolyploid offspring are produced by the mating of

two different species. While the hybrids are usually sterile, they may be quite vigorous and propagate asexually. In subsequent generations, various mechanisms may transform a sterile hybrid into a fertile polyploid. These polyploid hybrids are fertile with each other but cannot breed with either parent species. They thus represent a new biological species. The origin of polyploid plant species is common and rapid enough that scientists have documented several such speciations in historical times. For example, two new species of plants called goatsbeard (*Tragopodon*) appeared in Idaho and Washington in the early 1900s.

They are the results of allopolyploidy events between pairs of introduced European *Tragopodon* species. Many plants important for agriculture are polyploid. For example, wheat is an allohexaploid, with six sets of chromosomes from three different species. Oats, cotton, potatoes, and tobacco are polyploid. Plant geneticists now use chemicals that induce meiotic and mitotic errors to create new polyploid plants with special qualities. One example is an artificial hybrid combining the high yield of wheat with the hardiness and disease resistance of rye. While polyploid speciation does occur in animals, other mechanisms also contribute to sympatric speciation in animals. Reproductive isolation can result when genetic factors cause individuals to exploit resources not used by the parent. One example is the North American maggot fly, *Rhagoletis pomonella*. The fly's original habitat was native hawthorn trees. About 200 years ago, some populations colonized newly introduced apple trees. Because apples mature more quickly than hawthorn fruit, the apple-feeding flies have been selected for more rapid development and now show temporal isolation from the hawthorn-feeding maggot flies.

Speciation is underway. Sympatric speciation is one mechanism that has been proposed for the explosive adaptive radiation of cichlid fishes in Lake Victoria, Africa. This vast, shallow lake has filled and dried up repeatedly due to climate changes. The current lake is only 12,000 years old but is home to 600 species of cichlid fishes. The species are so genetically similar that many have likely arisen since the lake last filled. While these species are clearly specialized for exploiting different food resources and other resources, nonrandom mating in which females select males based on a certain appearance has probably contributed, too. Individuals of two closely related sympatric cichlid species will not mate under normal light because females have specific color preferences and males differ in color. However, under light conditions that de-emphasize color differences, females will mate with males of the other species and produce viable, fertile offspring. It seems likely that the ancestral population was polymorphic for color and that divergence began with the appearance of two ecological niches that divided the fish into subpopulations. Genetic drift resulted in chance differences in the genetic makeup of the subpopulations, with different male colors and female preferences.

Sexual selection reinforced the color differences. The lack of postzygotic barriers in this case suggests that speciation occurred relatively recently. As pollution clouds the waters of Lake Victoria, it becomes more difficult for female cichlids to see differences in male color. The gene pools of these two closely related species may blend again. We will summarize the differences between sympatric and allopatric speciation. In allopatric speciation, a new species forms while geographically isolated from its parent population. As the isolated population accumulates genetic differences due to natural selection and genetic drift, reproductive isolation from the ancestral species may arise as a by-product of the genetic change. Such reproductive barriers prevent breeding with the parent even if the populations reestablish contact. Sympatric speciation requires the emergence of some reproductive barrier that isolates a subset of the population without geographic separation from the parent population. In plants, the most common mechanism is hybridization between species or errors in cell division that lead to polyploid individuals.

In animals, sympatric speciation may occur when a subset of the population is reproductively isolated by a switch in food source or by sexual selection in a polymorphic population.

C. Adaptive Radiation The evolution of many diversely adapted species from a common ancestor when new environmental opportunities arise is called adaptive radiation. Adaptive radiation occurs when a few organisms make their way into new areas or when extinction opens up ecological niches for the survivors. A major adaptive radiation of mammals followed the

extinction of the dinosaurs 65 million years ago. The Hawaiian archipelago is a showcase of adaptive radiation. Located 3,500 km from the nearest continent, the volcanic islands were formed "naked" and gradually populated by stray organisms that arrived by wind or ocean currents. The islands are physically diverse, with a range of altitudes and rainfall. Multiple invasions and allopatric and sympatric speciation events have ignited an explosion of adaptive radiation of novel species.

1. Researchers study the genetics of speciation.

Researchers have made great strides in understanding the role of genes in particular speciation events. Douglas Schemske and his colleagues at Michigan State University examined two species of *Mimulus*. The two species are pollinated by bees and hummingbirds respectively, keeping their gene pools separate through prezygotic isolation. The species show no postzygotic isolation and can be mated readily in the greenhouse to produce hybrids with flowers that vary in color and shape. Researchers observed which pollinators visit which flowers and then investigated the genetic differences between plants. Two gene loci have been identified that are largely responsible for pollinator choice. One locus influences flower color; the other affects the amount of nectar flowers produce. By determining attractiveness of the flowers to different pollinators, allelic diversity at these loci has led to speciation.

2. The tempo of speciation is important. In the fossil record, many species appear as new forms rather suddenly (in geologic terms), persist essentially unchanged, and then disappear from the fossil record.

Darwin noted this when he remarked that species appeared to undergo modifications during relatively short periods of their total existence and then remained essentially unchanged.

Paleontologists Niles Eldredge and Stephen Jay Gould coined the term punctuated equilibrium to describe these periods of apparent stasis punctuated by sudden change. Some scientists suggest that these patterns require an explanation outside the Darwinian model of descent with modification. However, this is not necessarily the case. Suppose that a species survived for 5 million years, but most of its morphological alterations occurred in the first 50,000 years of its existence—just 1% of its total lifetime. Because time periods this short often cannot be distinguished in fossil strata, the species would seem to have appeared suddenly and then lingered with little or no change before becoming extinct. Even though the emergence of this species actually took tens of thousands of years, this period of change left no fossil record. Stasis can also be explained. All species continue to adapt after they arise, but often by changes that do not leave a fossil record, such as small biochemical modifications. Paleontologists base hypotheses of descent almost entirely on external morphology.

During periods of apparent equilibrium, changes in behavior, internal anatomy, and physiology may not leave a fossil record. If the environment changes, the stasis will be broken by punctuations that leave visible traces in the fossil record.

D. From Speciation to Macroevolution Speciation is at the boundary between microevolution and macroevolution. Microevolution is a change over generations in a population's allele frequencies, mainly by genetic drift and natural selection. Speciation occurs when a population's genetic divergence from its ancestral population results in reproductive isolation. While the changes after any speciation event may be subtle, the cumulative change over millions of speciation episodes must account for macroevolution, the scale of changes seen in the fossil record.

1. Most evolutionary novelties are modified versions of older structures. The Darwinian concept of descent with modification can account for the major morphological transformations of macroevolution. It may be difficult to believe that a complex organ like the human eye could be the product of gradual evolution, rather than a finished design created specially for humans. However, the key is to remember is that a very simple eye can be very useful to an animal. The simplest eyes are just clusters of photoreceptors, light-sensitive pigmented cells. These simple eyes appear to have had a single evolutionary origin. They are now found in a variety of animals, including limpets. These simple eyes have no lenses and cannot focus an image, but they do allow the animal to distinguish light from dark. Limpets cling tightly to their rocks when a shadow falls on them, reducing their risk of predation. Complex eyes have evolved several times

independently in the animal kingdom. Examples of various levels of complexity, from clusters of photoreceptors to camera-like eyes, can be seen in molluscs. The most complex types did not evolve in one quantum leap, but by incremental adaptation of organs that benefited their owners at each stage. Evolutionary novelties can also arise by gradual refinement of existing structures for new functions. Structures that evolve in one context, but become co-opted for another function, are exaptations. It is important to recognize that natural selection can only improve a structure in the context of its current utility, not in anticipation of the future.

An example of an exaptation is the changing function of lightweight, honeycombed bones of birds. The fossil record indicates that light bones predated flight. Therefore, they must have had some function on the ground, perhaps as a light frame for agile, bipedal dinosaurs. Once flight became an advantage, natural selection would have remodeled the skeleton to better fit their additional function. The wing-like forelimbs and feathers that increased the surface area of these forelimbs were co-opted for flight after functioning in some other capacity, such as courtship, thermoregulation, or camouflage.

2. Genes that control development play a major role in evolution. "Evo-devo" is a field of interdisciplinary research that examines how slight genetic divergences can become magnified into major morphological differences between species. A particular focus is on genes that program development by controlling 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. Allometric growth tracks how proportions of structures change due to different growth rates during development. Change relative rates of growth even slightly, and you can change the adult form substantially. Different allometric patterns contribute to the contrast of adult skull shapes between humans and chimpanzees, which both developed from fairly similar fetal skulls. Heterochrony appears to be responsible for differences in the feet of tree-dwelling versus ground-dwelling salamanders. The feet of the tree-dwellers are adapted for climbing vertically, with shorter digits and more webbing. This modification may have evolved due to mutations in the alleles that control the timing of foot development. Stunted feet may have resulted if regulatory genes switched off foot growth early. In this way, a relatively small genetic change can be amplified into substantial morphological change. Another form of heterochrony is concerned with the relative timing of reproductive development and somatic development. If the rate of reproductive development accelerates compared to somatic development, 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 have functioning gonads. Macroevolution can also result from changes in genes that control the placement and spatial organization of body parts. For example, genes called homeotic genes determine such basic features as where a pair of wings and a pair of legs will 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. One major transition in the evolution of vertebrates is the development of the walking legs of tetrapods from the fins of fishes. A fish fin that lacks external skeletal support evolved into a tetrapod limb that extends skeletal supports (digits) to the tip of the limb. This may be the result of changes in the positional information provided by Hox genes during limb development, determining how far digits and other bones should extend from the limb.

3. Evolution is not goal oriented. The fossil record shows apparent evolutionary trends. 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 to modern horses (Equus) with only one toe per foot and teeth modified for grazing on grasses. It is possible to arrange 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, 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 individuals. Speciation is their birth, extinction is their death, and new species are their offspring. In this model, Stanley suggest 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. To the extent that speciation rates and species longevity reflect success, the analogy to natural selection is even stronger. However, qualities unrelated to the overall success of organisms in specific environments may be equally important in species selection. As an example, the ability of a species to disperse to new locations may contribute to its giving rise to a large number of "daughter species." The appearance of an evolutionary trend does not imply some intrinsic drive toward a preordained state of being. Evolution is a response to interactions between organisms and their current environments, leading to changes in evolutionary trends as conditions change.

Evolution Review chapters 22-25

22.1 Darwin introduces revolutionary theory which challenged traditional views.

Natural selection sedimentary rocks uniformitarianism

Evolution paleontology Charles Darwin

Taxonomy catastrophism Jean Lamarck

Fossils gradualism James Hutton

George Cuvier Charles Lyell

22.2 Origin of Species

HMS Beagle Galapagos Islands Alfred Russel Wallace

Descent with modification artificial selection Ernst Mayr (Inferences/observations)

Thomas Malthus 3 points of natural selection 445 and 446

22.3 Darwins theory explains a wide range of observations

Guppies/moths homologous structures vestigial organs

Homology biogeography endemic

23.1 Evolution of Populations

Microevolution macroevolution population

Hardy-Weinberg Theorem 5 conditions for no evolution

23.2 Mutation and Sexual recombination produces variations

Mutations duplications point mutations

Sexual recombinations

23.3 Natural Selection, genetic drift, gene flow

Genetic drift bottleneck effect founder effect gene flow

23.4 Natural selection is the primary mechanism of adaptive evolution

Phenotypic polymorphism genetic polymorphism geographic variation

Cline fitness/relative fitness directional selection diploidy

Disruptive selection stabilizing selection balancing selection

Heterozygote advantage frequency dependent selection

Neutral variation sexual selection sexual dimorphism

Intrasexual selection intersexual selection 4 reasons why we aren't perfect 469

24.1 Reproductive isolation

Speciation anagenesis cladogenesis reproductive isolation

Prezygotic barriers Postzygotic barriers

Habitat reduced hybrid viability

Temporal reduced hybrid fertility

Behavioral hybrid breakdown

Mechanical

Gametic

Morphological species concept paleontological species concept ecological species concept

Phylogenetic species concept

24.2 Speciation

allopatric speciation sympatric speciation

Polyploidy adaptive radiation

Punctuated equilibrium gradualism

24.3 Macroevolutionary changes accumulate through speciation events

heterochrony allometric growth paedomorphosis

homeotic genes species selection

25.1 Phylogenies based on common ancestries inferred from fossils, morphological and molecular evidence

Phylogeny systematics molecular systematics

Fossil record analogy homoplasies

25.2 phylogenetic systematics connects classification with evolutionary history

Binomial genus 7 classification system phylogenetic trees

25.3 Phylogenetic trees

cladogram cladistics monophyletic paraphyletic  
polyphyletic out group ingroup phylogram  
ultrametric tree  
25.4 Genome evolutionary history  
orthologous genes paralogous genes  
25.5 Molecular clocks  
Molecular clock neutral theory 2 points of the tree

## CHAPTER 22: Objectives

### CHAPTER 22 Descent with Modification: A Darwinian View of Life

#### OBJECTIVES

##### The Historical Context for Evolutionary Theory

1. Explain the mechanism for evolutionary change proposed by Charles Darwin in *On the Origin of Species*.
2. Define evolution and adaptation.
3. Compare and contrast Aristotle's *scala naturae* to Carolus Linnaeus' classification scheme.
4. Describe the theories of catastrophism, gradualism, and uniformitarianism.
5. Explain the mechanism for evolutionary change proposed by Jean-Baptiste de Lamarck. Explain why modern biology has rejected Lamarck's theories.

##### The Darwinian Revolution

6. Describe how Darwin's observations on the voyage of the HMS Beagle led him to formulate and support his theory of evolution.
7. Explain how the principle of gradualism and Charles Lyell's theory of uniformitarianism influenced Darwin's ideas about evolution.
8. Explain what Darwin meant by "descent with modification."
9. Explain what evidence convinced Darwin that species change over time.
10. Explain how Linnaeus' classification scheme fit Darwin's theory of evolution by natural selection.
11. Describe the three inferences Darwin made from his observations that led him to propose natural selection as a mechanism for evolutionary change.
12. Explain how an essay by the Rev. Thomas Malthus influenced Charles Darwin.
13. Distinguish between artificial selection and natural selection.
14. Explain why an individual organism cannot evolve.
15. Describe the experiments that supported Reznick and Endler's hypothesis that differences in life-history traits between guppy populations are due to selective pressure based on predation.
16. Explain how the existence of homologous and vestigial structures can be explained by Darwin's theory of natural selection.
17. Explain how evidence from biogeography supports the theory of evolution by natural selection.
18. Explain the problem with the statement that Darwinism is "just a theory." Distinguish between the scientific and colloquial use of the word theory.

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## CHAPTER 23: Objectives

## CHAPTER 23 The Evolution of Populations

### OBJECTIVES

#### Population Genetics

1.

Explain the statement "It is the population, not the individual, that evolves."

2.

Explain how Mendel's particulate hypothesis of inheritance provided much-needed support for Darwin's theory of evolution by natural selection.

3.

Distinguish between discrete and quantitative traits. Explain how Mendel's laws of inheritance apply to quantitative traits.

4.

Explain what is meant by "the modern synthesis."

5.

Define the terms population, species, and gene pool.

6.

Explain why meiosis and random fertilization alone will not alter the frequency of alleles or genotypes in a population.

7.

List the five conditions that must be met for a population to remain in Hardy-Weinberg equilibrium.

8.

Write the Hardy-Weinberg equation. Use the equation to calculate allele frequencies when the frequency of homozygous recessive individuals in a population is 25%.

#### Mutation and Sexual Recombination

9.

Explain why the majority of point mutations are harmless.

10.

Explain why mutation has little quantitative effect on allele frequencies in a large population.

11.

Describe the significance of transposons in the generation of genetic variability.

12.

Explain how sexual recombination generates genetic variability.

#### Natural Selection, Genetic Drift, and Gene Flow

13.

Explain the following statement: "Only natural selection leads to the adaptation of organisms to their environment."

14.

Explain the role of population size in genetic drift.

15.

Distinguish between the bottleneck effect and the founder effect.

16.

Describe how gene flow can act to reduce genetic differences between adjacent populations.

#### Genetic Variation, the Substrate for Natural Selection

17.

Explain how quantitative and discrete characters contribute to variation within a population.

18.

Distinguish between average heterozygosity and nucleotide variability. Explain why average heterozygosity tends to be greater than nucleotide variability.

19.

Define a cline.

20.

Define relative fitness. a. Explain why relative fitness is zero for a healthy, long-lived, sterile

organism. b. Explain why relative fitness could be high for a short-lived organism.

21.

Distinguish among directional, disruptive, and stabilizing selection. Give an example of each mode of selection.

22.

Explain how diploidy can protect a rare recessive allele from elimination by natural selection.

23.

Describe how heterozygote advantage and frequency-dependent selection promote balanced polymorphism.

24.

Define neutral variations. Explain why natural selection does not act on these alleles.

25.

Distinguish between intrasexual selection and intersexual selection.

26.

Explain how female preferences for showy male traits may benefit the female.

27.

Describe the disadvantages of sexual reproduction.

28.

Explain how the genetic variation promoted by sex may be advantageous to individuals on a generational time scale.

29.

List four reasons why natural selection cannot produce perfect organisms.

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## CHAPTER 24: Objectives

### CHAPTER 24 The Origin of Species

#### OBJECTIVES

##### What Is a Species?

1.

Distinguish between anagenesis and cladogenesis.

2.

Define Ernst Mayr's biological species concept.

3.

Distinguish between prezygotic and postzygotic isolating mechanisms.

4.

Describe five prezygotic isolating mechanisms and give an example of each.

5.

Explain a possible cause for reduced hybrid viability.

6.

Explain how hybrid breakdown maintains separate species even if fertilization occurs.

7.

Describe some limitations of the biological species concept.

8.

Define and distinguish among the following: ecological species concept, paleontological species concept, phylogenetic species concept, and morphological species concept.

##### Modes of Speciation

9.

Distinguish between allopatric and sympatric speciation.

10.

Explain the allopatric speciation model and describe the mechanisms that may lead to divergence of isolated gene pools.

11.

Describe examples of adaptive radiation in the Galápagos and Hawaiian archipelagos.

12.

Explain how reproductive barriers evolve. Describe an example of the evolution of a prezygotic barrier and the evolution of a postzygotic barrier.

13.

Define sympatric speciation and explain how polyploidy can cause reproductive isolation.

14.

Distinguish between an autopolyploid and an allopolyploid species and describe examples of each.

15.

Describe how cichlid fishes may have speciated in sympatry in Lake Victoria.

##### Adaptive Radiation

16.

Define adaptive radiation and describe the circumstances under which adaptive radiation may occur.

17.

Describe the two gene loci implicated in speciation in *Mimulus*.

##### From Speciation to Macroevolution

18.

Explain in general terms how a complex structure can evolve by natural selection.

19.

Define exaptation and illustrate this concept with an example.

20.

Explain how slight genetic divergences may lead to major morphological differences between species.

21.

Explain how the evolution of changes in temporal and spatial developmental dynamics can result in evolutionary novelties.

22.

Define evo-devo, heterochrony, allometric growth, and paedomorphosis.

23.

Explain why extracting a single evolutionary progression from a fossil record can be misleading.

24.

Define and illustrate the concept of species selection.

25.

Explain why evolutionary change is not goal-directed.

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