

Evolution

Review

In general, **evolution** (or **organismic evolution**) is about changes in populations, species, or groups of species. More specifically, evolution occurs because populations vary by the frequency of heritable traits that appear from one generation to the next. These traits are represented by alleles for genes that modify morphology (form or structure), physiology, or behavior. Thus, evolution is changes in allele frequencies in populations over time.

There are two areas of evolutionary study, as follows:

1. **Microevolution** describes the details of how populations of organisms change from generation to generation and how new species originate.
2. **Macroevolution** describes patterns of changes in groups of related species over broad periods of geologic time. The patterns determine **phylogeny**, the evolutionary relationships among species and groups of species.

One of the earliest advocates for evolutionary ideas was **Lamarck**. His theory included the following three important ideas:

1. **Use and disuse** described how body parts of organisms can develop with increased usage, while unused parts weaken. This idea was correct, as is commonly observed among athletes who train for competitions.
2. **Inheritance of acquired characteristics** described how body features acquired during the lifetime of an organism (such as muscle bulk) could be passed on to offspring. This, however, was incorrect. Only changes in the genetic material of cells can be passed on to offspring.
3. **Natural transformation of species** described how organisms produced offspring with changes, transforming each subsequent generation into a slightly different form toward some ultimate, higher order of complexity. Species did not become extinct nor did they split and change into two or more species. This idea was also incorrect.

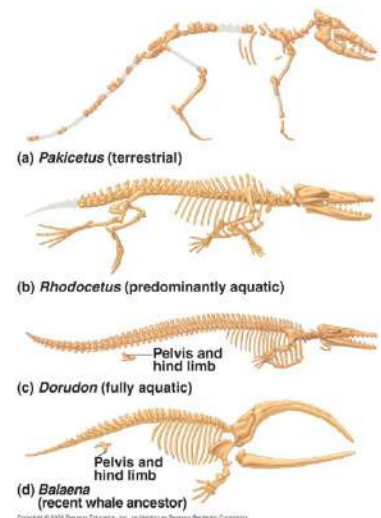
Fifty years after Lamarck published his ideas, Darwin published *The Origin of Species*. Darwin's theory that **natural selection**, or "survival of the fittest," was the driving force of evolution is now called **Darwinism**. Later, genetics was incorporated into evolutionary thinking, creating a new, more comprehensive view of evolution, now variously called **neo-Darwinism**, the **synthetic theory of evolution**, or the **modern synthesis**.

There is abundant evidence that evolution occurs—that some species change over time, that other species diverge and become one or more new species, and that still other species become extinct. The question that evolutionists try to answer is *how* evolution occurs. For this they propose theories. Lamarck theorized, incorrectly, that evolution occurs through the inheritance of acquired characteristics. Darwin's theory was that evolution progresses through natural selection. The synthetic theory of evolution combines natural selection with the influence of genetics. These theories, together with others discussed below, propose mechanisms responsible for the evolutionary patterns unequivocally observed in nature.

Evidence for Evolution

Evidence for evolution is provided by the following five scientific disciplines:

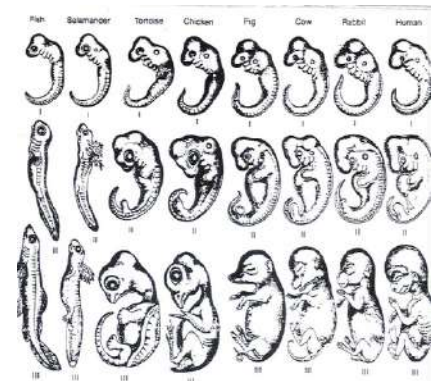
1. **Paleontology** provides fossils that reveal the prehistoric existence of extinct species. As a result, changes in species and the formation of new species can be studied.
 - Fossil deposits are often found among sediment layers, where the deepest fossils represent the oldest specimens. For example, fossil oysters removed from successive layers of sediment show gradual changes in the size of the oyster shell alternating with rapid changes in shell size. Large, rapid changes produced new species.



2. **Biogeography** uses geography to describe the distribution of species. This information has revealed that unrelated species in different regions of the world look alike when found in similar environments. This provides strong evidence for the role of natural selection in evolution.

- Rabbits did not exist in Australia until introduced by humans. A native Australian hare wallaby resembles a rabbit both in structure and habit. As similar as these two animals appear, they are not that closely related.

The rabbit is a placental mammal, while the wallaby is a marsupial mammal. The fetus of a placental mammal develops in the female uterus, obtaining nourishment from the mother through the placenta. The fetus of a marsupial leaves the mother's uterus at an early stage of development and completes the remaining development while attached to a teat in the abdominal pouch. The great similarity of the rabbit and the wallaby is the result of natural selection.



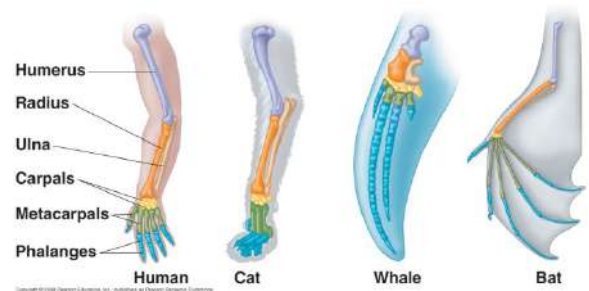
3. **Embryology** reveals similar stages in development (**ontogeny**) among related species. The similarities help establish evolutionary relationships (**phylogeny**).

- Gill slits and tails are found in fish, chicken, pig, and human embryos.

4. **Comparative anatomy** describes two kinds of structures that contribute to the identification of evolutionary relationships among species.

- Homologous structures** are body parts that resemble one another in different species because they have evolved from a common ancestor. Because anatomy may be modified for survival in specific environments, homologous structures may look different, but will resemble one another in pattern (how they are put together). The forelimbs of cats, bats, whales, and humans are homologous because they have all evolved from a common ancestral mammal.

- Analogous structures** are body parts that resemble one another in different species, not because they have evolved from a common ancestor, but because they evolved independently as adaptations to their environments. The fins and body shapes of sharks, penguins, and porpoises are analogous because they are adaptations to swimming.



5. **Molecular biology** examines the nucleotide and amino acid sequences of DNA and proteins from different species. Closely related species share higher percentages of sequences than species distantly related. In addition, all living things share the same genetic code. This data strongly favors evolution of different species through modification of ancestral genetic information.

- More than 98% of the nucleotide sequences in humans and chimpanzees are identical.

Darwin

Decent with Modification

- The phrase refers to the view that all organisms are related through descent from an ancestor that lived in the remote past

Natural Selection

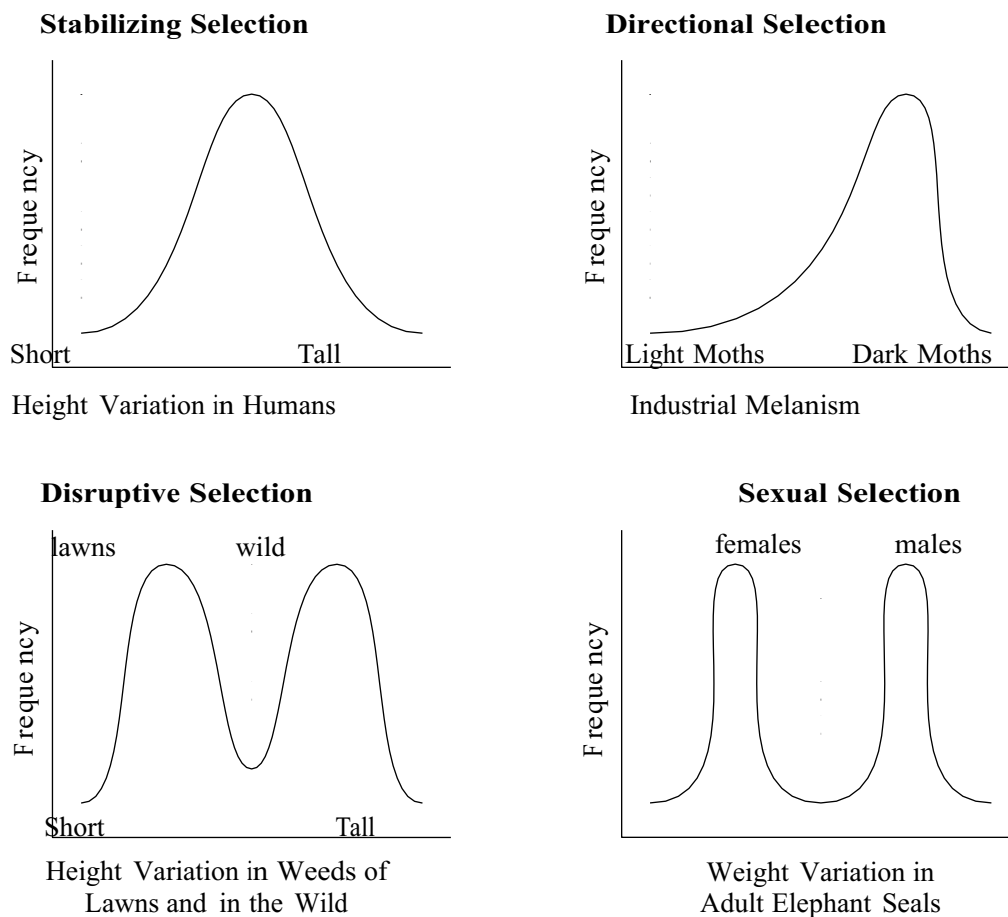
Natural selection is the differences in survival and reproduction among individuals in a population as a result of their interaction with the environment. In other words, some individuals possess alleles (genotypes) that generate traits (phenotypes) that enable them to cope more successfully in their environment than other individuals. The more successful individuals produce more offspring. Superior inherited traits are **adaptations** to the environment and increase an individual's **fitness**, or relative ability to survive and leave offspring. When the environment favors a trait, that is, when a trait increases the survival of its bearer, selection is said to act for that trait. In contrast, selection is said to act against unfavorable traits. Favorable traits are adaptive, while unfavorable traits are maladaptive.

Darwin presented his theory for evolution by natural selection using the following arguments:

1. **Populations possess an enormous reproductive potential.** Darwin calculated that two elephants would produce a population of 19 million individuals after 750 years if all offspring survived to reproductive maturity and fostered their normal number of offspring.
2. **Population sizes remain stable.** Darwin observed that populations generally fluctuate around a constant size.
3. **Resources are limited.** Resources, such as food, water, or light, do not increase as populations grow larger.
4. **Individuals compete for survival.** Eventually, the needs of a growing population will exceed the available resources. As a result, individuals must compete for resources
5. **There is variation among individuals in a population.** Most traits reveal considerable variety in their form. In humans, for example, skin, hair, and eye color occur as continuous variation from very dark to very light.
6. **Much variation is heritable.** Most traits are produced by the action of enzymes that are coded by DNA. DNA is the hereditary information that is passed from generation to generation. This contrasts with characteristics acquired during the life of an organism. The amputation of a limb, for example, is not heritable.
7. **Only the most fit individuals survive.** “Survival of the fittest” occurs because individuals with traits best adapted for survival and reproduction are able to outcompete other individuals for resources and mates.
8. **Evolution occurs as favorable traits accumulate in the population.** The best adapted individuals survive and leave offspring who inherit the traits of their parents. In turn, the best adapted of these offspring leave the most offspring. Over time, traits best adapted for survival and reproduction and the alleles that generate them accumulate in the population.

Natural selection may act upon a population in a variety of ways. These are illustrated in Figure 9-1 and discussed below.

arrows indicate strength of selection against a trait



1. **Stabilizing selection** eliminates individuals that have extreme or unusual traits. Under this condition, individuals with the most common trait are the best adapted, while individuals who differ from the common form are poorly adapted. As a result, stabilizing selection maintains the existing population frequencies of common traits while selecting against all other trait variations.
2. **Directional selection** favors traits that are at one extreme of a range of traits. Traits at the opposite extreme are selected against. If directional selection continues for many generations, favored traits become more and more extreme, leading to distinct changes in the allele frequencies of the population.
 - **Insecticide resistance** occurs as a result of directional selection. Because traits of individuals vary in a population, some individuals may possess some degree of resistance to the insecticide. These few individuals survive and produce offspring, most of whom will inherit the insecticide-resistance trait. After several generations of directional selection, the population will consist of nearly all insecticide-resistant individuals.
 - The **peppered moth** provides an example of directional selection of moth color from a light to a dark color. Before the industrial revolution, the light form of the moth was well camouflaged among the light-colored lichens that grew on tree barks around London. Since color variation is known to exist in other moths, the dark form of the moth probably existed but was never observed because it was so easily spotted and eaten by predator birds. With the advent of the industrial revolution, soot killed the pollution-sensitive lichens, exposing the dark tree bark below. As a result, the dark form of the moth became the better camouflaged of the two forms, and increased in frequency. A hundred years after the first dark moth was discovered in 1848, 90% of the moths were dark colored. Meanwhile, the light form of the moth continued to dominate populations in unpolluted areas outside London. The selection of dark-colored (melanic) varieties in various species of moths as a result of industrial pollution is called **industrial melanism**.
3. **Disruptive selection** (or **diversifying selection**) occurs when the environment favors extreme or unusual traits, while selecting against the common traits.
 - In the wild, many species of weeds occur in a range of heights, but tall forms predominate. Because of disruptive selection, however, only very short forms of these same weeds occur in lawns. On lawns, short weeds are selectively advantageous because they escape mowing. Weeds in the wild are primarily tall because tallness makes them better competitors for sunlight.
4. **Sexual selection** is the differential mating of males (sometimes females) in a population. Since females usually make a greater energy investment into producing offspring than males, they can increase their fitness by increasing the *quality* of their offspring by choosing superior males. Males, on the other hand, contribute little energy to the production of offspring and thus increase their fitness by maximizing the *quantity* of offspring produced. Thus, traits (physical qualities or behaviors) that allow males to increase their mating frequency have a selective advantage and, as a result, increase in frequency within the population. This leads to two kinds of sexual selection, as follows.
 - **Male competition** leads to contests of strength that award mating opportunities to the strongest males. The evolution of antlers, horns, and large stature or musculature are examples of this kind of sexual selection.
 - **Female choice** leads to traits or behaviors in males that are attractive to females. Colorful bird plumage (the peacock's tail is an extreme example) or elaborate mating behaviors are examples.
 - Sexual selection often leads to **sexual dimorphism**, differences in the appearance of males and females. When this occurs, sexual selection is a form of disruptive selection.
5. **Artificial selection** is a form of directional selection carried out by humans when they sow seeds or breed animals that possess desirable traits. Since it is carried out by humans, it is not "natural" selection, but is given here for comparison.
 - The various breeds of dogs have originated as a result of humans breeding animals with specific desirable traits.
 - Brussels sprouts, broccoli, cabbage, and cauliflower have all originated from a single species of wild mustard after artificial selection of offspring possessing specific traits.

Sources of Variation

In order for natural selection to operate, there must be variation among individuals in a population. Indeed, considerable variation exists in nearly all populations. The variation arises from or is maintained by the following mechanisms:

1. **Mutations** provide the raw material for new variation. All other contributions to variation, listed below, occur by rearranging existing alleles into new combinations. Mutations, however, can invent alleles that never before existed in the gene pool.
2. **Sexual reproduction** creates individuals with new combinations of alleles. These rearrangements, or **genetic recombination**, originate from three events during the sexual reproductive process, as follows.
 - **Crossing over**, or exchanges of DNA between nonsister chromatids of homologous chromosomes, occurs during prophase I of meiosis.
 - **Independent assortment of homologues** during metaphase I creates daughter cells with random combinations of maternal and paternal chromosomes.
 - **Random joining of gametes** during fertilization contributes to the diversity of gene combinations in the zygote.
3. **Diploidy** is the presence of two copies of each chromosome in a cell. In the heterozygous condition (when two different alleles for a single gene locus are present), the recessive allele is hidden from natural selection allowing variation to be “stored” for future generations. As a result, more variation is maintained in the gene pool.
4. **Outbreeding**, or mating with unrelated partners, increases the possibility of mixing different alleles and creating new allele combinations.
5. **Balanced polymorphism** is the maintenance of different phenotypes in a population. Often, a single phenotype provides the best adaptation, while other phenotypes are less advantageous. In these cases, the alleles for the advantageous trait increase in frequency, while the remaining alleles decrease. However, examples of polymorphism (the coexistence of two or more different phenotypes) are observed in many populations. These polymorphisms can be maintained in the following ways:
 - **Heterozygote advantage** occurs when the heterozygous condition bears a greater selective advantage than either homozygous condition. As a result, both alleles and all three phenotypes are maintained in the population by selection. For example, the alleles for normal and sickle-cell hemoglobins (*A* and *S*, respectively) produce three phenotypes, *AA*, *AS*, and *SS*. *AA* individuals are normal, while *SS* individuals suffer from sickle-cell disease, because the sickle-cell allele produces hemoglobin with an impaired oxygen-carrying ability. Most *SS* individuals die before puberty. *AS* individuals are generally healthy, but their oxygen-carrying ability may be significantly reduced during strenuous exercise or exposure to low oxygen concentrations (such as at high altitudes). Despite fatal effects to homozygote *SS* individuals and reduced viability of heterozygote individuals, the frequency of the *AS* condition exceeds 14% in parts of Africa, an unusually high value for a deleterious phenotype. However, *AS* individuals have a selective advantage (in Africa) because the *AS* trait also provides resistance to malaria. When *AS* phenotypes are selected, both *A* and *S* alleles are preserved in the gene pool, and all three phenotypes are maintained.
 - **Hybrid vigor** (or **heterosis**) describes the superior quality of offspring resulting from crosses between two different inbred strains of plants. The superior hybrid quality results from a reduction of loci with deleterious homozygous recessive conditions and an increase in loci with heterozygote advantage. For example, a hybrid of corn, developed by crossing two different corn strains that were highly inbred, is more resistant to disease and produces larger corn ears than either of the inbred strains.
 - **Frequency-dependent selection** (or **minority advantage**) occurs when the least common phenotypes have a selective advantage. Common phenotypes are selected against. However, since rare phenotypes have a selective advantage, they soon increase in frequency and become common. Once they become common, they lose their selective advantage and are selected against. With this type of selection, then, phenotypes alternate between low and high frequencies, thus maintaining multiple phenotypes (polymorphism). For example, some predators form a “search image,” or standard representation of their prey. By standardizing on the most common form of its prey, the predator optimizes its search effort. The prey that is rare, however, escapes predation.

Not all variation has selective value. Instead, much of the variation observed, especially at the molecular level in DNA and proteins, is **neutral variation**. For example, the differences in fingerprint patterns among humans represent neutral variation. In many cases, however, the environment to which the variation is exposed determines whether a variation is neutral or whether it has selective value.

Causes of Changes in Allele Frequencies

Natural selection was the mechanism that Darwin proposed for evolution. With the understanding of genetics, it became evident that factors other than natural selection can change allele frequencies and thus promote evolution. These factors, together with natural selection, are given here:

1. **Natural selection** is the increase or decrease in allele frequencies due to the impact of the environment.
2. **Mutations** introduce new alleles that may provide a selective advantage. In general, however, most mutations are **deleterious**, or harmful.
3. **Gene flow** describes the introduction or removal of alleles from the population when individuals leave (emigration) or enter (immigration) the population.
4. **Genetic drift** is a *random* increase or decrease of alleles. In other words, some alleles may increase or decrease for no other reason than by chance. When populations are small (usually fewer than 100 individuals) the effect of genetic drift can be very strong and can dramatically influence evolution.
 - An analogy of genetic drift can be made with the chances associated with flipping a coin. If a coin is flipped 100 times, the number of heads obtained would approach the expected probability of $\frac{1}{2}$. However, if the coin is flipped only 5 times (analogous to a small population), one may obtain, by chance, all tails. Similarly, gene frequencies, especially in small populations, may change by chance.

Two special kinds of genetic drift are commonly observed, as follows:

- The **founder effect** occurs when allele frequencies in a group of migrating individuals are, by chance, not the same as that of their population of origin. For example, one of the founding members of the small group of Germans that began the Amish community in Pennsylvania possessed an allele for polydactylism (more than five fingers or toes on a limb). After 200 years of reproductive isolation, the number of cases of this trait among the 8,000 Amish exceed the number of cases occurring in the remaining world's population.
 - A **bottleneck** occurs when the population undergoes a dramatic decrease in size. Regardless of the cause of the bottleneck (natural catastrophe, predation, and disease, for example), the small population that results becomes severely vulnerable to genetic drift. Destructive geological or meteorological events such as floods, volcano eruptions, and ice ages have created bottlenecks for many populations of plants and animals.
5. **Nonrandom mating** occurs when individuals choose mates based upon their particular traits. For example, they may always choose mates with traits similar to their own or traits different from their own. Nonrandom mating also occurs when mates choose only nearby individuals. In all of these cases, mate selection is not random, and only the alleles possessed by the mating individuals are passed to the next generation. The following two kinds of nonrandom mating are commonly observed.
 - **Inbreeding** occurs when individuals mate with relatives.
 - **Sexual selection** occurs when females choose males based upon their attractive appearance or behavior or their ability to defeat other males in contests.

Genetic Equilibrium

When the allele frequencies in a population remain constant from generation to generation, the population is said to be in **genetic equilibrium**, or **Hardy-Weinberg equilibrium**. *At genetic equilibrium, there is no evolution.* In order for equilibrium to occur, the factors that normally change gene frequencies do not occur. Thus, the following conditions hold:

1. **All traits are selectively neutral (no natural selection).**
2. **Mutations do not occur.**
3. **The population must be isolated from other populations (no gene flow).**
4. **The population is large (no genetic drift).**
5. **Mating is random.**

Genetic equilibrium is determined by evaluating the following values:

1. Allele frequencies for each allele (p , q)
2. Frequency of homozygotes (p^2 , q^2)
3. Frequency of heterozygotes ($pq + qp = 2pq$) Also, the

following two equations hold:

1. $p + q = 1$ (all alleles sum to 100%)
2. $p^2 + 2pq + q^2 = 1$ (all individuals sum to 100%)

As an example, suppose a plant population consists of 84% plants with red flowers and 16% with white flowers. Assume the red allele (R) is dominant and the white allele (r) is recessive. Using the above notation and converting percentages to decimals:

$$q^2 = 0.16 = \text{white flowered plants (} rr \text{ trait)}$$

$$p^2 + 2pq = 0.84 = \text{red flowered plants (} RR \text{ and } Rr \text{ trait)}$$

To determine the allele frequency of the white flower allele, calculate q by finding the square root of q^2 .

$$q = \sqrt{0.16} = 0.4$$

Since $p + q = 1$, p must equal 0.6.

You can also determine the frequency (or percentages) of individuals with the homozygous dominant and heterozygous condition.

$$2pq = (2)(0.6)(.4) = 0.48 \text{ or } 48\% = \text{heterozygotes}$$

$$p^2 = (0.6)(0.6) = 0.36 \text{ or } 36\% = \text{homozygotes dominant}$$

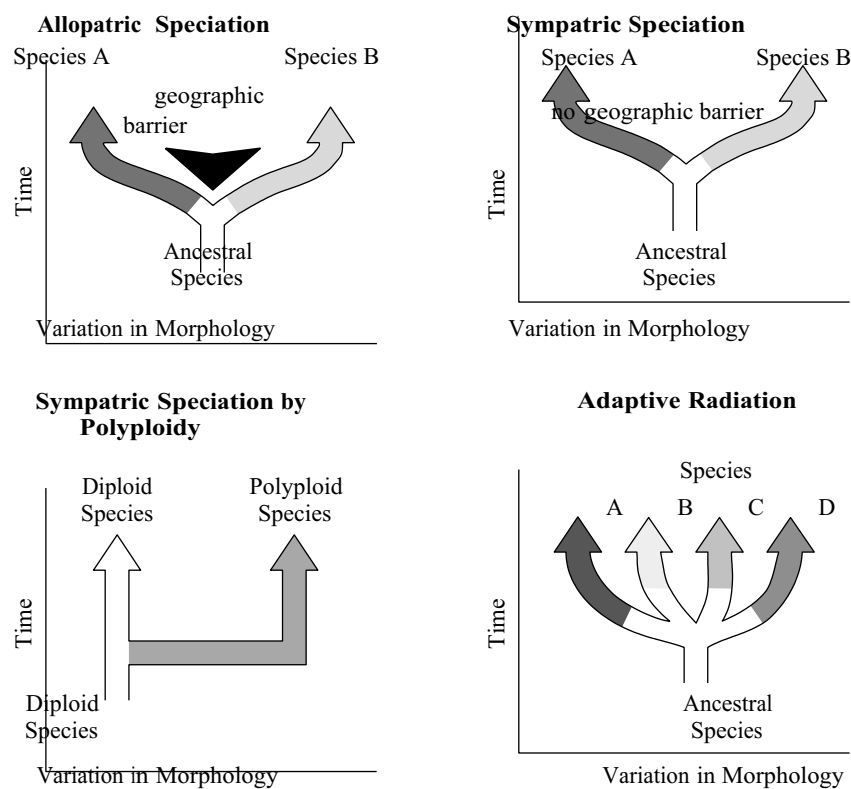
In most natural populations, the conditions of Hardy-Weinberg equilibrium are not obeyed. However, the Hardy-Weinberg calculations serve as a starting point that reveal how allele frequencies are changing, which equilibrium conditions are being violated, and what mechanisms are driving the evolution of a population.

Speciation

A **species** is usually defined as a group of individuals capable of interbreeding. **Speciation**, the formation of new species, occurs by the following processes, as illustrated in Figure 9-2.

1. **Allopatric speciation** begins when a population is divided by a geographic barrier so that interbreeding between the two resulting populations is prevented. Common barriers include mountain ranges or rivers, but any region that excludes vital resources, such as a region devoid of water, a burned area devoid of food, or an area covered with volcanic lava, can act as a barrier because individuals cannot survive its crossing. Once reproductively isolated by the barrier, gene frequencies in the two populations can diverge due to natural selection (the environments may be slightly different), mutation, or genetic drift. If the gene pools sufficiently diverge, then interbreeding between the populations will not occur if the barrier is removed. As a result, new species have formed.
2. **Sympatric speciation** is the formation of new species without the presence of a geographic barrier. This may happen in several different ways, as follows:
 - **Balanced polymorphism** among subpopulations may lead to speciation. Suppose, for example, a population of insects possesses a polymorphism for color. Each color provides a camouflage to a different substrate, and if not camouflaged, the insect is eaten. Under these circumstances, only insects with the same color can associate and mate. Thus, similarly colored insects are reproductively isolated from other subpopulations, and their gene pools diverge as in allopatric speciation.

- **Polyploidy** is the possession of more than the normal two sets of chromosomes found in diploid ($2n$) cells. Polyploidy often occurs in plants (and occasionally animals) where triploid ($3n$), tetraploid ($4n$), and higher ploidy chromosome numbers are found. Polyploidy occurs as a result of nondisjunction of all chromosomes during meiosis, producing two viable diploid gametes and two sterile gametes with no chromosomes. A tetraploid zygote can be established when a diploid sperm fertilizes a diploid egg. Since normal meiosis in the tetraploid individual will continue to produce diploid gametes, reproductive isolation with other individuals in the population (and thus speciation) occurs immediately in a single generation.
- **Hybridization** occurs when two distinctly different forms of a species (or closely related species that are normally reproductively isolated) mate and produce progeny along a geographic boundary called a **hybrid zone**. In some cases, the genetic variation of the hybrids is greater than that of either parent and permits the population of hybrids to evolve adaptations to environmental conditions in the hybrid zone beyond the range of either parent. Exposed to different selection pressures, the hybrids eventually diverge from both parent populations.



Processes of Speciation

Figure 9-2

3. **Adaptive radiation** is the relatively rapid evolution of many species from a single ancestor. It occurs when the ancestral species is introduced to an area where diverse geographic or ecological conditions are available for colonization. Variants of the ancestral species diverge as populations specialize for each set of conditions.
 - The marsupials of Australia began with the colonization and subsequent adaptive radiation of a single ancestral species.
 - The fourteen species of Darwin's finches on the Galapagos Islands evolved from a single ancestral South American mainland species.

Maintaining Reproductive Isolation

If species are not physically separated by a geographic barrier, various mechanisms commonly exist to maintain reproductive isolation and prevent gene flow. These mechanisms may appear randomly (genetic drift) or may be the result of natural selection.

There are two categories of isolating mechanisms. The first category, **prezygotic isolating mechanisms**, consists of mechanisms that prevent fertilization.

1. **Habitat isolation** occurs when species do not encounter one another.
2. **Temporal isolation** occurs when species mate or flower during different seasons or at different times of the day.
3. **Behavioral isolation** occurs when a species does not recognize another species as a mating partner because it does not perform the correct courtship rituals, display the proper visual signals, sing the correct mating songs, or release the proper chemicals (scents, or pheromones).
4. **Mechanical isolation** occurs when male and female genitalia are structurally incompatible or when flower structures select for different pollinators.
5. **Gametic isolation** occurs when male gametes do not survive in the environment of the female gamete (such as in internal fertilization) or when female gametes do not recognize male gametes.

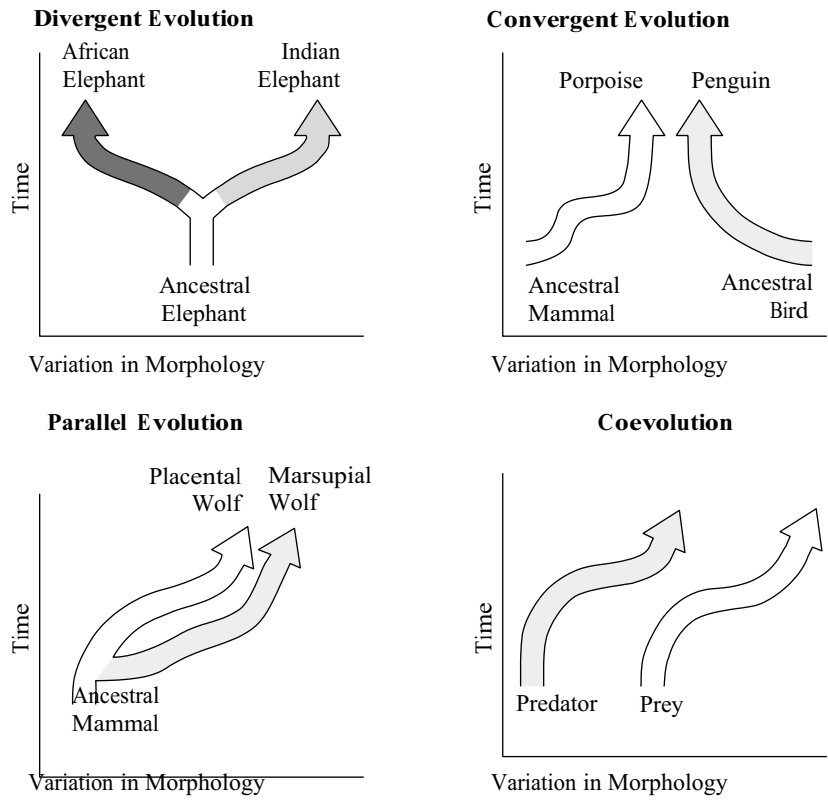
The second category, **postzygotic isolating mechanisms**, consists of mechanisms that prevent the formation of fertile progeny.

6. **Hybrid inviability** occurs when the zygote fails to develop properly and aborts, or dies, before reaching reproductive maturity.
7. **Hybrid sterility** occurs when hybrids become functional adults, but are reproductively sterile (eggs or sperm are nonexistent or dysfunctional). The mule, a sterile offspring of a donkey and a horse, is a sterile hybrid.
8. **Hybrid breakdown** occurs when hybrids produce offspring that have reduced viability or fertility.

Patterns of Evolution

The evolution of species is often categorized into the following four patterns (Figure 9-3):

1. **Divergent evolution** describes two or more species that originate from a common ancestor and become increasingly different over time. This may happen as a result of allopatric or sympatric speciation or by adaptive radiation.
2. **Convergent evolution** describes two unrelated species that share similar traits. The similarities arise, not because the species share a common ancestor, but because each species has independently adapted to similar ecological conditions or lifestyles. The traits that resemble one another are called **analogous** traits.
 - Sharks, porpoises, and penguins have torpedo-shaped bodies with peripheral fins. These traits arise as a result of adaptations to aquatic life and not because these animals inherited the traits from a recent, common ancestor.
 - The eyes of squids and vertebrates are physically and functionally similar. However, these animals do not share a recent common ancestor. That the eyes in these two groups of animals originate from different tissues during embryological development confirms that they have evolved independently.
3. **Parallel evolution** describes two related species or two related lineages that have made similar evolutionary changes after their divergence from a common ancestor.
 - Species from two groups of mammals, the marsupial mammals and the placental mammals, have independently evolved similar adaptations when ancestors encountered comparable environments.
4. **Coevolution** is the tit-for-tat evolution of one species in response to new adaptations that appear in another species. Suppose a prey species gains an adaptation that allows it to escape its predator. Although most of the predators will fail to catch prey, some variants in the predator population will be successful. Selection favors these successful variants and subsequent evolution results in new adaptations in the predator species.
 - Coevolution occurs between predator and prey, plants and plant-eating insects, pollinators and flowering plants, pathogens and the immune systems of animals.

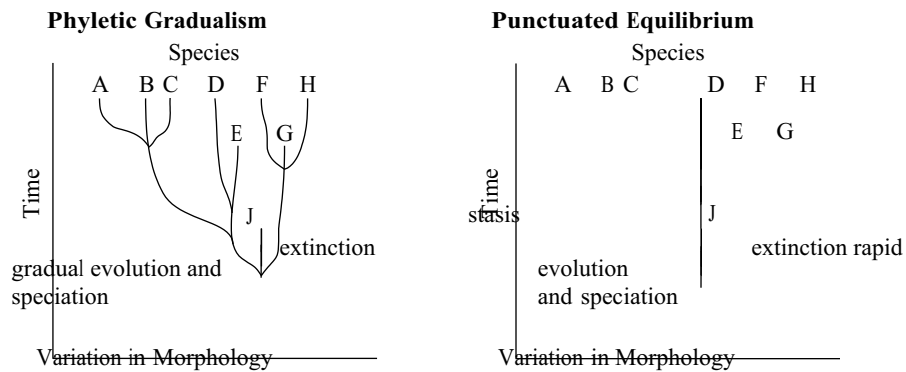


Patterns of Evolution

Figure 9-3

Macroevolution

The previous two sections describe the evolution of individual species. **Macroevolution** describes patterns of evolution for groups of species over extended periods of geologic time. The two distinct macroevolution theories listed below reflect philosophical differences in interpretations of fossil evidence and explanations for the development of evolutionary history (Figure 9-4).



Patterns of Macroevolution

Figure 9-4

1. **Phyletic gradualism** argues that evolution occurs by the gradual accumulation of small changes. Individual speciation events or major changes in lineages occur over long periods of geologic time. Fossil evidence provides snapshots of the evolutionary process, revealing only major changes in groups of organisms. That intermediate stages of evolution are not represented by fossils merely testifies to the incompleteness of the available fossil record.
2. **Punctuated equilibrium** argues that evolutionary history consists of geologically long periods of stasis with little or no evolution, interrupted, or “punctuated,” by geologically short periods of rapid evolution. The fossil history, then, should consist of fossils mostly from the extended periods of stasis with few, if any, fossils available from the short bursts of evolution. Thus, in this theory, the absence of fossils revealing intermediate stages of evolution is considered data that confirms rapid evolutionary events.

The Origin of Life

A topic related to evolution is the study of how life began, or **chemical evolution**. This kind of evolution describes the processes that are believed to have contributed to the formation of the first living things. The **heterotroph theory** for the origin of life proposes that the first cells were **heterotrophs**, organisms incapable of making their own food. The steps hypothesized to have led to the first primitive cell and the subsequent steps that led to more complex living cells are outlined below with supporting information.

1. The earth and its atmosphere formed.

- The primordial atmosphere originated from outgassing of the molten interior of the planet (through volcanos) and consisted of CO, CO₂, H₂, N₂, H₂O, S, HCl (hydrochloric acid), and HCN (hydrogen cyanide), but little or no O₂.

2. The primordial seas formed.

- As the earth cooled, gases condensed to produce primordial seas consisting of water and minerals.

3. Complex molecules were synthesized.

- Energy catalyzed the formation of organic molecules from inorganic molecules. An organic “soup” formed.
- Energy was provided mostly by ultraviolet light (UV), but also lightning, radioactivity, and heat.
- Complex molecules included acetic acid, formaldehyde, and amino acids. These kinds of molecules would later serve as monomers, or unit building blocks, for the synthesis of polymers.
- **A. I. Oparin** and **J. B. S. Haldane** independently theorized that simple molecules were able to form only because oxygen was absent. As a very reactive molecule, oxygen, had it been present, would have prevented the formation of organic molecules by supplanting most reactants in chemical reactions.
- **Stanley Miller** tested the theories of Oparin and Haldane by simulating an experiment under primordial conditions. He applied electric sparks to simple gases (but no oxygen) connected to a flask of heated water. After one week, the water contained various organic molecules including amino acids.

4. Polymers and self-replicating molecules were synthesized.

- Monomers combined to form polymers. Some of these reactions may have occurred by dehydration condensation, in which polymers formed from monomers by the removal of water molecules.
- **Proteinoids** are abiotically produced polypeptides. They can be experimentally produced by allowing amino acids to dehydrate on hot, dry substrates.

5. Organic molecules were concentrated and isolated into protobionts.

- **Protobionts** were the precursors of cells. They were able to carry out chemical reactions enclosed within a border across which materials can be exchanged, but were unable to reproduce. Borders formed in the same manner as hydrophobic molecules aggregate to form membranes (as phospholipids form plasma membranes).
- **Microspheres** and **coacervates** are experimentally (and abiotically) produced protobionts that have some selectively permeable qualities.

6. Primitive heterotrophic prokaryotes formed.

- **Heterotrophs** are living organisms that obtain energy by consuming organic substances. Pathogenic bacteria, for example, are heterotrophic prokaryotes.
- The organic “soup” was a source of organic material for heterotrophic cells. As these cells reproduced, competition for organic material increased. Natural selection would favor those heterotrophs most successful at obtaining food.

7. Primitive autotrophic prokaryotes were formed.

- As a result of mutation, a heterotroph gained the ability to produce its own food. As an **autotroph**, this cell would be highly successful.
- Autotrophs manufacture their own organic compounds using light energy or energy from inorganic substances. Cyanobacteria (photosynthetic bacteria), for example, are autotrophic prokaryotes that obtain energy and manufacture organic compounds by photosynthesis.

8. Oxygen and the ozone layer formed and abiotic chemical evolution ended.

- As a by-product of the photosynthetic activity of autotrophs, oxygen was released and accumulated in the atmosphere. The interaction of UV light and oxygen produced the ozone layer.
- As a result of the formation of the ozone layer, incoming UV light was absorbed, preventing it from reaching the surface of the earth. Thus, the major source of energy for the abiotic synthesis of organic molecules and primitive cells was terminated.

9. Eukaryotes formed (endosymbiotic theory).

- According to **endosymbiotic theory**, eukaryotic cells originated from a mutually beneficial association (symbiosis) among various kinds of prokaryotes. Specifically, mitochondria, chloroplasts, and other organelles established residence inside another prokaryote, producing a eukaryote.

There is considerable evidence for the endosymbiotic theory. A sample of that evidence follows:

1. Mitochondria and chloroplasts possess their own DNA. The DNA is circular and “naked” (without proteins) as is the DNA of bacteria and cyanobacteria.
2. Ribosomes of mitochondria and chloroplasts resemble those of bacteria and cyanobacteria, with respect to size and nucleotide sequence.
3. Mitochondria and chloroplasts reproduce independently of their eukaryotic host cell by a process similar to the binary fission of bacteria.
4. Mitochondria and chloroplasts have two membranes (both phospholipid bilayers). The second membrane could have been acquired when the introduced prokaryote is surrounded, in endocytosis fashion, by a vesicle produced by the host prokaryote.
5. The thylakoid membranes of chloroplasts resemble the photosynthetic membranes of cyanobacteria.