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.

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.

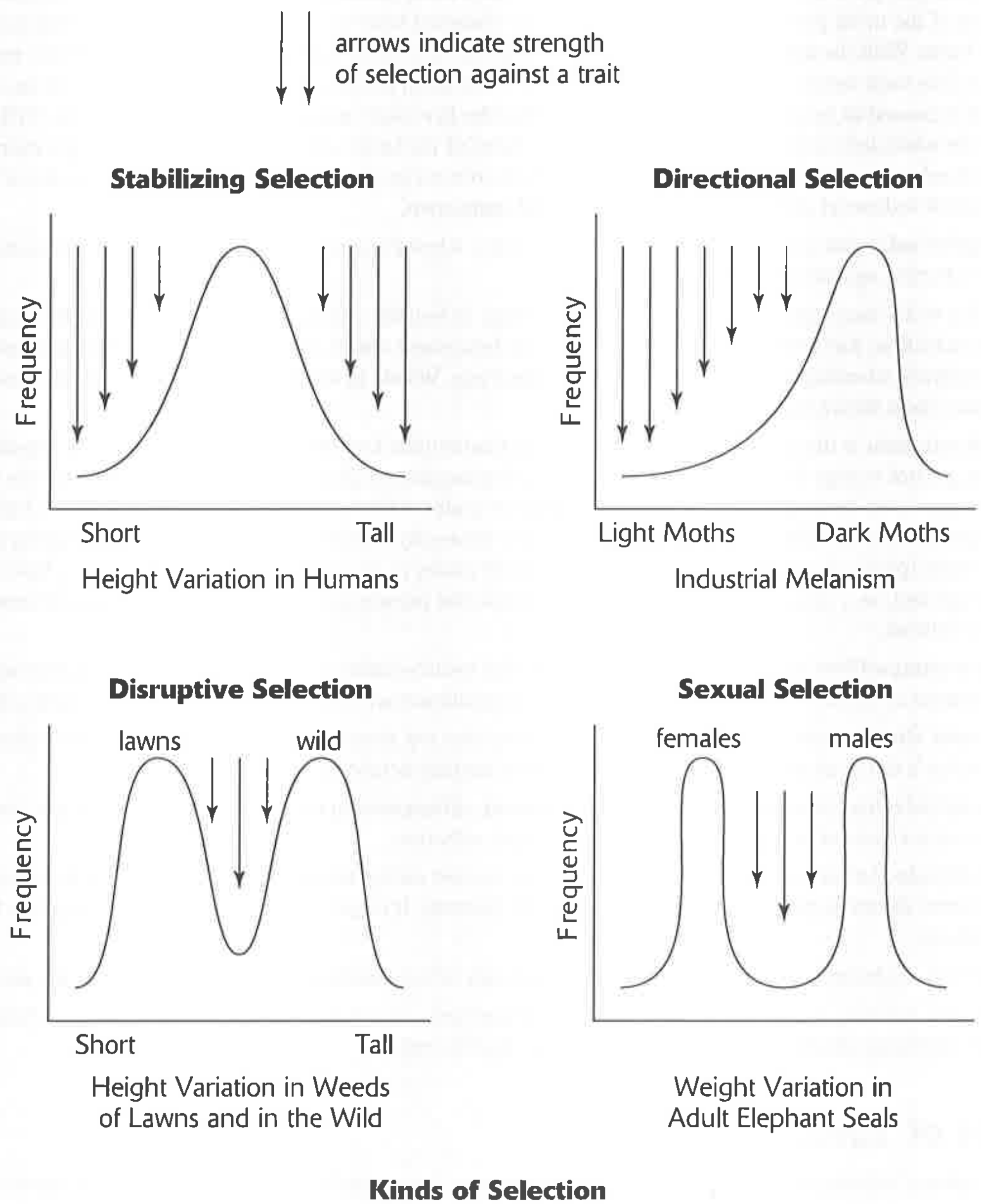

Figure 9-1

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 that 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.

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.

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.

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, CO_2, H_2, N_2, H_2O, S, HCl (hydrochloric acid), and HCN (hydrogen cyanide), but little or no O_2.
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.

Sample Questions and Answers

Multiple-Choice Questions

Directions: Each of the following questions or statements is followed by five possible answers or sentence completions. Choose the one best answer or sentence completion.

1. Which of the following was most responsible for ending chemical evolution?

- **A.** Natural selection
- **B.** Heterotrophic prokaryotes
- **C.** Photosynthesis
- **D.** Viruses
- **E.** The absence of oxygen in the atmosphere

2. Which of the following generates the formation of adaptations?

- **A.** Genetic drift
- **B.** Mutations
- **C.** Gene flow
- **D.** Sexual reproduction
- **E.** Natural selection

3. The B blood-type allele probably originated in Asia and subsequently spread to Europe and other regions of the world. This is an example of

- **A.** artificial selection
- **B.** natural selection
- **C.** genetic drift
- **D.** gene flow
- **E.** sexual reproduction

4. The appearance of a new mutation is

- **A.** a random event
- **B.** the result of natural selection
- **C.** the result of artificial selection
- **D.** the result of sexual reproduction
- **E.** usually a beneficial event

5. Which of the following is an example of sexual selection?

- **A.** Dark-colored peppered moths in London at the beginning of the industrial revolution
- **B.** The mane of a lion
- **C.** Insecticide resistance in insects
- **D.** Darwin's finches in the Galapagos Islands
- **E.** The ability of certain insects to avoid harm when consuming toxic plants.

6. A population consists of 9% white sheep and 91% black sheep. What is the frequency of the black-wool allele if the black-wool allele is dominant and the white-wool allele is recessive?

- **A.** 0.09
- **B.** 0.3
- **C.** 0.42
- **D.** 0.49
- **E.** 0.7

7. After test-cross experiments, it was determined that the frequencies of homozygous dominant, heterozygous, and homozygous recessive individuals for a particular trait were 32%, 64%, and 4% respectively. The dominant and recessive allele frequencies

- **A.** are 0.2 and 0.8, respectively
- **B.** are 0.32 and 0.68, respectively
- **C.** are 0.36 and 0.64, respectively
- **D.** are $\sqrt{0.32}$ and $1 - \sqrt{0.32}$, respectively
- **E.** cannot be determined because the population is not in Hardy-Weinberg equilibrium

8. *Cepaea nemoralis* is a land snail. Individual snails have shells with zero to five dark bands on a yellow, pink, or dark brown background. The various shell patterns could have occurred by all of the following EXCEPT:

- **A.** convergent evolution
- **B.** natural selection
- **C.** a balanced polymorphism
- **D.** chance
- **E.** mutations

9. All of the following are homologous structures EXCEPT:

- **A.** a bat wing
- **B.** a bird wing
- **C.** a butterfly wing
- **D.** a human arm
- **E.** a penguin flipper

Answers to Multiple-Choice Questions

1. **C.** Chemical evolution was able to occur because highly reactive oxygen was not present. The production of oxygen from photosynthesis ended abiotic synthesis because oxygen interfered with the abiotic chemical reactions. Also, the oxygen interacted with UV light to form the ozone layer, which absorbed most incoming UV, the major energy source for abiotic reactions.

2. **E.** Only natural selection generates adaptations. Changes in gene frequencies from other factors may contribute to increases in fitness but not because they produce adaptations. For example, mutations may introduce a new allele, but the allele will lead to an adaptation only if it increases in the population as a result of natural selection.

3. **D.** Gene flow is the increase in allele frequencies due to transfer from other populations.

4. **A.** Mutations occur randomly and are usually harmful. Whether or not the mutation increases or decreases in frequency in the population is the result of natural selection, genetic drift, gene flow, or nonrandom mating.

5. **B.** Only male lions have a mane. Differences in appearance between males and females (sexual dimorphisms) not directly required for reproduction are usually the result of sexual selection.

6. **E.** The information given in the question is summarized as follows:

$$q^2 = 0.09 = \text{white sheep (homozygous recessives)}$$
$$p^2 + 2pq = 0.91 = \text{black sheep (homozygous dominants and heterozygotes)}$$

Then, calculate

$$q = 0.3$$
$$p = 1 - q = 0.7 \text{ (since } p + q = 1)$$

7. **E.** This population is not in Hardy-Weinberg equilibrium. The values given for p^2, $2pq$, and q^2 correctly total 1. Calculating the value of q from q^2 gives $q = \sqrt{0.04}$ or 0.2, and the value of p from p^2 gives $p = \sqrt{0.32}$, which is approximately 0.57. The sum of these *calculated* values for p and q gives 0.77. Since $p + q$ *must* equal 1 (there are only two alleles and their frequencies must total 1), the population cannot be in equilibrium. This can be caused by the nonrandom nature of a test cross, as a population in equilibrium must be mating randomly.

8. **A.** The maintenance of various patterned shells in the snail population is an example of a balanced polymorphism. It may be (and there is good evidence that it is) maintained by natural selection, genetic drift (chance), mutations, and other factors as well. Convergent evolution does not apply here because it refers to two or more species not of common ancestral origin that share similar traits. This question deals with phenotypic variation within a single species.

9. **C.** Structures in different species are homologous because they have been inherited from a common ancestor. Insects (butterflies) are not closely related to the other listed animals. Mammals (bats and humans) and birds (birds and penguins) are related by descent from an early reptile.

10. **A.** A bottleneck occurs when population size precipitously falls. Surviving individuals may possess only a limited amount of the total genetic variation present previously. In addition, the effect of genetic drift intensifies when populations are small.

11. **D.** A consequence of sexual reproduction is that crossing over during prophase I of meiosis, mixing of maternal and paternal chromosomes, and random union of gametes produce new combinations of alleles in every generation. Except for identical twins, no two individuals will ever have exactly the same genetic makeup.

12. **C.** As a result of genetic variation, there will be some bacteria that are resistant to antibiotics. Extensive use of antibiotics kills bacteria that are susceptible, but resistant variants survive and reproduce. After many generations of (directional) selection for resistant bacteria, most surviving bacteria are antibiotic resistant.