SECTION 3

OBJECTIVES

- **Relate** the biological species concept to the modern definition of species.
- **Explain** how the isolation of populations can lead to speciation.
- **Compare** two kinds of isolation and the pattern of speciation associated with each.
- **Contrast** the model of punctuated equilibrium with the model of gradual change.

VOCABULARY

speciation
morphology
biological species concept
geographic isolation
reproductive isolation
gradualism
punctuated equilibrium

FORMATION OF SPECIES

How many species of organisms exist on Earth today? Undiscovered species may be so numerous that we have no accurate answer. For example, even small areas of tropical rain forests can contain thousands of species of plants, animals, and microorganisms. New species are discovered and others become extinct at an increasing rate. In this section, you will learn how one species can become two through a process called speciation.

THE CONCEPT OF SPECIES

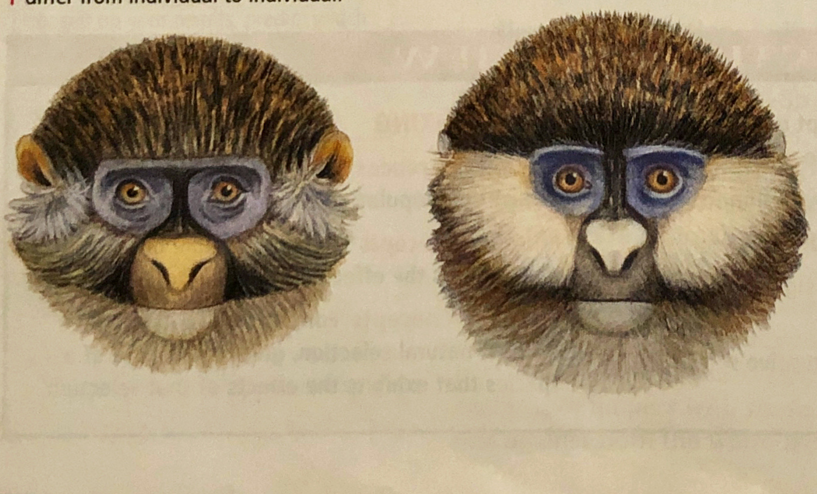
You have learned that existing species are essentially changed versions of older species. The process of species formation, **speciation** (SPEE-shee-AY-shun), results in closely related species. Some are very similar to their shared ancestral species, whereas other descendant species become quite different over time.

Morphological Concept of Species

For many years, scientists used the internal and external structure and appearance of an organism—its **morphology** (mawr-FAHL-uh-jee)—as the chief criterion for classifying it as a species. Using the morphological concept of species, scientists defined species primarily according to structure and appearance. Because morphological characteristics are easy to observe, making species designations based on morphology proved convenient.

The morphological concept of species has limitations, however. There can be phenotypic differences among individuals in a single population. Notice, for example, the variation between the two red-tailed monkeys shown in Figure 16-9. To further complicate the matter, some organisms that appear different enough to belong to different species interbreed in the wild and produce fertile offspring. In response to the capacity of dissimilar organisms to reproduce, the biological species concept arose.

FIGURE 16-9
The facial features of red-tailed monkeys, *Cercopithecus ascianus*, can differ from individual to individual.



The Biological Species Concept

According to the **biological species concept,** as proposed by German-born, American biologist Ernst Mayr (1904–2005), a species is a population of organisms that can successfully interbreed but cannot breed with other groups. Although this definition is useful for living animals, the biological species concept does not provide a satisfactory definition for species of extinct organisms, whose reproductive compatibility cannot be tested. Nor is it useful for organisms that do not reproduce sexually. Thus, our modern definition of species includes components of both the morphological and biological species concepts. A species is a single kind of organism. Members of a species are morphologically similar and can interbreed to produce fully fertile offspring. The many species alive today diverged from a smaller number of earlier species.

ISOLATION AND SPECIATION

How do species give rise to other, different species? Speciation begins with isolation. In isolation, two parts of a formerly interbreeding population stop interbreeding. Two important types of isolation frequently drive speciation.

Geographic Isolation

Geographic isolation is the physical separation of members of a population. Populations may be physically separated when their original habitat becomes divided. A deep canyon could develop, a river could change course, or a drying climate in a valley could force surviving fragments of an original population into separate mountain ranges. Once the subpopulations become isolated, gene flow between them stops. Natural selection and genetic drift cause the two subpopulations to diverge, eventually making them incompatible for mating.

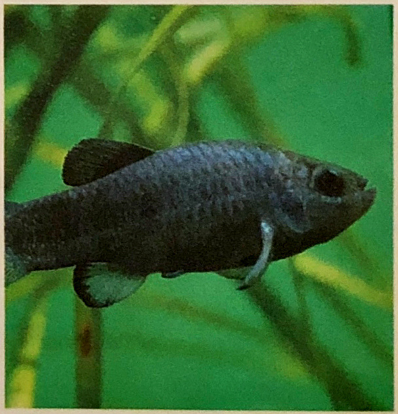
In pupfish, small freshwater fish shown in Figure 16-10, speciation following geographic isolation apparently took place in parts of the western United States, including the desert of Death Valley. Death Valley has a number of isolated ponds formed by springs. Each pond contains a species of fish that lives only in that one pond, but the fish species of various ponds in the area are quite similar.

How did these different populations of fish become isolated in Death Valley? Geologic evidence indicates that most of Death Valley was covered by a lake during the last ice age. When the ice age ended, the region became dry, and only small, spring-fed ponds remained. Members of a fish species that previously formed a single population in the lake may have become isolated in different ponds. The environments of the isolated ponds differ enough that the separate populations of fish diverged. Eventually, the fishes in the different ponds diverged enough to be considered separate species.

FIGURE 16-10

These two types of pupfish live in isolated water sources in the western United States. Both types appear to have evolved from a common ancestor after undergoing geographic isolation.

(a) desert pupfish, *Cyprinodon macularius*



(b) Amargosa pupfish, *Cyprinodon nevadensis*

(a) white-tailed antelope squirrel, *Ammospermophilis leucurus*

(b) Harris's antelope squirrel, *Ammospermophilis harrisi*

FIGURE 16-11

These two closely related squirrels are probably the result of allopatric speciation. The white-tailed antelope squirrel (a) is found on the north rim of the Grand Canyon, and Harris's antelope squirrel (b) is found on the south rim.

Geographic barriers can be formed by canyons, mountain ranges, bodies of water, deserts, or other geographic features that organisms cannot cross. In addition, parts of a population may be accidentally transported to new islands or slowly drift apart on separate continents. On the geologic time scale, the processes of geology frequently rearrange populations.

Whether or not a geographic barrier will isolate a particular group of organisms depends on the organisms' ability to move around. Birds, for example, can easily fly back and forth across a deep canyon. However, a canyon might be a major barrier to a small, crawling mammal. An example of such a barrier is the Grand Canyon in Arizona. The ever-deepening canyon separates the habitats of two closely related populations of squirrels, shown in Figure 16-11. These two populations are different enough to be considered separate species, but similar enough that scientists debate whether they might simply be subspecies. Because their ranges do not overlap, the two populations do not interbreed.

Allopatric Speciation

Allopatric speciation happens when species arise as a result of geographic isolation. *Allopatric* means "different homelands." Populations separated by a geographic barrier no longer experience gene flow between them. So, the gene pools of each separate population may begin to differ due to genetic drift, mutations, and natural selection.

Allopatric speciation is more likely to occur in small populations because a smaller gene pool will be changed more significantly by genetic drift and natural selection. The key question in this type of speciation is whether or not the separated populations become different enough to be reproductively isolated from one another. In other words, if the geographic barrier is removed, could the two groups interbreed and produce fertile offspring?

Reproductive Isolation

Sometimes, groups of organisms within a population become genetically isolated without being geographically isolated. **Reproductive isolation** results from barriers to successful breeding between population groups in the same area. Reproductive isolation and the species formation that follows it may sometimes arise through disruptive selection. Remember that in disruptive selection, the two extremes of a trait in a given population are selected for and the organisms begin to diverge. Once successful mating is prevented between members of the two subpopulations, the effect is the same as what would have occurred if the two subpopulations had been geographically isolated. There are two general types of reproductive isolation: prezygotic (pree-zie-GAHT-ik) isolation and postzygotic isolation. *Prezygotic isolation,* or *premating isolation,* occurs before fertilization, and *postzygotic isolation,* or *postmating isolation,* occurs after fertilization.

Word Roots and Origins

prezygotic

from the Latin *prae,* meaning "before," and the Greek *zygotos,* meaning "yoked"

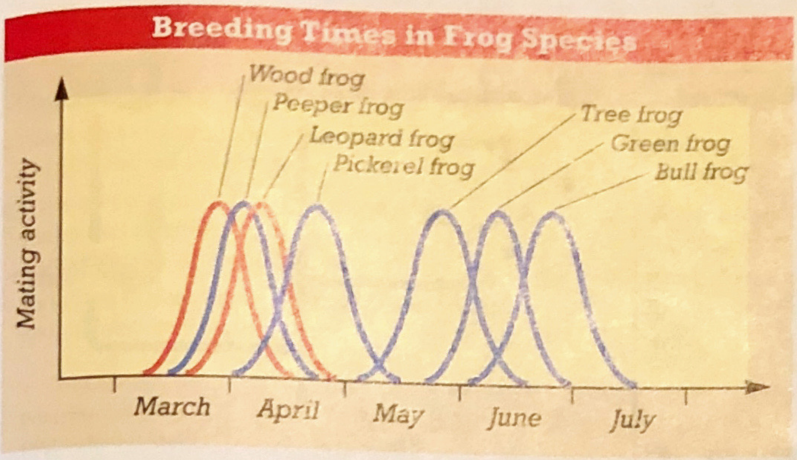


FIGURE 16-12

As the graph shows, frogs that share habitats may be reproductively isolated by differences in timing of mating activity.

If two potentially interbreeding species mate and fertilization occurs, success is measured by the production of healthy, fully fertile offspring. But this may be prevented by one of several types of postzygotic isolation. The offspring of interbreeding species may not develop completely and may die early, or, if healthy, they may not be fertile. From an evolutionary standpoint, if death or sterility of offspring occurs, the parent organisms have wasted their gametes producing offspring that cannot, in turn, reproduce.

In contrast, prezygotic isolating mechanisms can reduce the chance of hybrid formation. For example, a mating call that is not recognized as such by a potential mate can contribute to isolation. Differences in mating times are another type of prezygotic isolation. Both mechanisms are in effect for the frogs shown in Figure 16-12. The time of peak mating activity differs for each frog, reducing the chance of interbreeding. As a result, the wood frog and the leopard frog, shown in Figure 16-13, are reproductively isolated. Though these two frogs interbreed in captivity, they do not interbreed where their ranges overlap in the wild. The wood frog usually breeds in late March, and the leopard frog usually breeds in mid-April.

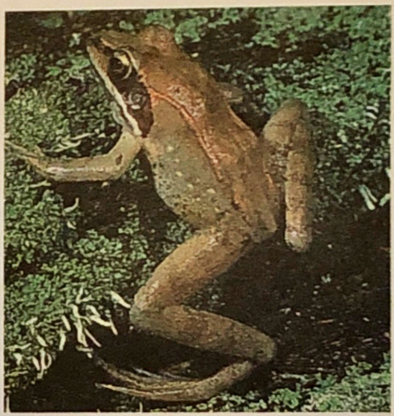
Sympatric Speciation

Sympatric speciation occurs when two subpopulations become reproductively isolated within the same geographic area. Charles Darwin proposed this model of speciation in the 1850s. He hypothesized that competing individuals within a population could gain an adaptive advantage by using slightly different niches. This specialization could lead each group to become reproductively isolated from the other.

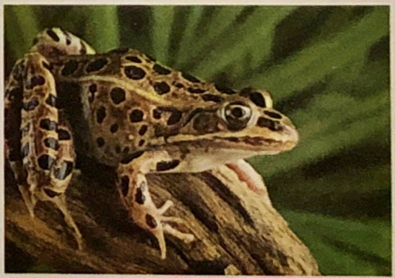
For example, a population of insects might live on a single type of plant. If some of the individuals from this population began to live on another type of plant, they might no longer interbreed with the original population. The two groups of insects would then be able to evolve independently and could eventually become two different species.

FIGURE 16-13

Differences in peak mating times and in mating calls appear to have led to reproductive isolation of the wood frog (a) from its close relative, the leopard frog (b).



(a) wood frog, *Rana sylvatica*



(b) leopard frog, *Rana pipiens*

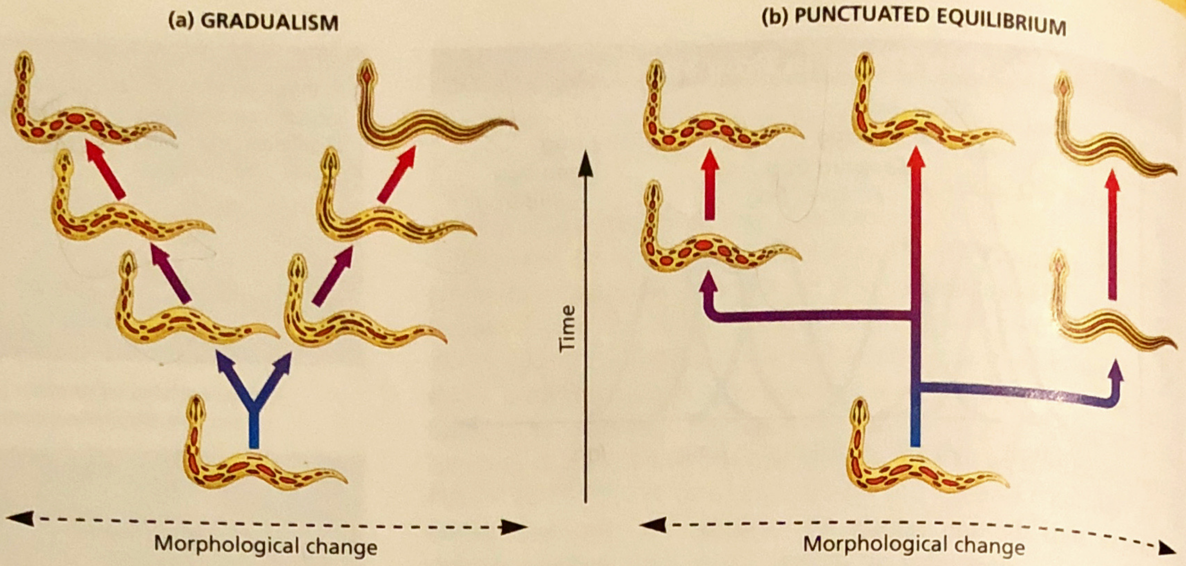


FIGURE 16-14

In the model of speciation shown on the left, species evolve gradually, at a stable rate. In the model of speciation shown on the right, species arise abruptly and differ noticeably from the root species. These species then change little over time.

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RATES OF SPECIATION

Speciation sometimes requires millions of years. But apparently some species can form more rapidly. For example, Polynesians introduced banana trees to the Hawaiian Islands about a thousand years ago. Today, there are several species of moths that are unique to the Hawaiian Islands and that feed only on bananas. These species likely descended from ancestral moths during the past thousand years, since bananas were introduced to Hawaii.

The idea that speciation occurs at a regular, gradual rate is called **gradualism.** However, some scientists think that speciation happens in "bursts" relative to the geologic time scale. The fossil record holds evidence that many species existed without change for long periods of time, whereas in some cases a great diversity of new forms seems to have evolved rapidly. That is, change occurred in a few thousand, rather than a few million, years. Scientists call this pattern of species formation **punctuated equilibrium.** The term *punctuated* refers to sudden, rapid change, and *equilibrium* refers to periods of little change. Figure 16-14 illustrates these two contrasting models as they might apply to the evolution of snakes.

SECTION 3 REVIEW

1. What role did Ernst Mayr play in the development of the modern biological species concept?
2. Explain how geographic isolation can lead to allopatric speciation.
3. Explain how reproductive isolation can lead to sympatric speciation.
4. Contrast the model of punctuated equilibrium with the model of gradualism.

CRITICAL THINKING

5. **Critiquing Explanations** What are two shortcomings of the biological species concept?
6. **Analyzing Concepts** Describe one possible scenario of postzygotic reproductive isolation in an animal species.
7. **Drawing Conclusions** How might the generation time of a population affect future speciation?

THE PURPOSE SET FORTH (FROM *ON MORPHOLOGY*)

JOHANN WOLFGANG VON GOETHE

In observing objects of nature, especially those that are alive, we often think the best way of gaining an insight into the relationship between their inner nature and the effects they produce is to divide them into their constituent parts. Such an approach may, in fact, bring us a long way toward our goal. In a word, those familiar with science can recall what chemistry and anatomy have contributed toward an understanding and overview of nature.

But these attempts at division also produce many **adverse** effects when carried to an extreme. To be sure, what is alive can be dissected into its component parts, but from these parts it will be impossible to restore it and bring it back to life. This is true even of many inorganic substances, to say nothing of things organic in nature.

adverse— negative, unhelpful

Thus scientific minds of every **epoch** have also exhibited an urge to understand living formations as such, to grasp their outward, visible, **tangible** parts in context, to see these parts as an indication of what lies within and thereby gain some understanding of the whole through an exercise of **intuitive perception**. It is no doubt unnecessary to describe in detail the close relationship between this scientific desire and our need for art and imitation.

epoch— a great age, like a century or a millennia, marked by revolutionary happenings

tangible— able to be touched

intuitive perception— thoughtful observation

Thus the history of art, knowledge, and science has produced many attempts to establish and develop a theory which we will call "morphology." The historical part of our discourse will deal with the different forms in which these attempts have appeared.

Morphos – form

…

When something has acquired a form it metamorphoses immediately to a new one. If we wish to arrive at some living perception of nature we ourselves must remain as quick and flexible as nature and follow the example she gives.

In anatomy, when we dissect a body into its parts, and further separate these parts into their parts, we will at last arrive at elementary constituents called "similar parts." These will not concern us here. Instead we will concentrate on a higher principle of the organism, a principle we will characterize as follows.

No living thing is unitary in nature; every such thing is a plurality. Even the organism which appears to us as individual exists as a collection of independent living entities. Although alike in idea and **predisposition**, these **entities**, as they materialize, grow to become alike or similar, unalike or dissimilar. In part these entities are joined from the outset, in part they find their way together to form a union. They diverge and then seek each other again; everywhere and in every way they thus work to produce a chain of creation without end.

predisposition — a tendency to be a certain way or to do certain things

entities— things that exist, here "living material things"

The less perfect the creation, the more its parts are alike or similar and the more they resemble the whole. The more perfect the creation the less similar its parts become. In the first instance the whole is like its parts to a degree, in the second the whole is unlike its parts. The more similar the parts, the less they will be **subordinated** to one another. Subordination of parts indicates a more perfect creation.

subordinated — under the authority of something greater

...

Although a plant or tree seems to be an individual organism, it undeniably consists only of separate parts which are alike and similar to one another and to the whole. How many plants are propagated by runners! In the least variety of fruit tree the eye puts forth a twig which in turn produces many identical **eyes**; propagation through seeds is carried out in the same fashion. This propagation occurs through the development of innumerable identical individuals out of the womb of the mother plant.

eyes— the buds or bud scares of a twig

Here it is immediately apparent that the secret of propagation by seeds is already present in the principle cited above, and upon closer consideration we will find that even the seed, seemingly a single unity, is itself a collection of identical and similar entities. The bean is usually offered as a good example of the process of germination. If we take a bean in its completely undeveloped state prior to germination, and cut it open, we will first find two seed leaves. These are not to be compared to a **placenta**, for they are two genuine leaves: though **distended** and stuffed with a mealy substance, they also turn green when given light and air. In addition we will discover the presence of plumules which are again two leaves capable of further and more extensive development. We may also observe that behind every leaf stalk there is an eye, if not actual then at least in latent form. Thus even a seed, seemingly simple, we find a collection of several individual parts which we may characterize as alike in idea and similar in appearance.

placenta— a sac of nutrients used by fetuses in the womb, yolk

distended— swollen,

What is alike in idea may manifest itself in **empirical reality** as alike, or similar, or even totally unalike and dissimilar: this gives rise to the ever-changing life of nature. It is this life of nature which we propose to outline in these pages.

empirical reality— the world as we experience it

...

Plants and animals in their least perfect state are scarcely to be **differentiated**. Hardly perceptible to our senses, they are a pinpoint of life, mutable or semimutable. Are these beginnings—**determinable** in either direction—destined to be transformed by light into plant, or by darkness into animal? This is a question we would not trust ourselves to answer no matter how well we are supplied with relevant observations and analogies. We can say, however, that the creatures which gradually emerge from this barely differentiated relationship of plant and animal pursue diametrically opposite paths in their development toward perfection. Thus plants attain their final glory in the tree, enduring and rigid, while the animal does so in man by achieving the highest degree of mobility.

differentiated — distinguished from one another

determinable — here "able to go..."

SECTION 3

OBJECTIVES

- **Describe** how convergent evolution can result among different species.
- **Explain** how divergent evolution can lead to species diversity.
- **Compare** artificial selection and natural selection.
- **Explain** how organisms can undergo coevolution.

VOCABULARY

convergent evolution
divergent evolution
adaptive radiation
artificial selection
coevolution

EVOLUTION IN ACTION

Evolution is a continuous process. Evolution is going on today in populations of living species and can be observed, recorded, and tested. Patterns of evolution repeat in different times and places. Interactions between species, including humans, affect their ongoing evolution.

CASE STUDY: CARIBBEAN ANOLE LIZARDS

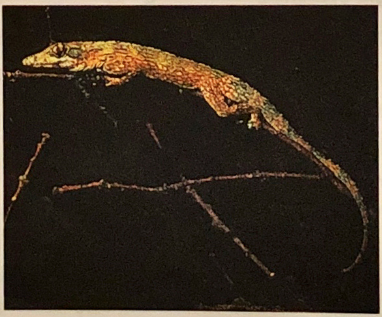
Often, when scientists compare groups of species, the scientists find patterns that are best explained as evolution in progress. An example is the comparison of anole lizard species (genus *Anolis*) on the Caribbean islands of Cuba, Hispaniola, Jamaica, and Puerto Rico. Among these lizards, each species' body type correlates with the habitat in which the species lives, as shown in Figure 15-11. For example, anole species that live mainly on tree trunks have stocky bodies and long legs. In contrast, those that reside on slender twigs have thin bodies, short legs and tails, and large toe pads. Grass-dwelling anoles tend to be slender and have very long tails. In all, there are at least six anole body types that are each adapted to their environment in a unique way. Also, distinct species of anoles with the same body types occur on different islands. For example, a distinct species of twig-dwelling anole is found on each island.

Many different hypotheses could explain these observations. Two possibilities are that (1) an ancestral anole species specialized for living on twigs originally lived on one island and later migrated to other islands or that (2) each twig-dwelling species evolved independently on each island from distinct ancestor anole species.

FIGURE 15-11

Each of these lizards is a member of the genus *Anolis* and lives on the island of Hispaniola in the Caribbean. One species (a) dwells mainly on tree trunks and on the ground and has much longer legs than a species (b) that mostly inhabits tree branches. Another species (c) stays mainly in the grass and has a long tail.

(a) *Anolis cybotes*



(b) *Anolis insolitus*

(c) *Anolis pulchellus*

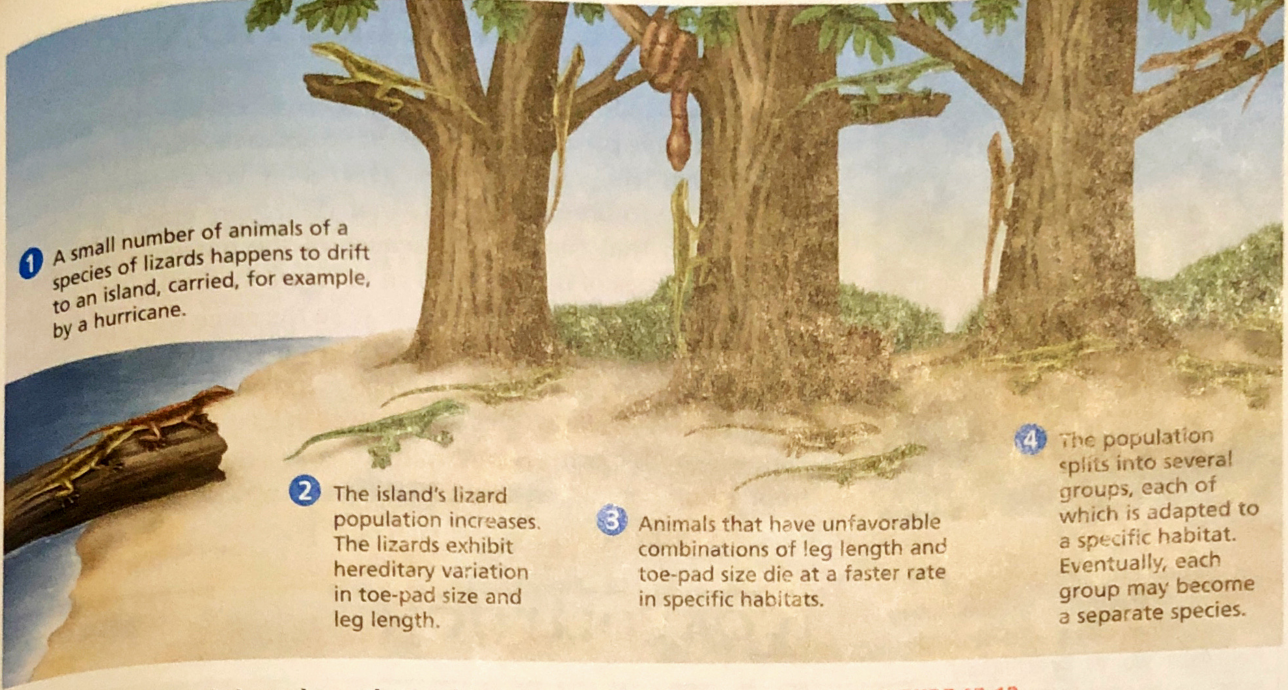


FIGURE 15-12

This diagram shows a possible scenario to explain, through natural selection, the evolution of a variety of anole lizard species in the Caribbean islands by descent from common ancestors.

Biologists tested these hypotheses by comparing DNA from various species to look for closely related species. The DNA evidence supported hypothesis 2—twig-dwelling species evolved independently on each island. In other words, each twig-dwelling species came from different ancestors but evolved similar adaptations to similar habitats. The process by which different species evolve similar traits is called **convergent evolution.** Many other examples of convergent evolution can be found in nature.

Divergence and Radiation

A model of Caribbean anole evolution must also explain how the lizards became adapted to their particular habitats. Studies showed that long-legged trunk-dwelling species could run faster on flat surfaces than short-legged twig-dwelling species, but the twig-dwelling species could cling to twigs better and did not fall as often. However, both kinds of lizards on each island were closely related.

The best explanation for this pattern of phylogeny is that divergent evolution occurred on each island. **Divergent evolution** is a process in which the descendants of a single ancestor diversify into species that each fit different parts of the environment. Lizards with genes for large toe pads and short legs ran so slowly on the trunk and ground that predators often caught them, and lizards with long legs and small toe pads often slipped if they climbed thin branches.

Sometimes, a new population in a new environment, such as an island, will undergo divergent evolution until the population fills many parts of the environment. This pattern of divergence is called **adaptive radiation.** Figure 15-12 illustrates a possible scenario for the evolution of Caribbean anole lizards. Fossil evidence suggests many cases of adaptive radiation on the geologic time scale.

Quick Lab

Observing Adaptations Around You

Materials paper and pencil

Procedure Observe organisms around your school grounds or around your home. Describe any traits that seem to be adaptations to a particular environment or way of life. Also, look for and describe variations within groups of organisms that you see. Explain your reasoning for each inference you make about adaptations. Do not touch or disturb any organism, even plants, during your observation.

Analysis Which variations in the traits that you observed might increase or decrease the fitness of the organisms? Explain your reasoning.

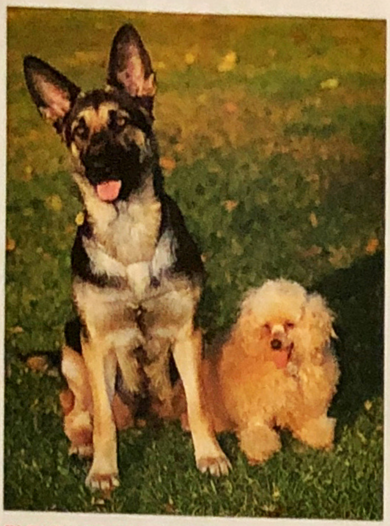


FIGURE 15-13

Recent DNA evidence shows that despite the enormous variation among domestic dogs, all varieties descended from Asian wolves. By artificially selecting the dogs that will be the parents of the next generation, people have increased the rate of divergent evolution among domestic dogs.

ARTIFICIAL SELECTION

Darwin started his famous book with a chapter on **artificial selection.** This process occurs when a human breeder chooses individuals that will parent the next generation. For example, humans may choose to breed oat plants that yield more grain per stalk or greyhounds that run faster. Because of the immense differences among varieties of dogs, as shown in Figure 15-13, Darwin doubted that all domestic dog breeds arose from the same wild species. But in the 2000s, geneticists analyzed DNA from 654 dog breeds, including ancient dog remains. Their findings indicated that all breeds of dogs share DNA similarities with wolves in East Asia. These findings support the hypothesis that humans first selected domestic dogs from a wolf population about 15,000 years ago.

COEVOLUTION

It is important to keep in mind that evolution is ongoing and that in a given environment, many species may be evolving at once. Each species is part of the forces of natural selection that act upon the other species. When two or more species have evolved adaptations to each other's influence, the situation is called **coevolution.**

Through coevolution, some species have evolved strategies to avoid being eaten, while the animals that eat them have evolved strategies to keep eating them. Many flowering plants have evolved such that specific insects carry pollen to other plants. Some microbes have evolved to live within certain animals, while these animals have adapted to either benefit from or avoid the microbes.

Humans are also involved in many cases of coevolution. For example, humans have developed and used antibiotics, such as penicillin, to kill disease-causing bacteria. But as antibiotic use has increased, many populations of bacteria have evolved adaptations to resist the effects of some antibiotics. This kind of adaptation is called *resistance*. Similarly, the evolution of resistance to pesticides is observed among populations of insects in agricultural settings.

SECTION 3 REVIEW

1. Explain how the anole lizard species on Caribbean islands demonstrate both convergent and divergent evolution.
2. What are the key differences and similarities between natural selection and artificial selection?
3. Give examples of species that are likely to be coevolving. Describe how each species influences the evolution of the other species.

CRITICAL THINKING

4. **Inferring Meaning** What is the meaning of *radiation* as used in the term *adaptive radiation*?
5. **Constructing Models** Draw a phylogenetic tree to match each of the two proposed hypotheses for the evolution of the anole lizards.
6. **Analyzing Patterns** Propose a reason why some Caribbean islands lack lizard species.